FORAGING IN THE CAVE ENVIRONMENT: THE ECOLOGY OF THE CAVE SPIDER
META OVALIS (ARANAE: TETRAGNATHIDAE)

Thesis

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Science in the Graduate School of The Ohio State University

By

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ABSTRACT

Much focus in cave biology has been placed on the evolution and population dynamics of troglobitic (cave-adapted) organisms. Troglophiles (non-adapted cave residents) have been largely ignored in studies of distribution, dispersal, and foraging in cave ecosystems. The purpose of this study was to examine the relationship between distribution, dispersal, and foraging behaviors, and the patterns of environmental variation and light gradients in caves, and consider their potential effects on population structure in a troglophilic cave resident. To examine these relationships, I used the orb-weaving cave spider *Meta ovalis* (Araneae: Tetragnathidae), a troglophilic, predatory species common in caves across the eastern United States. These spiders are differentially distributed throughout caves, with sub-adults primarily in the entrance and twilight zones and adults in the twilight and dark zones. This distribution of spiders correlates with availability (capture rate) of aerial and terrestrial prey in each zone. Aerial prey items, the primary source of prey for surface orb-weavers, are most commonly captured in the entrance zone and larger, terrestrial prey the most common in dark zones. Sub-adult webs have capture spirals composed of narrowly spaced spiral lines (compared to adults) that should improve overall capture efficiency and are better suited for the entrance and twilight zones of caves where the web may act as a screen to intercept
many aerial prey of low mass. The capture areas of adult webs are not significantly larger than sub-adult webs, but consist of mesh width that is wider than sub-adult webs, resulting in a more energetically efficient web that may be better suited for the lower prey availability in the twilight and dark zones of cave habitats. The distribution of a non-obligate arthropod predator throughout the terrestrial zones of caves may impact multiple aspects of the cave ecosystem, as spiders may be specialized for available prey types at specific zonal locations within a cave.
DEDICATION

Dedicated to my parents, Loren and Nancy Rector, for their continuous support and encouragement from the very beginning of my scientific explorations.
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CHAPTER 1:
INTRODUCTION

Animal foraging can be viewed as a compromise between the energetic needs of the individual and the costs or risks associated with foraging activity (Lima & Dill 1990). The degree of these foraging trade-offs may vary with the condition of the forager and the state of the foraging patch and available prey (Krebs & Kacelnik 1991). Optimal foraging models predict that the range of diet and the intensity of the foraging effort of animals change in response to their energetic state (Charnov 1976). Other factors must also be considered when determining foraging effort, such as the type of foraging activity (stationary or active) (Leclerc 1991), density of prey in a foraging patch (Heiling 1999; Diaz-Fleischer 2005; Barraquand et al. 2009), competition for prey (Pimm et al. 1985), and predation risk (Aisenberg et al. 2009), all of which could impact foraging behaviors.

Studies of foraging in caves are uncommon among reviews of foraging theory. The foraging ecology of various species of bats and crickets has been examined, but these animals forage primarily external to the cave environment rather than within it (Gillieson 1996). Organisms that reside within and rely upon resources available in a cave habitat are likely to have different foraging strategies
relative to the organisms that reside within but utilize resources outside the cave environment.

Caves are characterized by a combination of darkness or low light (Poulson & White 1969; Culver 1982), stable relative humidity, minimal temperature variation (Poulson & White 1969; Howarth 1993), and scarcity of nutritional resources (Gillieson 1996; Fagan et al. 2007). This combination of ecological factors results in subterranean habitats that are quite different from surrounding surface landscapes. Despite their multitude of distinctive traits, cave habitats are relatively understudied, with much about the relationships between the habitat and resident organisms unknown.

A single cave can contain three different terrestrial light zones (the entrance, twilight, and dark zones), each of which is defined by the amount of ambient light. The entrance zone contains the area of the cave immediately around and including the actual cave entrance. It is the only area of the cave that is physically connected to the surface environment, and is the most exposed to climatic variations. The twilight zone is the region extending from the entrance zone to the dark zone (the point at which light from the surface is no longer detectable), containing minimal light levels and is subject to short term fluctuations based on surface events (Howarth 1993). The dark zone of the cave is the region where no light from the entrance zone can be detected. The sizes of these zones are fluid, and depend on the size of the cave entrance and the overall size and structure of the cave. The decreased exposure of each terrestrial light zone to the environment of the surrounding surface habitat
provide for a comparatively stable environment across the karst landscape (relative to the surrounding surface habitat), allowing cave systems to maintain a relatively constant and aseasonal internal environment (Culver 1982).

Many other ecological cues are also missing in subterranean environments compared to surrounding terrestrial areas; low temperatures, high humidity, and lack of airflow are just a few factors that characterize a cave ecosystem. Nutrients are also generally limited in cave systems; all but a few cave interiors feature zero on-site primary productivity (Poulson & White 1969; Culver 1982; Gillieson 1996) and thus utilize external sources for energy and nutrients. Caves primarily depend on the initial transport of nutrients and energy from the surface via foraging efforts of troglobilhic (e.g. beetles, spiders, etc.) and trogloxenic (e.g. crickets, bats, etc.) organisms, as well as floods, air transport, and other environmental processes (Gillieson 1996; Fagan et al. 2007). Nutrients in the form of microflora, microfauna, guano, and reproductive material (e.g. eggs, larvae, etc.) are the main sources of energy (Gillieson 1996). Due to the nature of transport, nutrients often end up patchily distributed throughout the cave making them a difficult resource for cave dwelling organisms to locate and exploit (Howarth 1993).

There are close to 1000 described species in the United States that are known to live in only cave or associated subterranean habitats (Culver et al. 2000). Obligate cave residents (troglobites) are characterized by morphological, physiological, and behavioral traits that make them unsuitable for survival aboveground (Culver 1982; Holsinger & Culver 1988). There are many organisms
found residing in cave habitats that do not, however, exhibit obvious modified traits for subterranean life. Troglophiles are common in caves, but are not obligate cave dwellers (Gillieson 1996). Trogloxenes are organisms that may reside in caves, but must leave the habitat for foraging or reproduction (Gillieson 1996). These two classifications of organisms are typically also residents of the habitats surrounding caves, and as such they provide a link between surface and subterranean ecosystems.

Troglophiles and trogloxenes represent key elements of cave ecosystems (Taylor et al. 2005; Fagan et al. 2007). Organisms such as cave crickets (Orthoptera: Raphidiophoridae) and harvestmen (Opiliones: Sclerosomatidae) act as invaluable transporters of nutrients and energy from the surface into the resource limited ecosystem. The distribution of these organisms in cave systems is key for the distribution of resources and energy throughout the habitat. There are many levels of trophic interchange in a cave habitat; one must consider the aquatic and terrestrial landscapes as well as the floor and ceiling communities (Gillieson 1996). Trogloxenes often provide the input of food and resources for the secondary consumers, such as beetles and spiders, in the terrestrial cave ecosystem. In such communities, spiders are often placed as the top invertebrate predator (Gillieson 1996). Spiders are common predators in terrestrial ecosystems, and are frequently used in studies of population distribution and foraging ecology.

Spiders are capable of inhabiting a broad range of environments with differential resource availability, leading to wide variations in behavioral and
feeding ecology. Spiders primarily utilize one of two methods of prey capture, silk snares or active hunting (Foelix 1996). Spiders that build specialized snares exhibit a wide variety web-types used for capturing prey, including funnel-webs (Agelenidae), tangle-webs (Theridiidae), sheet and dome webs (Linyphiidae), and orb-webs (Araneidae, Nephilidae, Tetragnathidae, and Uloboridae). Feeding ecology varies with the different web types to best suit the type of snare and the available habitat.

Of the web-building spiders, the largest group is the orb-weavers, representing four spider families (Araneae; Araneidae, Nephilidae, Tetragnathidae, and Uloboridae). Orb-weaving spiders are dispersed all over the world and occupy most terrestrial habitats – from the high arctic (Emerton 1921; Koponen 1992) to tropical rainforests (Guevara & Aviles 2007; Powers & Aviles 2007). Orb-web building spiders are considered to be an especially informative group of animals upon which to examine principles of population distribution and foraging theory (Diaz-Fleischer 2005). As sit-and-wait foragers that are more or less immobile within their web, they utilize the sticky spiral threads of the capture area to intercept and ensnare prey, typically aerial insects, long enough for the spider to bite or wrap the prey (Reichert 1976; McReynolds 2000). With such emphasis placed on the structure of the web for foraging success, foraging decisions of orb-weaving spiders must include the time invested in web construction, the cost of silk production (size and shape of web), and the distribution of available prey in the habitat (Uetz 1992).
As successful foraging depends on the success of the orb-web at intercepting prey items, it is important to consider factors that may impact the structure of the web. Environmental variation is known to influence web structure and engineering, indirectly affecting the foraging success of web-building spiders (Sherman 1994; Harwood et al. 2003; Prokop 2005; Bruce 2006; Folz et al. 2006; Blamires et al. 2007). Changes in ambient temperature can have a direct effect on foraging efficiency (Herberstein & Fleisch 2003) and may even effect foraging decisions by altering behavior and prey availability. Other factors such as air pressure and relative humidity also have an impact on foraging activity in arthropods (Durou et al. 2001). Additionally, the spatial distribution of webs is also integral to the foraging success of orb-weaving spiders (McReynolds 2000; Harwood 2003; Nakata et al. 2003; Iwata 2007; Powers & Aviles 2007).

Orb-weavers are relatively abundant in surface ecosystems (Platnick 2008) where there is an abundance of aerial prey, but are not common in cave habitats though spiders of other groups regularly occur there (Culver et al. 2000; Christman & Culver 2001; Elliot 2007). Cave habitats are generally thought to be unsuitable for orb-weavers, as they have few aerial prey items beyond the entrance of the cave and are characterized by high relative humidity, which is known to result in significant levels of stress on the silk fibers (Agnarsson et al. 2009; Blackledge et al. 2009). Spiders residing in caves must also combat the constant low temperatures (relative to the fluctuating surface temperatures) and near constant darkness that characterizes the typical cave environment (Howarth 1993; Gillieson 1996).
The following two chapters of this thesis focus on the relationships between the cave environment and the web structure, feeding ecology, and population distribution of the troglophilic orb-weaving spider *Meta ovalis* (Tetragnathidae, Gertsch 1933). The orb-weaving spider is a common cave dweller known to build webs in the region extending from the cave entrances to the recesses of the twilight zone, though recently have been observed building webs well into the dark zone (personal observation). Though spiders are regular inhabitants of cave systems, *M. ovalis* is the one of the few widespread and commonly found orb-weaving species (Culver et al. 2000; Christman & Culver 2001; Elliot 2007). While terrestrial arthropods are frequently used to examine population dispersal and distribution (Culver 1982; Moulds et al. 2007; Culver et al. 2009) and the effects of this movement on cave community structure (Kane 1974; Kane & Poulson 1976; Van Zant et al. 1978), cave spiders have been largely ignored and are typically only examined as part of biodiversity surveys (Culver 1973; Culver et al. 2000; Elliot 2007). Interactions among terrestrial arthropods such as predation (Kane 1974) and competition (Van Zant et al. 1978) are known to play are large role in the control of cave community structure. As such, the distribution and dispersal of arthropod predators in a cave system can give insight into the regulation of community structure at each trophic level (Culver 1982).

In Chapter 2, I examine distribution, site fidelity, and dispersal of a troglophilic cave resident relative to spatial structure and patterns of environmental variation (light, temperature, and humidity) and consider their potential effects on
population structure. The distribution and dispersal of troglophiles is important for understanding the ecological role they hold in relation to other organisms in the cave community. Additionally, the level of dispersal that troglophilic cave residents exhibit offers insight into the level of exaptations (pre-adaptation) to cave life that they may have, and whether or not they are restricted to the cave habitat.

In order to address the above concepts, I looked at the relationship between the cave habitat and the populations found at each site, including zonal location, cave temperature, and cave humidity. I also examined demographic variables of the population in relation to the cave environment, including the proportion of adults and sub-adults at each site, zonal preference of these individuals, measurements of spatial web overlap and nearest neighbor tolerance, and dispersal.

The distribution of a species depends largely on the presence and accessibility of suitable habitats and availability of resources. As sit-and-wait predators, the foraging ecology of web spiders is directly affected by the efficiency of the web at intercepting and retaining prey. Web structure and habitat distribution should greatly affect the rate and effectiveness of prey capture (McReynolds 2000; Blackledge & Gillespie 2002; Opell 2002; Blackledge & Zevenbergen 2006). Habitat variables such as light, moisture, and prey density are common factors that affect web structure, location, and efficiency in prey capture (Sherman 1994; Harwood et al. 2003; Herberstein & Fleish 2003; Prokop 2005; Bruce 2006; Folz et al. 2006; Blamires et al. 2007).
In Chapter 3, I explored the relationship between web structure, location, and efficiency and the abiotic and biotic factors of the cave environment. The size and shape of the capture area of orb-webs greatly affects the rate and retention of prey capture (McReynolds 2000; Blackledge & Gillespie 2002; Opell 2002; Blackledge & Zevenbergen 2006). Orb-weaving spiders depend on the sticky spirals in the capture area to intercept and trap insects, so the structure and spacing of the spiral is important for effective captures (Blackledge & Zevenbergen 2006) and when considering interactions between predator and prey. As *M. ovalis* are sit-and-wait foragers relying on their webs for prey capture, web structure is key for determining the size and type of prey that can be successfully captured (Blackledge & Zevenbergen 2006). In order to examine the potential capture efficiency of orb-webs in cave habitats, I took measurements of the capture area and radial spacing of adult and sub-adult webs throughout all zonal locations. These measurements allowed me to determine any relationships between the environment, web location, prey encounters, and capture efficiency.

These studies of population distribution, dispersal, and web ecology allow us to examine foraging by a troglophile in the cave habitat and offer new insight into population structure in caves. The common presence and foraging success of orb-weaving spiders in a resource-limited environment expands our understanding of the impact of habitat structure, environmental variables, and prey distribution on predator distribution and web construction in a new habitat. Information from this study can be used in conjunction with other studies of cave ecology, foraging
dynamics, and orb-web construction to further develop our understanding of habitat influence on behavioral ecology.

LITERATURE CITED


CHAPTER 2:

DISTRIBUTION AND DISPERASAL IN A TROGLOPHILIC SPIDER

ABSTRACT

Much focus in cave biology has been placed on the evolution and population dynamics of troglobitic (cave-adapted) organisms. Troglophiles (non-adapted cave residents) have been largely ignored in studies that examine the effects of distribution and dispersal on cave ecosystems. The purpose of this study was to examine the dispersal and distribution patterns of a troglophilic predator, the orb-weaving spider *Meta ovalis* (Gertsch 1933) relative to the patterns of environmental variation and light gradients in caves and consider their potential effects on population structure. Only within site dispersal was found to occur in this species; no individuals were found to move between different caves or even between sites within a single cave. Individuals were also not found in the surface habitat surrounding cave entrances. Spiders were active year-round and have overlapping generations (spiderlings, sub-adults, adults) residing in the cave throughout. Populations of these spiders are distributed differentially across the three terrestrial light zones (entrance, twilight, and dark) of cave habitats. Adults are found more commonly in the twilight and dark zones whereas sub-adults are most
common in the entrance zone. As a troglophile with no apparent traits specialized to the cave habitat, it is unusual to have a consistent presence in the dark zone. The distribution of a non-obligate arthropod predator across all terrestrial zones of caves, may impact multiple aspects of the cave ecosystem, as individuals will preferentially forage for the available prey types in each zone. In the twilight and dark zones of caves, this likely means more predation on other cave residents, rather than the incidental surface prey found in the entrance zone of caves. This predation on obligate cave dwellers and other cave residents may be important in terms of understanding community regulation and conservation of endemic species.

INTRODUCTION

The distribution of a species depends largely on the presence and accessibility of suitable habitats and availability of resources. Habitats that are common and widely distributed or those that are well connected allow for easy dispersal and exploitation. In contrast, areas of suitable habitat that are surrounded by unsuitable habitats, or those that are isolated by lack of connection to other similar habitats, are difficult for species to exploit. There are many habitats that are isolating by nature of having extreme climatic variables (e.g. deserts), inhospitable surrounds (e.g. islands), or altitudinal gradients (e.g. mountaintops or valleys). Others are not isolated by distance but by lack of connectivity (e.g. multiple lakes in the same vicinity). Caves offer up a habitat with distinct environmental differences (e.g. lack of direct light & constant darkness, limited resources, relatively stable
temperature and humidity) from the surrounding surface environment and are often found as single caves or small networks isolated from like habitats in the geographic area. With so few connections, caves are another example of isolating habitats that limit the interactions of resident species (Howarth 1993; Christman & Culver 2001; Palmer 2007).

Many residents of caves are limited in their ability to disperse outside of the subterranean habitat due to physical or physiological adaptations to cave life (Culver 1982; Howarth 1993; Christman et al. 2005). Other cave residents have no physical adaptations to cave life, but may have exaptations (pre-adaptation) allowing cave residence. These organisms, known as troglophiles, are characteristic residents of the entrance (highly variable area characterized by direct light from the surface) and twilight (area of indirect light accompanied by higher humidity extending from the entrance zone) zones of caves (Gillieson 1996). Troglophiles are not common in the cave dark zone (area extending from the twilight zone, where light from the surface is no longer visible), as it is less hospitable for non-obligate (cave adapted) residents (Gillieson 1996). The substrate of the dark zone is perpetually wet and the relative humidity is often at levels beyond the tolerance of terrestrial arthropods (Poulson & White 1969). Common troglophiles include some species of snails, scorpions, centipedes, millipedes, ground beetles, crickets, and spiders (Reddell 1994; Reeves et al. 2000).

Dispersal of cave-dwelling animals is usually limited by their reliance on the cave environment (limited light, high humidity, constant temperature). Due to the
difficulties of dispersal within and between caves, the distribution of these animals is naturally restricted. Caves, and the microhabitats within, become representative of hospitable islands surround by inhospitable habitats (Howarth 1993). Troglophilic organisms as residents not confined to caves, represent a system where movement and dispersal is less restricted by the cave habitat (in comparison to obligate cave dwellers) and so offer insight into population interactions in the subterranean environment.

The most obvious change for organisms residing in caves is the progressive decrease in light levels as they move from the entrance zone to the dark zone. Consequently, the base of the ecosystem structure in most terrestrial environments (primary producers) is lacking in caves, and cave fauna are dependent on food and resources produced external to the subterranean environment (Gillieson 1996). Primary subterranean sources of energy are 1) organic debris washed in or air-fall from surface crack systems and 2) guano and/or reproductive material of bats, crickets, and other cave organisms that forage on the surface but return to caves to roost or reside for a portion of each day (Culver 1982; Gillieson 1996). Organisms residing in the entrance zone are exposed to greater amounts of organic debris and a greater diversity of potential food may be available in the form of surface plant production and surface organisms. With such differences in source and amount of available energy throughout a cave, many studies have examined how the patchy cave habitat affects the distribution and dispersal of cave organisms (Hill 1981; Holsinger & Culver 1988; Howarth 1991; Humphreys 1993).
Terrestrial arthropods are frequently used to examine population dispersal and distribution within and between caves (Culver 1982; Moulds et al. 2007; Culver et al. 2009; Martinsen et al. 2009; Medeiros et al. 2009) and the effects of this movement on population structure in subterranean habitats (Kane 1974; Van Zant et al. 1978; Norton et al. 1975; Kane & Poulson 1976; Culver 1982). As consumers, terrestrial arthropods are principal organisms in the primary (crickets, some beetles, and springtails) and secondary (some beetles and spiders) trophic levels in cave ecosystems. The amount of available energy in caves is variable both from the entrance to the back and the floor to the ceiling, resulting in segregated floor/wall, ceiling, and light zone communities (Whitten et al. 1988; Gillieson 1996). Studies have shown that interactions among species in these communities such as predation (Kane 1974), or competition between predators (Van Zant et al. 1978) play a large role in the control of cave populations. Therefore the distribution and dispersal of arthropod predators in cave systems can give insight into the regulation of populations at each trophic level (Culver 1982).

Aside from studies of the distribution of cricket eggs and beetle populations in caves (Norton et al. 1975; Kane & Poulson 1976; Hubbell & Norton 1978; Griffith & Brown 1992; Griffith & Poulson 1993) and the relationship between the predator population (beetles) and prey distribution (cricket eggs), the ecological roles of arthropod secondary consumers have not been well studied, yet it is thought that these organisms play a large role in regulating communities (Gillieson 1996). The orb-weaving cave spider *Meta ovalis* (Tetragnathidae, Gertsch 1933) is a secondary
consumer known to reside on cave walls extending from the entrance to the recesses of the twilight zone, but have been found distributed well into the dark zone (personal observation). They are solitary spiders, not found in aggregations of connected webs, though sub-adult webs are often found in close associations with spatial overlap (personal observation). Aggregations of orb-webs are common among colonial spiders (Uetz & Hieber 1997), however some solitary spiders tend to form temporary aggregations in relation to higher prey abundance (Burgess & Uetz 1982; Gillespie 1987). The formation and spacing among individuals in groups is thought to result from a compromise between increased foraging success, intraspecific aggression due to proximity, and predation risk (Rayor & Uetz 2000). The degree of spatial overlap has been speculated to be beneficial in orb-weavers, as it may increase accidental prey deflection from nearby webs. This occurrence is called the ‘ricochet’ effect, where spiders with closely spaced webs benefit by capturing prey items escaping from those nearby webs increasing the overall probability of prey interception (Uetz 1989; Rao 2009). Potential increases in prey interception would be beneficial to individuals throughout the food-limited cave habitat. As a trogophile, *M. ovalis* are dependent on the resources available within the cave, and both individual spiders and those in spatial overlap should demonstrate a distribution pattern within caves that is related to the availability of resources. However, as they are not strictly limited the cave environment, *M. ovalis* could also take advantage of additional surface resources and exhibit dispersal tendencies between caves (see Tercafs 1988; Smithers 2005).
In this study, I examined the distribution and dispersal of *M. ovalis* populations in cave habitats (Carter Co. and Elliot Co., KY) in order to explore relationships between the isolated cave habitat and the distribution and population dynamics of a secondary consumer. The physical structure and relative isolation of the cave environment allows for examination of the spatial distribution of *Meta ovalis* populations as it relates to environmental variables. In particular, I tested the following hypotheses: 1) light zones impact the distribution of adult and sub-adult spiders throughout the cave habitat, 2) spider population size and distribution across zones fluctuates with seasonal climate change, 3) webs in spatial overlap are differentially distributed through the cave light zones, and 4) spiders rarely disperse between separate caves. Accordingly, I predicted that 1) sub-adults would be more common in the entrance zone and adults more common in the dark zone of caves, 2) population sizes in the entrance and twilight zones would decrease during winter months and increase during summer months, while the dark zone would remain stable, 3) spatially overlapping webs will be most common among in the entrance zone, and 4) spiders would rarely be found dispersing between different caves, but should demonstrate dispersal throughout a single cave.

To examine these predictions, I conducted a survey of the population size and distribution of individuals. The surveys used the location (light zone) of spiders, spider maturity/sex, nearest neighbor association, and seasonal changes (temperature and humidity) to explore the stated hypotheses.
METHODS

Mark-Recapture:

A mark-recapture survey of the spider population was conducted from October 2007 to March 2009. Mark-recapture was chosen as the least intrusive method of estimating population density over the course of multiple surface seasons, as cave ecosystems can be sensitive to changes in ecosystem make-up (Gillieson 1996). Nutrients are a major limiting factor in caves and the disruption of a food pathway, such as the removal of a large number of predators, can negatively impact other organisms (e.g. prey populations) in the cave. Mark-recapture allowed for an analysis of the population without the removal of individual spiders.

Adult spiders were marked with a small dot on the cephalothorax using Utrecht ® acrylic paints blue (series 1), green (series 1), yellow (series 1), and orange-red (series 2). As the paint was applied directly to the spider, both toxicity and the wet and humid habitat had to be taken into consideration. Acrylic paint, a common method for marking arthropods, was chosen for its low toxicity levels, it can be applied on damp surfaces, and is relatively waterproof (Rypstra 1984; Blamires et al. 2007; Delaney et al. 2007). Each field site used in the mark-recapture survey was assigned a different color to assess any site-specific dispersal occurring within and between any of the four caves used. Tarkiln Cave (TK) (N 38° 14.577’, W 083° 06.917’, Elliot Co., KY) contained four sites: Main Entrance (ME), Rockpile (RP), Sinkholes (SH), and Waterfall (WF), used to explore dispersal within a single cave system. Tarkiln Cave is a privately owned cave, and was chosen because there is
little regular pedestrian traffic through the cave. The remaining three caves (Carter Co., KY; located at Carter Caves State Resort Park, scientific research permit #0901), each containing a single site, were located along a continuous streambed, and were used for exploring dispersal between caves. The three caves located downstream of each other, listed in order, were: Cobblestone Crawl Cave (CC) (N 38° 22.836’, W 083° 06.959’), Horn Hollow Cave (HH) (N38° 22.665’, W 083° 06.911’), and Laurel Cave (LA) (N 38° 22.481’, W 083° 06.917’). Cobblestone Crawl is an ungated but restricted access cave that is not open to the public. Horn Hollow is accessible to the public by permit only, but receives regular pedestrian traffic year-round. Laurel Cave was a permit cave at the start of this study, but became a gated, restricted access cave in 2008 to conserve and protect the resident endangered bat populations (Coy Ainsley, Carter Caves State Resort Park, pers. com.).

In order to obtain an accurate estimate of the population density over the course of the surface seasons, a survey of the spider populations was conducted regularly from October 2007 to March 2009. Due to weather (e.g. high water, ice, etc.) and seasonal conservation restrictions at Carter Caves SRP, not all caves/sites were sampled equally across the study period. Tarkiln Cave (TK) was surveyed 11 times (ME = 11; RP = 10; SH = 11; WF = 8), Cobblestone Crawl (CC) was surveyed 8 times, Horn Hollow (HH) was surveyed 9 times, and Laurel Cave (LA) was surveyed 5 times. Estimates of population size were calculated using the Lincoln Index (Lincoln Index: N = (M*n)/m; N = Population estimate, M= Number previously counted and marked, n= Number caught in recapture, m= Number of marked
individuals in recapture), a common ecological method for estimating populations assessed by mark-recapture technique (Tinkle & Milstead 1960; Edgar 1971; Greenstone 1978; Henschel et al. 1995; Gerber & Templeton 1996; Trombulak et al. 2001). The survey period lasted until all animals within the designated site had been recorded and no new animals could be found. Due to differences in the size of cave sites there was no specified length of time for each survey.

**Population Distribution:**

The zonal distribution of individuals throughout each field site was also included in every survey. Each site was divided according to the three natural light zones of caves, which were defined for a given cave by the amount of natural light present from the entrance of the cave at 12:00pm for all sites. The full extent of the zones depends on the time of day, size, shape, and location of entrances as well as the structure of the passageways. Zone parameters were marked so as to be consistent across all survey periods and included: 1) The cave entrance zone, which includes the area immediately surrounding the entrance inside the cave, where light from the surface is present; 2) The cave twilight zone, which is immediately beyond the entrance zone and reaches as far as the light from the surface penetrates; and 3) The cave dark zone, which extends from the twilight zone into complete darkness. The separation of the entrance zone and twilight zone was marked at the point where direct light from the surface was no longer physically present (twilight is characterized by reflected light). Separation of the twilight zone from the dark zone
was determined by locating the distance from the entrance where light is no longer
detectable to the human eye (see Howarth 1980; Gillieson 1996).

During each survey, the presence and location of adult spiders, sub-adults,
and egg sacs were recording according to their zonal location. Adult males and
females were visually distinguished from sub-adult spiders by the presence or
absence of mature sex organs. All sub-adult instars were grouped together, except
for spiderlings (2\textsuperscript{nd} instar spiders), which were distinguished by their clumping
behavior immediately around their egg sac.

\textit{Nearest Neighbors}

Nearest neighbor distance between adjacent spiders was used to measure
the close associations of webs found in spatial overlap. Nearest neighbor distance
was determined using digital calipers (Mitutoyo, Model \#CD-6"CS). The number of
individuals and the zonal location for each association were also recorded.

RESULTS

\textbf{Mark-Recapture:}

There was no evidence (for adult spiders) of dispersal behavior for short-
distances (within a cave: Tarkiln) or long-distances (between different caves:
Laurel, Horn Hollow, Cobblestone Crawl). All marked individuals were recaptured in
the same cave where originally located. Spiderling dispersal was observed to be by
mechanical movement (locomotion) within the cave environment instead of
ballooning – which is the characteristic method of spiderling dispersal in species where individuals release a thread of silk into the air and disperse via air currents. Spiderlings expanded slowly from the central egg sac, constructing webs in close contact with neighboring spiders, a typical behavior for orb-weavers prior to ballooning (Foelix 1996). While ballooning behavior cannot be ruled out for spiderlings that exit the system, it was not observed within or outside the cave system during the sample periods.

Due to the size and structure of the caves, population size and rate of recapture was variable from site to site (Table 2.1). Population estimates based on the Lincoln Index are highly variable across sites (Table 2.2), with the estimates for Tarkiln Cave (ME) and Cobblestone Crawl being the most comparable to observed population numbers during the mark-recapture surveys. Of the surveyed populations, sub-adults are the most common (Mean 19.4 individuals ± 1.8 S.E. per site across surveys) followed by females (10.9 ± 0.9) and males (6.0 ± 0.6). Surface seasonality (Figure 2.1) had an affect on population counts at individual caves, but the overall size of the population was not found to fluctuate significantly throughout the year (Two-way ANOVA, F3, 92=1.78, p=0.15). The presence of active egg sacs did vary somewhat by season and zone, but not significantly, with a higher proportion found in the twilight zone during summer (7.0 ± 1.5) and fall (3.8 ± 1.0).
Population Distribution:

Distribution data was square root transformed for analysis. Adults are distributed differentially across the three light zones (Two-way ANOVA, $F_{2,51}=10.73$, $p<0.01$), but there is no seasonal effect on distribution patterns (Two-way ANOVA, $F_{3,51}=0.60$, $p=0.62$) or interaction between season and zone (Two-way Anova, $F_{6,51}=1.01$, $p=0.42$). Sub-adults populations are highly variable and are not differentially distributed across the three light zones (Two-way ANOVA, $F_{2,51}=1.14$, $p=0.32$) or impacted by seasonal change (Two-way ANOVA, $F_{3,51}=0.92$, $p=0.43$) (Fig. 2.2b).

Adults are found significantly more often in the twilight and dark zones (One-way ANOVA, $F_{57}=9.24$, $p<0.01$) than the entrance zone. Adults and sub-adults are found equally in the twilight zone, but adults are more common in the dark zone (Fig. 2.3). Adults are least common in the entrance zone during winter and spring and most common in the summer (Fig. 2.2a).

Nearest Neighbors

Sub-adults spiders were frequently found on orb-webs constructed in close proximity to each other, resulting in considerable spatial overlap. Webs in the dark zone were significantly more widely spaced (Mean 13.90 cm ± 0.44 S.E. distance between webs) than webs in the entrance zone (11.81 cm ± 0.68) (One-way ANOVA, $F=3.34$, $p=0.04$, df=77). The number of individuals in the overlapping groups was
not significantly different across the three terrestrial light zones (One-way ANOVA, 
F=0.89, p=0.42, df=19).

Groups of overlapping webs were most frequently found in the dark zone (11 
groups) followed by the twilight zone (6 groups) and in entrance zone (5 groups). 
Adults were largely not found with connected or overlapping webs, although males 
and females located off of a web were occasionally found in close proximity (1-5cm).

DISCUSSION

Adult *Meta ovalis* displayed no dispersal within or between cave systems 
throughout the duration of the study. Individuals that were marked as residents of a 
specific cave site were continuously found within that site and there were no 
recaptures of individuals at sites other than their original site of residence. Within 
the confines of a single cave site, marked spiders were found occupying all three 
terrestrial light zones, however due to the method of marking we were unable to 
determine if individuals demonstrate zone fidelity or move freely across light zones 
at a single site.

Sub-adults and spiderlings were not marked as it could interfere with the 
molting process (potentially killing marked animals), but dispersal was observed to 
differ from the characteristic method of ballooning seen in other orb-weaving 
spiders (Foelix 1996). Although long-distance dispersal was not observed, the 
locomotory method of dispersal for spiderlings and sub-adults does give insight into 
the movement of *M. ovalis* populations. Dispersal of spider populations occurs
primarily during the initial dispersal of spiderlings and sub-adults (Foelix 1996). While adults are by no means immobile, they are for the most part unable to balloon due to their larger mass (Foelix 1996). Dispersal by mechanical movement (walking; observed in *M. ovalis*, but see Tercafs 1988; Smithers 2005) occurs over shorter distances and at a slower rate than ballooning, which could explain the lack of within and between cave dispersal seen among the populations surveyed. Dispersal may be occurring, but at a rate that was undetectable over the survey period. It is also likely that in dispersal within a single cave system, spiders utilize areas of the cave habitat, such as cracks and crevices, which cannot be successfully surveyed (Howarth 1991; Humphreys 1993; Gillieson 1996). In some caves, spatial scale was a problem for accurate sampling. Upper levels, tight passageways, and other inaccessible areas existed at many of the study sites, and while spiders could be seen they could not be positively identified or counted.

Population movement may be impacted by seasonal changes in the cave environment. While characteristics of the cave environment (temperature and humidity) do, on average, represent the annual surface mean (13-16 °C) of the surrounding habitat, caves undergo a remarkable amount of environmental fluctuation. Variability decreased the further from the entrance of the cave, resulting in a more stable habitat for the organisms residing within.

While seasonality affects overall population size, it was not found to affect the zonal distribution patterns. Adults were most common in the twilight and dark zones throughout all seasons. Sub-adults were more common in the entrance and
twilight zones, but were found residing in all three terrestrial light zones. Population sizes in each zone decreased during winter months, but there is no significant increase in residence in the back of the caves. It is most likely that spiders are utilizing cracks and crevices in the cave structure as protection from the changing environment. These areas were visible during surveys but were impossible to accurately sample due to their size.

In the entrance zone, sub-adults were the most common, but adults outnumber them in the remainder of the cave habitat. It has been proposed that size of available prey impacts the distribution of spiders in a population (Diaz-Fleischer 2005; Prokop 2006; Blamires et al. 2007), and this is supported by the distribution of M. ovalis in cave habitats. Sub-adults spiders were distributed throughout the cave and commonly found in the entrance zone where there are numerous aerial prey items of a relatively small mass (Gillieson 1996; See Results Chapter 3). Adult spiders would not benefit as much from the smaller prey, and were found in the twilight and dark zones where larger terrestrial prey items are more common, if fewer in number (Gillieson 1996; See Results Chapter 3). It is possible that competitive exclusion is occurring between adults and sub-adults in the dark zone. The differential distribution of spiders within the cave light zones may allow for reduced competition for specific prey types, with sub-adults specializing on the numerous small aerial prey and adults on infrequent but larger terrestrial prey (See Results Chapter 3).
Sub-adults were also frequently found in collections of overlapping webs. These associations could be beneficial or detrimental to the spiders involved. Overlapping webs can result in ‘shadow competition’, indirect competition from the close association with surrounding webs (Rao 2009). However this association may be advantageous for the sub-adults involved – prey that strike and escape from one web are more likely to become entangled in a nearby web, a result of the ‘ricochet effect’ previously described for aggregations of orb weavers (Uetz 1989; Rao 2009). While both concepts are traditionally applied to orb-web aggregations found in high densities (hundreds to thousands of individuals per group), they can operate at a smaller scale and in lower densities (Rao 2009).

Sub-adult groups were found throughout all three terrestrial zones (adults were not found in these associations). The number of individuals per group did not vary significantly but the frequency of groups was not even across all zones. Sub-adults in such groups were found most often in the dark zone; the webs in these groups were also the most widely spaced of all grouped webs. The ‘ricochet effect’ may be beneficial for sub-adults in the dark zone due to the reduced prey availability (compared to the entrance) and larger prey size (terrestrial prey) – webs that are part of a close association will be more likely to capture prey items than single webs.

It has been suggested that the position of an individual spider web in these spatially overlapping groups can significantly impact the number of prey intercepted (Rypstra 1985; Lloyd & Elgar 1997; Rao et al. 2007; Rao 2009). The
degree of overlap and spacing between webs also impacts the distribution of prey capture among spiders in spatially overlapping groups (Rao 2009). Webs from groups in the dark zone were the widest spaced; those in the entrance zone were the nearer each other. While I did not measure degree of overlap or frequency of prey interception in this study, it is possible that the differences seen between zones are in response to the frequency of available prey types in each zone.

In conclusion, it is known that arthropod predators play a large role in regulating cave communities and trophic level interactions (Gillieson 1996). The study presented here represents an investigation of the population distribution in a troglobilic cave resident and how it is impacted by environmental variables (temperature and humidity). As a relatively abundant predator in cave habitats, these spiders can provide insight into the community structure of subterranean ecosystems that has been largely unexplored (Culver 1982). The distribution of spiders is likely determined by the distribution of prey in the habitat. In areas of the cave where there is less influx from the surface (the dark zone), it would be advantageous to spiders to reside near prey aggregations. In some locations in Mammoth Cave National Park, there is a positive correlation between cave cricket abundance and M. ovalis number and reproduction, suggesting that prey numbers and distribution have a strong influence on the success of the spiders (Lavoie et al. 2007).

This study demonstrates that spider maturity (and likely mass differences) is a factor in the distribution of individuals throughout a cave habitat and implies that
maturity may also play a role in their predation behavior. The differential location of adults and sub-adults may be a result of specialization for available prey types that differ by zone. Although spiders were not found to disperse external to the cave environment, it is assumed that they are capable of moving, if slowly, throughout a single cave, which would affect the movement of energy and resources in the ecosystem (Hill 1981; Holsinger 1988; Howarth 1991; Humphreys 1993). To better understand the relationship between troglophilic consumers and their effect on community structure, relationships between distribution and predation activities need to be explored.

LITERATURE CITED


<table>
<thead>
<tr>
<th>Site</th>
<th>Mean Number of Adults Counted Per Survey Period</th>
<th>Mean Number of Adults Recaptured on Site Per Survey Period</th>
<th>Percent Recaptured On Site</th>
<th>Percent Recaptured Off Site</th>
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<tbody>
<tr>
<td>Tarkiln Main</td>
<td>23.7 ± 11.5</td>
<td>8.8 ± 5.7</td>
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<td>Tarkiln Rockpile</td>
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<td>Tarkiln Sinkhole</td>
<td>7.3 ± 7.6</td>
<td>0.7 ± 1.4</td>
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<td>Tarkiln Waterfall</td>
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<td>0.06 ± 0.2</td>
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<tr>
<td>Cobblestone</td>
<td>18.8 ± 7.5</td>
<td>4.2 ± 3.8</td>
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<tr>
<td>Horn Hollow</td>
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<tr>
<td>Laurel</td>
<td>8.1 ± 4.1</td>
<td>1.6 ± 2.3</td>
<td>19.6%</td>
<td>0%</td>
</tr>
</tbody>
</table>

Table 2.1. Average adult population counts determined for the seven cave sites used for the mark-recapture survey. Survey periods lasted until all animals at each site were recorded and represent a thorough exploration of the area. Tarkiln Cave is privately owned and located in Elliot Co., KY. Cobblestone Crawl Cave, Horn Hollow Cave, and Laurel Cave are part of Carter Caves State Resort, Cart Co., KY.
<table>
<thead>
<tr>
<th>Cave</th>
<th>Mean Number of Individuals Per Survey Period</th>
<th>Lincoln Index (Mean ± SD)</th>
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<tr>
<td>Tarkiln (WF)</td>
<td>Adults 3.5</td>
<td>Sub-Adults 17.9</td>
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<td>Tarkiln (SH)</td>
<td>Adults 7.1</td>
<td>Sub-Adults 23.0</td>
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<td>Tarkiln (RP)</td>
<td>Adults 7.7</td>
<td>Sub-Adults 18.7</td>
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<tr>
<td>Laurel</td>
<td>Adults 8.2</td>
<td>Sub-Adults 27.2</td>
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</tbody>
</table>

Table 2.2. Estimates of spider population size. Populations were calculated for each site using the Lincoln Index. Survey periods represent an exhaustive exploration of the area and lasted until all animals found at each site were recorded.
Figure 2.1. Mean seasonal variation of a) temperature (± S.E.) and b) relative humidity (± S.E.) in the cave environment across all caves. While seasonal variation does exist in all three terrestrial light zones, the cave habitat is, on average, stable across the three zones in both temperature and relative humidity.
Figure 2.2. Seasonal distribution of populations of a) adult and b) sub-adult spiders by cave zone (entrance, twilight, dark). Numbers reflect the mean percent of the population counted across all caves used in the study.
Figure 2.3. Percent (± S.E.) of sub-adult and adult spiders found in each cave light zone, across all caves.
CHAPTER 3

FORAGING IN A CAVE HABITAT: WEB STRUCTURE OF THE ORB-WEAVING CAVE SPIDER, *META OVALIS* (TETRAGNATHIDAE)

ABSTRACT

Studies of foraging in subterranean environments have been centered on organisms that leave caves to forage (e.g. crickets and bats). As resources are limited in cave ecosystems, the resulting transfer of energy to other cave residents is important for understanding ecological interactions of subterranean habitats. Secondary consumers in cave systems are impacted by the distribution and availability of prey in the habitat and play an important role the regulation of predator and prey populations. The orb-weaving spider *Meta ovalis* (Gertsch 1933) is a top invertebrate predator commonly found throughout caves in North America. This study examined the relationship between the cave habitat, population distribution, and available prey on web construction and foraging behavior in this spider. Spiders exhibit a differential use of habitat and webs of adults and sub-adults may be specialized for available prey types at specific zonal locations (entrance, twilight, and dark) within a cave. As such, the structure of orb-webs in each of the
terrestrial light zones may be a key factor for successful foraging and regulation of cave populations.

INTRODUCTION

The act of foraging involves a collection of decisions where the animals make efficient choices regarding suitable prey types and suitable foraging patches. It is assumed that optimal foraging behaviors are shaped by natural selection, and therefore predators should behave in a manner that maximizes prey capture efficiency (Charnov 1976; Pyke et al. 1977; Krebs 1978; Janetos 1982; Olive 1982; Nakata & Ushimaru 1999; Adams 2000; Green 2006). Under optimal foraging parameters, the predator should discriminate between various prey and focus on the most profitable prey among those available, weighing the costs to subdue and handle against the gain of nutrients and energy (MacArthur & Pianka 1966; Krebs 1978; Diaz-Fleischer 2005). Other factors must also be considered within a foraging strategy, such as the activity of the forager, density of prey, competition, and predation, all of which can impact foraging behaviors.

The importance of available prey types in foraging patches depends on the predation activity of the forager. Patch choices vary for active foragers moving throughout the habitat, and for sit-and-wait foragers remaining sessile within a chosen patch (MacArthur & Pianka 1966; Heiling 1999). Within patches, predators are confronted with prey densities that vary in time and spatial distribution (Bianchi et al. 2009). The density and distribution of prey in a patch will in turn,
affect decisions of the forager (Olive 1980; MacKay 1982; Riechert & Gillespie 1986; Uetz 1986, Spiller 1992; Bianchi et al. 2009). For instance, ladybeetles (Coleoptera: Coccinellidae) utilize alternate foraging strategies that depend on multiple landscapes of prey distribution and density. They reach maximum predation rates when prey distribution is varied among two or more foraging patches of different size and spatial density (Bianchi et al. 2009). Ladybeetles foraging in fewer patches or those where prey exhibit a more regular distribution, do not have a high rate of foraging success.

However, some predators will switch foraging behaviors when densities of an alternate, or less preferred, prey type reach a threshold level (Persson & Bronmark 2008; Kobler et al. 2009; Randa et al. 2009). Prey switching or changes in the rates of prey consumption occurs in vertebrate predators and is often caused by fluctuations in prey abundance (Jaksic et al. 1992; Dale et al. 1994; Randa et al. 2009), especially when primary prey densities decline (Kjellander & Nordström 2003; Sundell et al. 2003). This behavioral response can affect reproductive success of predators (Kjellander & Nordström 2003; Rosenberg et al. 2003) and facilitate the survivorship of primary prey types (Miller et al. 2006). In sympatric species, such as coyotes and red foxes, a combination of prey selectivity and switching is the most effective method of foraging allowing for resource partitioning between predators in the same habitat (Azvedo et al. 2006; Randa et al. 2009). Prey switching also occurs in various species of fish, commonly as a result of increased predator population density (Svanbäck & Bolnick 2007). Sticklebacks (Gasterosteus
*aculeatus* L.) are known to add alternative prey types to their diet under increased population densities (Svanbäck & Bolnick 2007) and pike (*Esox lucius* L.) will adjust their habitat choice according to variations in conspecific density (Kobler et al. 2009).

As predator populations increase, so does competition for space and resources within a patch, affecting the time a predator will spend in a foraging patch. A patch with high densities of suitable prey may be less optimal if the gains in energy do not outweigh the energy costs of competing with other foragers. Predation risk may also make an otherwise optimal foraging patch less suitable (Lubin 1973; Uetz 1992; Heiling 1999). Animals in structurally complex habitats face patches where they must balance access to resources against competitive interactions and predatory risks (Rypstra et al. 2007). Spiders of the genus *Schizocosa* are influenced by the presence of conspecifics in a foraging patch (Wagner & Wise 1997), prey density (Persons & Uetz 1997,1998; Wagner & Wise 1997), and age-specific foraging strategies (Persons 1999), utilizing the information perceived from the environment to determine how long to remain in an area.

Web-building spiders are considered an especially informative group of animals upon which to examine principles of foraging theory (Heiling 1999; Watanabe 2001; Diaz-Fleischer 2005). As sit-and-wait foragers that are more or less immobile within their web, foraging decisions consist of time invested in web construction, size and shape of the web (cost of silk production), foraging response behaviors, and the diet selected (Uetz 1992). Spiders that build specialized snares
exhibit a wide variety of web types used for capturing prey, including funnel-webs (Agelenidae), tangle-webs (Theridiidae), sheet and dome webs (Linyphiidae), and orb-webs (Araneidae, Nephilidae, Tetragenathidae, and Uloboridae). Feeding ecology varies with the different web types to best suit the type of snare and available habitat (Foelix 1996).

Of the web-building spiders, the largest group is the orb-weavers (Araneae) (Foelix 1996; Griswold et al. 1998). Foraging in orb-weaving spiders is primarily based on their web structure and the location of the orb-web. Orb-webs are used to intercept and capture prey items, typically aerial insects, by snaring them in the sticky spiral threads long enough for the spider to bite or wrap the prey (Reichert 1976; McReynolds 2000). The size and shape of the capture area can greatly affect the rate and retention of prey capture (McReynolds 2000; Blackledge & Gillespie 2002; Opell 2002; Blackledge & Zevenbergen 2006). Orb-webs depend upon the spirals of sticky silk in the capture area to trap insects, and the structure and spacing of these spirals serve multiple functions. The elastic spirals absorb the impact of the prey striking the web and the sticky silk must adhere to the prey (Opell 1996; Blackledge & Zevenbergen 2006). The combination of these factors prevents the prey from escaping prior to being subdued by spiders. The capture area of the web is then important when considering interactions between predator and prey. As sit-and-wait predators that rely on webs to intercept and capture their prey, the size and spacing of the spiral area determines the size and type of prey that can be successfully captured (Blackledge & Zevenbergen 2006).
As successful foraging depends on success of the orb-web at stopping prey items, it is important to consider factors that may impact the structure of the web. Environmental variation within and between habitats can influence web structure and engineering, indirectly affecting the foraging success of web-builder (Sherman 1994; Lin et al. 1995; Vollrath et al. 1997; Vollrath et al. 2001; Harwood et al. 2003; Prokop 2005; Bruce 2006; Folz et al. 2006; Blamires et al. 2007). Spiders are known to alter their foraging behavior in response to abiotic factors such as temperature and light levels (Herberstein & Fleisch 2003) and relative humidity (Durou et al. 2001). Light can be a major factor in spider foraging behavior, affecting web orientation (Bishop & Connolly 1992), thermoregulatory behavior (Krakauer 1972; Biere & Uetz 1981), and web construction (Blackledge 1998a; Bruce & Herberstein 2006).

Orb-weavers are relatively abundant in terrestrial ecosystems (Platnick 2008) where there is an abundance of aerial prey, but are not common in all habitats. Cave habitats are an example of a system where only one orb-weaving species is regularly found, although spiders of other groups often occur there (Culver et al. 2000; Christman & Culver 2001; Elliot 2007). Caves are generally unsuited for orb-weaver foraging, as they have few aerial insects beyond the entrance of the cave (Gillieson 1996). Spiders residing in caves must also combat the low temperatures (relative to surface environments), high relative humidity, and near constant darkness that characterizes the typical cave environment (Howarth 1993; Gillieson 1996).
Obligate cave residents (troglobites) often exhibit morphological, physiological, and behavioral traits necessary for subterranean survival as a result of the relatively limiting environmental characteristics of caves (Culver 1982; Holsinger & Culver 1988). There are many organisms that are found in the subterranean environment that do not, however, exhibit obvious modified traits for cave life. These residents are known as troglobiphiles, and though common in caves are not obligate cave dwellers (Gillieson 1996). These organisms are typically residents of the habitats surrounding caves, which can range from temperate forests to arid landscapes. Many troglobiphiles are key elements of cave ecosystems (Taylor et al. 2005; Fagan et al. 2007). Troglobiphiles and trogloxenes (visitors, non-residents) such as cave crickets (Orthoptera: Raphiodphoridae) and harvestmen (Opiliones: Sclerosomatidae) act as invaluable transporters of nutrients and energy into the resource limited ecosystem (Willemart & Gnaspini 2004; Taylor et al. 2005; Fagan et al. 2007). Despite their important role of transporting plant and animal material into caves, studies of cave organisms and foraging are largely limited to mammals (e.g. bats: Hurst & Lacki 1999; Brack & Whitaker 2001; Levin et al. 2006; Biscardi et al. 2007; Johnson & Gates 2007; Almenar et al. 2008; Lundberg & McFarlane 2009) and select arthropods (e.g.: cave crickets: Poulson et al. 1995; Taylor et al. 2005; Fagan et al. 2007; Lavoie et al. 2007). While these model systems demonstrate foraging behaviors outside of caves, they do not consider other aspects of resource interchange in the bottom-up trophic community. Predators such as carabid cave beetles (see Kane & Poulson 1976; Griffith & Brown 1992; Griffith &
Poulson 1993) and spiders forage primarily within the cave environment, feeding opportunistically upon other troglobilites, troglobenotes, and surface prey items. As they are not dependent on exiting the cave for nutrients and resources, these organisms represent another level of trophic interchange to explore.

Spiders are common predators in terrestrial ecosystems and are frequently used in studies of surface foraging ecology, with particular focus placed on the orb-weaving spiders (e.g. Brown 1981; Craig 1989; Sandoval 1994; Higgins 1995; Herberstein et al. 2000; Adams 2000; Venner et al. 2003; Herberstein & Fleisch 2003; Blackledge & Zevenbergen 2006; Prokop 2006; Blamires et al. 2007; Rao 2009; Edwards et al. 2009). Studies of orb-weaver foraging have examined factors such as web design, prey availability, and environmental characters (e.g. temperature and light) across most surface habitats, but the role of orb-weavers in cave ecosystems has yet to be explored.

The orb-weaving spider *Meta ovalis* (Tetragnathidae, Gertsch 1933) is a troglobilic cave dweller known to build webs in the region extending from the cave entrance to the recesses of the twilight zone (defined by minimal light levels, extends from the entrance to the dark zone), but have been seen building webs well into the dark zone (region where no light from the entrance can be detected). As an orb-weaver, *M. ovalis* likely utilize their webs in a similar manner to other members of the orb-weaving families and therefore web structure will greatly affect the rate and retention of prey capture (McReynolds 2000; Blackledge & Gillespie 2002; Opell 2002; Blackledge & Zevenbergen 2006).
If *M. ovalis* use webs as other orb-weavers do, webs should be utilized to intercept primarily aerial prey, of which there is neither a great diversity nor abundance in typical cave environments (Gillieson 1996; Culver et al. 2000). However *M. ovalis* has been observed to deviate from typical foraging behavior and feed on terrestrial arthropods such as millipedes (Diplopoda) and crickets (Orthoptera: Ceuthophilinae, Hadenoecinae) in addition to available aerial prey (see also Smithers 2005). As a member of a typically surface-dwelling group, these orb-weavers provide an opportunity to examine principles of foraging theory in cave habitats. In addition, their role as a troglobilic predator in cave ecosystems highlights the need to study the influence of the habitat structure on foraging success in these spiders by examining web components and prey captures.

In this study, I explored the influence of web structure and location on the foraging success of this troglobilic orb-weaver. In particular, I tested the following hypotheses: 1) habitat location (terrestrial light zones) impacts the size and structure of the capture area of orb-webs, 2) size and structure of the capture area differs between adult and sub-adult webs, 3) available prey type differs by zonal location, and 4) web structure correlates with prey availability. Accordingly, I predicted that 1) webs in the entrance zone will have more compact radial lines than webs in the dark zone, 2) the capture area of sub-adult webs would be smaller than adult webs, 3) aerial prey will be more common in the entrance zone and terrestrial prey more in the dark zone, and 4) webs capturing more aerial prey will have closer spaced capture spirals than webs capturing more terrestrial prey.
To examine these predictions, I measured the physical structure of adult and sub-adult webs and calculated the capture area and size differences of orb-webs. These measurements, along with web location (light zone), spider maturity/sex, spider mass, and prey availability were used to test the stated hypotheses.

METHODS

Four separate caves were used for the duration of this study. Each site was chosen as a representative of cave type (public/private) and accessibility (regular/restricted). The variability in cave type and accessibility allowed us to control for any tampering that may occur in public sites while maintaining a large sample population. Tarkiln Cave (N 38° 14.577’, W 083° 06.917’, Elliot Co., KY) is a privately owned cave, and was chosen because there is little regular pedestrian traffic through the cave. The remaining three caves (Carter Co., KY) were located along a continuous streambed, downstream of each other: Cobblestone Crawl Cave (CC) (N 38° 22.836’, W 083° 06.959’), Horn Hollow Cave (HH) (N38° 22.665’, W 083° 06.911’), and Laurel Cave (LA) (N 38° 22.481’, W 083° 06.917’). Cobblestone Crawl is an ungated but restricted access cave that is not open to the public. Horn Hollow is accessible to the public by permit, and receives regular pedestrian traffic year-round. Laurel Cave was a permit-access cave at the start of this study, but became a gated, restricted access cave in 2008 to conserve and protect the resident endangered bat populations (Coy Ainsley, Carter Caves State Resort Park).
Orb-webs of male, female, and sub-adult (1-2 molts prior to adult instar) spiders were measured in the field throughout each of the terrestrial light zones from December 2007 to March 2009. The physical measurement of webs in situ, versus the measurement of webs powdered with cornstarch and photographed or the removal of webs (Blackledge & Gillespie 2002), was chosen so as to limit disturbance in the cave. The addition of cornstarch, or other powder, helps to visualize the strands but adds external nutrients to the silk in the web, which would then be ingested by the spiders during web recycling and alter their normal nutrient intake. As these spiders live in a food-limited environment (Gillieson 1996), adding external nutrients could have altered their web-construction and predation behaviors, interfering with the objective of this study.

Spiders were captured and removed from the web, and held in 20ml plastic sample vials for the duration of web measurements. Measurements of spider mass were also taken while spiders were contained, and maturity (adult/sub-adult), sex, the number/type of captured prey in the web, and location of the web (terrestrial light zone) were recorded. The three light zones were defined for a given cave by the amount of natural light present from the entrance of the cave at 12:00pm for all sites. The full extent of the zones depends on the time of day, size, shape, and location of entrances as well as the structure of the passageways. Zone parameters were marked so as to be consistent across all survey periods and included: 1) The cave entrance zone, which includes the area immediately surrounding the entrance inside and outside the cave, where direct light from the surface is present; 2) The
cave twilight zone, which is just beyond the entrance zone and reaches as far reflected light from the surface penetrates; and 3) The cave dark zone, which is the region of the cave that is in complete darkness. The separation of the entrance zone and twilight zone was marked at the point where direct light from the surface was no longer physically present (twilight is characterized by reflected light). Separation of the twilight zone from the dark zone was determined by locating the distance from the entrance where light is no longer detectable to the human eye (see Howarth 1980; Gillieson 1996). Relative humidity and air temperature were recorded for each light zone using a Kestral pocket weather meter (Model 3000).

Web Structure:

In order to explore the structure of the web in relation to its capacity to intercept prey, digital calipers (Mitutoyo, Model #CD-6"CS) were used to measure the following web components: hub diameter (H), horizontal web diameter (d_h), vertical web diameter (d_v), and sticky spiral spacing. These web parameters were used to calculate the capture area of each orb using the Ellipse-Hub estimation formulae from Blackledge and Gillespie (2002).

\[ \text{Capture Area} = \text{Ellipse} - \text{Hub} = \left(\frac{d_v}{2}\right)\left(\frac{d_h}{2}\right)\pi - \left(\frac{H}{2}\right)^2\pi \]

Web Recycling and Site Fidelity:

To examine web construction/recycling and site fidelity behavior by zone, webs were surveyed after being intentionally damaged. Approximately 24 hours
after web damage, each web was surveyed and categorized as abandoned, occupied
damage ignored, or occupied damaged repaired. One-third of the capture spiral
(sticky threads) was removed from each web by burning out every third row of
sticky silk using a portable soldering iron (Weller, model #BP645MP) (Blackledge &
Zeivenbergen 2006).

Assessment of Available Prey:

To categorize available prey items and rate of capture in caves, we used
artificial sticky traps following the method of Uetz and Biere (1980). These artificial
traps were constructed of nylon mesh coated in Tanglefoot® adhesive supported by
a wire ring set to the average capture area of adult webs (size determined using
preliminary web measurements, Rector & Roberts, unpubl. data).

Orb-webs of adults and sub-adults were surveyed in each of the three
terrestrial light zones to determine the actual rates and types of prey captured over
a 24-hour period. To calibrate the sticky trap data and confirm it as comparable to
actual web captures, we determined the actual capture rate over 24-hours then
compared that to 24-hour captures using sticky traps (see results). Actual capture
rates for a 24-hour period were determined through observations of 20 individual
orb webs that were clear of prey items at the start of the observation period.

Following the observation period, the number of prey and remnants of prey found
in the spider web were recorded. As these were not significantly different, we
placed two sticky traps per zone for 30-day periods (5 trials) to explore the
daily/weekly/monthly capture rates and type of prey striking a web. The traps were placed in each of the entrance, twilight and dark zones of Tarkiln Cave (Main Entrance). I did not place traps at all caves (Cobblestone Crawl, Horn Hollow, Laurel Cave) due to the higher risk of tampering or removal by visitors at the other locations or increased chance of flash flood related damage.

RESULTS

Web Structure

Zonal location of webs and maturity affect the hub size of spider webs (Two-way ANOVA, F_{2,272}=5.10, p<0.01). Adults construct webs with larger hubs than those of sub-adult webs (Two-way ANOVA, F_{1,272}=10.75, p<0.01), but not across all zones (Figure 3.1a). No differences were found between the overall vertical diameters of adult and sub-adult webs, but adult webs in the twilight zone have significantly greater vertical height (One-way ANOVA, F=7.50, p<0.01, df=102) with an average vertical radius of 83mm (SE=3.8mm) over the sub-adult of 67mm (SE=4.2mm) (Figure 3.1b). Adult webs in the twilight zone are significantly wider (horizontal diameter) than sub-adult webs (One-way ANOVA, F=5.18, p=0.02, df=102) with an average horizontal radius of 86mm (SE=3.6mm) over the sub-adult radius of 74mm (SE=4.0mm) (Figure 3.1b).
Capture Area

Zonal location of webs has an effect on capture area size (Two-way ANOVA, $F_{2, 272} = 3.53, p = 0.03$). Capture areas of webs found in the entrance and twilight zones are significantly larger (One-way ANOVA, $F = 3.82, p = 0.02$, df=275) than the capture areas found in the dark zone (Figure 3.1). Maturity has no impact on capture area size (Two-way ANOVA, $F_{1, 272} = 1.19, p = 0.27$) (Figure 3.2) and there is no interaction between maturity and zone (Two-way ANOVA, $F_{2, 272} = 2.17, p = 0.11$). Spiders of average mass (0.18g ± 0.10g) tend to have larger capture areas, but the relationship between mass and capture area is not correlated (Correlation: $r = -0.03, p = 0.74$).

Sticky Spiral

While the capture areas of adult and sub-adult webs are not significantly different, the capture areas of adult webs have fewer spiral lines with significantly wider spacing than sub-adult webs (One-way ANOVA, $F = 35.87, p < 0.01$, df=276). Adult webs average 7.1mm between spiral lines (SE=0.30mm) whereas sub-adult webs average 4.4mm (SE=0.31mm). The zonal distribution of webs does not alter spiral line spacing with maturity (Two-way ANOVA, $F_{2, 272} = 0.41, p = 0.65$). Spiral line spacing is positively correlated with spider mass (Figure 3.3) (Correlation: $r = 0.52$, $p < 0.01$). Spiders of higher mass have wider spaced spiral lines than spiders of lower mass (One-way ANOVA, $F = 32.03, p < 0.01$, df=85). There is no significant interaction between maturity, spider mass, and spiral line spacing.
Spider Mass

Adults are heavier than sub-adults in all three terrestrial light zones (One-way ANOVA; Entrance: $F=15.54$, $p<0.01$, $DF=12$; Twilight: $F=9.15$, $p<0.01$, $DF=41$; Dark: $F=4.28$, $p=0.04$, $DF=38$). Females tend to be the heaviest (0.23g ± 0.01g) and weigh significantly more than males and sub-adults in the entrance (One-way ANOVA, $F=22.27$, $p<0.01$, $df=11$) and twilight (One-way ANOVA, $F=7.37$, $p<0.01$, $df=40$). Spiders in the dark zone (0.24g ± 0.01g) are significantly heavier than spiders in the entrance (0.13g ± 0.02g) and twilight (0.16g ± 0.01g) zones (One-way ANOVA, $F=8.23$, $p<0.01$, $df=94$).

Web Recycling and Site Fidelity

Spider response to web damage, maturity (adult vs. sub-adult), and zone (web location) are all mutually independent factors in the population sampled (37 adult webs and 31 sub-adult webs) (Contingency Analysis for mutual independence: $X^2=13.516$, $df=12$, $0.5 \leq p \leq 0.25$). Repair was the most common response (Table 3.1) followed by Ignore and Abandon.

Within age classes, sub-adults are most likely to repair a damaged web whereas adults are equally likely to repair or ignore the damage. Abandonment of the web following damage is the least common response behavior for both adults and sub-adults. In the web location category, damage is most likely to be repaired in the entrance and twilight zones and most likely to be ignored in the twilight and
dark zones. Web abandonment following damage is maintained at low levels throughout all three cave zones.

**Assessment of Available Prey**

**24-hour Capture Rates**

The observed capture rates over 24-hours were comparable between sticky traps and actual webs (Students t Test, t=0.42, p>0.33, df=135). There were no significant differences between observed and sticky trap captures in observed prey types or capture rates across zones.

**30-Day Capture Rates**

The mean total number of prey captured in sticky traps over the 30 day trials varied significantly across the three zones (One-Way ANOVA, F = 23.44, p < 0.01, df=42), with the 46% (27.8 ± 2.7) of the total captures occurring in the entrance zone, 35% (21.0 ± 1.15) in the twilight zone and 19% (11.1 ± 0.8) in the dark zone. Of the prey items captured in the entrance zone, 93% were aerial insects with the remaining prey consisted of terrestrial prey items. Of those captured in the twilight zone, aerial prey comprised 87% and in the dark zone aerial prey captures comprised 43% (Figure 3.4). The prey types across the aerial and terrestrial categories are not of equal size, the aerial insect groups (Diptera: Chironomidae, Tipulidae, Culicidae) average a body length of 10mm and terrestrial prey groups
(Diplopoda, Orthoptera: Ceuthophilinae and Hadenoecinae) average a body length of 26 mm (Borrør & White 1970).

When the 30-day capture rates are scaled per week, the sticky trap data is comparable (4.98 ± 0.20) to the 24-hour capture rates (Table 3.2). However, the sticky traps scaled for daily captures are much lower (0.66 ± 0.03) than found in the 24-hour capture rates. The capture rates between terrestrial light zones are not significantly different when scaled per day. The proportion of aerial and terrestrial prey groups captured remain steady throughout each zone, and demonstrate no overall differences.

DISCUSSION

Populations of *Meta ovalis* utilize the structure of the cave environment and available prey differentially throughout the habitat. Much of the variation observed between adults and juveniles is due to differences in web structure across some of the terrestrial light zones. The major differences in web structure between adults and sub-adults occur in the twilight zone, where adult webs are significantly larger across all web factors. While maturity did not have an effect on zonal location of webs, the location of the webs did affect the overall capture size of all webs found in each distinct zone. The larger sizes of capture areas in the entrance and twilight zone is likely related to available prey types in these zones. Many spiders actively alter the size and shape of their webs in response to prey (Higgins & Buskirk 1992; Pasquet et al. 1994; Sherman 1994; Vollrath et al. 1997; Blackledge 1998b) and the
construction of the web can directly influence foraging success in orb-weavers (Rypstra 1982; Eberhard 1986; Blackledge & Wenzel 1999). As the available prey types differ from the entrance of a cave through the dark zone (Gillieson 1996), it is reasonable to suggest that *M. ovalis* are actively responding to prey type availability and constructing webs differentially across the cave zones.

The success of an orb-web in intercepting and capturing prey is determined by more than the overall size of the web and capture area (Blackledge & Eliason 2007). The mesh width of the capture area, constructed of the sticky spiral lines, also influences prey interception and retention (Blackledge & Zevenbergen 2006). The structure of *M. ovalis* capture areas is significantly different between adults and sub-adults. While the overall capture area is not different between adults and sub-adults, the structure of the capture area and the spacing of the spiral lines is significantly wider in adult webs. Adult webs contain fewer, wider-set spiral lines, whereas sub-adult web contain more, narrowly spaced spiral lines. The retention of prey in spider webs is based on how the kinetic energy of prey is absorbed in a web (Opell & Bond 2001; Blackledge & Zevenbergen 2006), and therefore depends on the density of lines in the capture spiral. Spider webs with narrow-meshed capture areas are more likely to capture large, rare prey than webs with wider-spaced mesh (Blackledge & Eliason 2007). Additionally, webs with a higher density of spiral lines per capture area may capture more incidental small prey items.

Sub-adult webs of *M. ovalis*, with their tighter capture spiral, may function primarily as a capture screen for the numerous small prey in the entrance zone with
the added benefit of being structurally more sound for the capture of large, rare prey from which they would have higher energetic gains. This web-structure corresponds with the prey variety found in the entrance and twilight zones, where sub-adults are most common.

The looser spiral found in adult webs are thought to be more energetically efficient for intercepting prey (Chacón & Eberhard 1980) and may represent a greater foraging effort (Sherman 1994; Vener & Casas 2005). Adults were also observed to actively forage from their web, capturing terrestrial prey on the cave wall or by swinging out on a silk dragline and capturing aerial prey in the air. The increased spacing of adult webs may be a response to both saving energy on the production of silk for a web and periodic bouts of active foraging.

Analysis of spider mass in comparison to the spacing of spiral lines supports that spiders with more to gain from the large, rare prey will construct a web that increases the likelihood of interception – spiders of lower mass construct webs with narrower mesh width. Additionally, spiders of higher and lower mass are differentially distribution across cave light zones. Individuals in the entrance and twilight zones are significantly lighter than those in the dark zone. Based on the web structure analysis, it is likely that the heavier spiders are constructing webs with wider spaced capture areas than the lighter spiders.

The differences present between sub-adults and adults in the components of web structure also indicate that juveniles invest more silk in each new web they construct. The study of web recycling behavior and site fidelity found that sub-
adults are most likely to repair a damaged web, rather than abandon the web or ignore the damage. As repairing a web is less of an energetic investment than building a new web (Opell 1998; Venner et al. 2003), sub-adults seem to be making the most energetically efficient decision in repairing an already existing web. The repair behavior is also most common among spiders residing in the entrance and twilight zones, where the trade-off in energy investment is likely balanced by an increased likelihood of prey capture. Ignoring web damage is likely optimal in the twilight to dark zone, as the frequency of prey capture decreases. Abandonment was the least common response among all spiders, as would be expected in a food and energy limited habitat.

The distribution of available prey in the cave habitat supports the distribution of web types and recycling behaviors. Aerial prey is most common in the entrance zone and terrestrial prey most common in the dark zone. The aerial prey items captured in the artificial webs were on average much smaller than the terrestrial prey captured, supporting that individuals who capture the larger Diplopoda and Orthoptera gain significantly more energy per predation activity. Spiders located in the entrance zone of caves are relying on the relative availability of small, aerial prey to supplement the chances of capturing a rare, large prey item. As artificial capture rates are much lower in the dark zone, individuals residing here would be able to optimize foraging success by constructing webs with wider mesh (Chacón & Eberhard 1980; Sherman 1994; Vener & Casas 2005), as was found in this study.
It is interesting that the 30-day artificial webs were not comparable on a
daily rate to the observed 24-hour capture rates. There are several possibilities for
the decrease in prey numbers when scaled per week and day. First, with the
extended exposure and high relative humidity, the adhesive on the sticky traps may
have weakened, resulting in a ‘web’ that was easier for insects to escape from.
Additionally, large prey are more capable of struggling out of spider webs (Opell
1999; de Crespigny et al. 2001) and without a predator actively capturing prey that
intercept the web, there may be loss of prey over time. Finally, as the webs were run
for 30-day trials, it is also possible that we lost some insects, especially smaller ones,
to decomposition, resulting in lower estimates of actual prey captures.

In summary, the findings of this study partially support my initial hypothesis
that the size and structure of the capture area would differ between adults and sub-
adults. The overall size of the capture area did not differ as predicted, but its
structural components were influenced by maturity. The overall size and structure
of the capture area was influenced by the zonal location of the web, supporting my
second hypothesis. Webs in the entrance zone were larger and more compact than
in the dark zone. Prey type availability was found to be different across cave zones,
with aerial prey captured more often in the entrance zone and terrestrial prey more
often in the dark zone. And lastly, web structure was correlated with prey
availability, but while webs with more compact capture spiral do capture aerial
prey, they are likely more important for capturing the large, rare prey.
The results of this study demonstrate that the habitat zonation of cave environments does influence the foraging behavior and success of *Meta ovalis*. Despite their role of a top invertebrate predator in cave ecosystems, these spiders are active foragers of surface prey in the entrance and dark zones of caves, relying on predation of other cave dwellers for supplemental food and resources. In many spider species, net energetic gains of adults influence growth rates, and in females the time of egg laying and the number and/or size of the eggs (Fritz & Morse 1985; Vollrath 1987; Morse 1988; Spiller 1992; Uetz 1992). Therefore foraging decisions of sub-adults and adult spiders may have consequences for future energetic gains, growth, and reproductive success.

LITERATURE CITED


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Table 3.1. Contingency table of spider response to web damage. Response, maturity, and zonal location are all mutually independent factors. Independently, sub-adults are most likely to repair and adults are most likely to repair or ignore damaged webs.
<table>
<thead>
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<th></th>
<th>Aerial Prey</th>
<th></th>
<th>Terrestrial Prey</th>
<th></th>
<th>Total Prey</th>
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<tbody>
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<td>Twilight</td>
<td>Dark</td>
<td>Entrance</td>
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<td>0.15</td>
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Table 3.2. Average prey captures of spider webs and sticky traps. The 30-day traps underestimate the frequency of prey capture observed over a 24-hour period and are thus used as a conservative estimate of prey capture. Prey may be escaping the sticky traps or they may be located in lower prey traffic areas, resulting in fewer captures than actual webs.
Figure 3.1. Web architecture measurements for *Meta ovalis* webs across all study sites. a) Mean hub area of adult and sub-adult webs in the three light zones and b) mean vertical and horizontal web dimensions of adult and sub-adult webs.
Figure 3.2. Mean capture areas of *Meta ovalis* orb-webs (± S.E.) across study sites.

Capture areas of webs found in the entrance and twilight zones are significantly larger (One-way ANOVA, $F=3.82$, $p=0.02$, $df=275$) than the capture areas found in the dark zone. Maturity does not significantly impact capture size (General Linear Model ANOVA, $F=1.20$, $p=0.27$, $df=272$) and does not interact with zone location of the web (General Linear Model ANOVA, $F=2.17$, $p=0.11$, $df=272$).
Figure 3.3 Mean capture spiral line spacing of *Meta ovalis* orb webs, scaled by spider mass. Increasing line spacing is positively correlated with increasing spider mass ($r = 0.52$). As adults are heavier than sub-adults, this supports the trend for larger webs in adults.
Figure 3.4. Percent of aerial and terrestrial prey captured during the 30-day sticky trap trial. Numbers reflect the percent of the total prey captured in each terrestrial light zone. Aerial insects were captured in higher proportions in the entrance (93.3%) and twilight (86.7%) zones and terrestrial prey were captured most often in the dark zone (57.2%).
REFERENCES


