FACTORS AFFECTING DISPERSAL AND WEB TENACITY IN THE LAMPSHADE SPIDER, *HYPOCHILUS POCOCKI* PLATNICK (ARANEAE: HYPOCHILIDAE)

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By

Sarah Ruth Batte Corkern

Director: Dr. Kefyn M. Catley
Department of Biology

Committee Members: Dr. Beverly Collins, Biology
Dr. Ron Davis, Natural Resources

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ABSTRACT

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Sarah R. B. Corkern, M. S.
Western Carolina University (November 2012)
Director: Dr. Kefyn M. Catley

The ability of a species to disperse is a key component in maintaining gene flow and therefore genetic diversity between populations. Dispersal in the lampshade spider *Hypochilus*, may be adversely affected by their extreme habitat specialization, restricting them to habitats consisting of damp, shaded rock faces in montane regions. These habitats are often patchy in nature and in some areas may be threatened by destructive fragmentation due to human activities. Movement of adult females within a population of *Hypochilus pococki* Platnick were observed in the Pisgah National Forest, Canton, NC. Eighty-nine individuals were marked within five designated plots. Web use and movement within plots was tracked over multiple visits over a breeding season. Females were shown to have a greater propensity toward web-tenacity than toward movement between web-sites. Individuals that did re-locate were more likely to travel a shorter distance than a greater distance between visits than was expected by chance. Results provide empirical support for previous genetic study conclusions and anecdotal observations that females exhibit limited movement and are therefore dispersal limited.

The role that juvenile spiders and mature males might play in maintaining gene flow among populations is discussed as is how understanding the processes of gene flow among *Hypochilus* populations is critical to the conservation biology of all three species in Western North Carolina.

INTRODUCTION

Movement of individuals throughout and between populations of an animal species is important in maintaining gene flow and therefore genetic diversity (Slatkin 1987; Bohonak 1999). Spiders, because of the two modes by which species disperse, are a particularly good taxon to study. Spiders can disperse by ballooning, a somewhat random yet active method that can achieve great distances, or by walking along the substrate, which may be more restrictive in terms of distance. Certain non-ballooning species may be especially restricted in their ability to disperse, which presents challenges in maintaining gene flow within a species. The genus *Hypochilus* is a group of spiders that are not known to balloon suggesting dispersal is by walking along the substrate. However *Hypochilus* are tightly coupled to their habitat and may not be able to travel through areas that do not meet specific habitat parameters. Much of the habitat that *Hypochilus* occupy is fragmented, which could create a dilemma for dispersing individuals that may not be able to survive outside of their microhabitat. While it is likely that *Hypochilus* have limited dispersal, this has not been tested empirically. Observing and tracking movements of *Hypochilus* individuals in the field may lead to a better understanding of dispersal within these species, and perhaps dispersal in other species that are likely to experience similar selection pressures.

Ballooning vs. Non-Ballooning Dispersal

The order Araneae (spiders) is the seventh most diverse animal taxon. Occupying a wide variety of niches, their success in certain habitats can, in part, be attributed to the ability of certain species to disperse by ballooning. Ballooning is a method of spider dispersal, in which spiderlings, and sometimes adults, become displaced by being carried by air currents, and is often instigated by a "tiptoe" behavior where the opisthosoma is lifted and a strand of silk is released into the air. When meteorological conditions are conducive, ballooning is thought to be an efficient means of long distance or short distance passive airborne transport that allows travel to a variety of different habitats (Duffey 1998; Reynolds et al. 2007). However, not all spider species disperse by ballooning. While many species have evolved well-developed ballooning behaviors, such as "tiptoeing," there are many others in which ballooning dispersal appears to have been selected against.

Dispersal in non-ballooning species appears to be largely cursorial, where the individual walks along the substrate, but it has not been well studied in most species. Since many non-ballooning species have been described as being limited dispersers, it may be particularly important to study dispersal in those groups, as conservation may be warranted in some cases. In addition, non-ballooning species appear to be more frequent in the more basal spider groups, such as Mesothelae, Mygalomorphae, and lower Araneomorphae (Haplogynes and lower Entelegynes), than in more derived spider groups (higher Entelegynes), but ballooning is not always a monomorphic behavior within families (Bell et al. 2005). Therefore, understanding mechanisms for dispersal in non-ballooning species may provide important implications about the evolution of ballooning dispersal and may contribute to the overall understanding of spider evolution.

The evolution of ballooning vs. non-ballooning dispersal in spiders has only been touched upon by Bell and colleagues (2005), but appears to be largely synonymous with the evolution of adaptations to habitat characteristics and landscape features of which a particular species occupies. Bell and colleagues (2005) suggest that evolution of ballooning behaviors most likely became highly selected for during the Cretaceous, as a result of the diversification of habitats caused by the radiation of angiosperms. Ballooning may have become a more feasible option for dispersal during this time, as more open habitats developed, such as grasslands, that provided better air flow needed to facilitate ballooning (Bell et al. 2005). However, while ballooning may have been selected for in generalist species, it may not have been favored in evolving habitat specialists that remained within very narrow niches, particularly in habitats that did not provide wind conditions necessary for ballooning, such as caves, leaf litter, and dense forests (Bell et al. 2005).

A ballooning individual's destination is largely dependent on the strength and direction of the air current by which it is carried, therefore ballooning is thought to be a lottery and is selected for in risk spreading generalists, and selected against in specialists because of the increased risk of reaching unsuitable habitat (Bonte et al. 2003). A simulation model by Halley and colleagues (1996) of linyphiid dispersal in mixed agricultural landscapes with changing field types indicates that the ability of a spider to balloon frequently and to great distances can increase their survival and abundance in changing heterogeneous landscapes. Thus, individuals in unpredictable and ephemeral habitats are likely to evolve higher rates of dispersal (Travis and Dytham 1999). In comparison, a simulation model by Kisdi (2002) showed that dispersal may co-evolve with a habitat specialization trait that when selected for increases local adaptation and decreases dispersal.

In habitat specialists, in which ballooning dispersal is not as prevalent, the risk of extinction can increase with increasing habitat fragmentation (Bonte et al. 2003; Bonte et al. 2004). This is because non-ballooning species commonly disperse by walking, and therefore some degree of connectivity between habitat patches may be required to maintain gene flow between populations in different habitat patches. In contrast, ballooning species may be able to maintain some degree of gene flow in highly fragmented habitats because they are able to disperse by ballooning (Ramirez and Haakonsen 1999).

In some non-ballooning spiders, studies have revealed that long time genetic divergence between species or between populations within a species can either be explained in relation to historical geographical barriers that physically separated groups or by a combination of temporal and spatial isolation created by low dispersal rates and habitat fragmentation (*Lutica*, Ramirez and Beckwitt 1995; *Habronattus pugillis*, Masta 2000; *Aptostichus simus*, Bond et al. 2001; *Hypochilus*, Hedin 2001; *Hypochilus thorelli*, Hedin and Wood 2002; *Apomastus*, Bond et al. 2006; *Homalonychus*, Crews and Hedin 2006). Not all non-ballooning species appear to be isolated to such a degree (some species of *Agelenopsis* (Ayoub et al. 2005) and some populations within the non-ballooning salticid species *Habronattus pugillis* (Masta 2000) appear to have significant degrees of gene flow), but habitat destruction and fragmentation does seem to have potentially detrimental effects on populations of particular non-ballooning species. For example, in *Apomastus* spp., a GIS simulated model showed that population loss appeared to have resulted from loss of genetic diversity and adaptability due to loss of habitat and fragmentation (Bond et al. 2006). Thus, studying dispersal in non-ballooning species may become increasingly more important as it will not only help to assess potential risks that a particular species might face, but will also contribute to the knowledge and understanding about the evolution of ballooning and non-ballooning dispersal in spiders.

Non-Ballooning Dispersal in Hypochilus spp.

Of particular interest is the non-ballooning spider family Hypochilidae, which is the most basal group of the infraorder Araneomorphae, and thus a critical taxon for the study of spider biology (Platnick 1977; Forster et al. 1987). All species within the two genera that comprise the family Hypochilidae (*Hypochilus*, consisting of 10 species, and *Ectatostica*, containing two described species) possess a unique combination of plesiomorphic characters: two pairs of book lungs, semidiaxial positioning of the chelicerae, and a cribellum and calamistrum (Marx 1888). *Ectatostica* spp. are known only from China, but *Hypochilus* spp. are endemic to North America and are separated into three disjunct geographical clades (Catley 1994; Hedin 2001). Each clade is restricted to a distinct montane region: the California Mountains (*H. kastoni* Platnick, *H. petrunkevitchi* Gertsch, and *H. bernardino* Catley); the Rocky Mountains (*H. bonneti* Gertsch, and *H. jemez* Catley, as well as *H. cf. jemez,* an undescribed species proposed by Hedin (2001)); and the Southern Appalachian Mountains (*H. gertschi* Hoffman, *H. thorelli* Marx, *H. pococki* Platnick, *H. sheari* Platnick, and *H. coylei* Platnick). Current range distributions of *Hypochilus* species do not appear to overlap (Hedin 2001; Huff and Coyle 1992; Catley 1994). Molecular data analyses of *Hypochilus* species relationships suggest that species may be highly divergent at the mtDNA level, indicating long time separation (Hedin 2001). However, despite this genetic divergence, *Hypochilus* species all have very similar morphology and ecology and often are solely distinguished based on differences in genital characters (Catley 1994). All *Hypochilus* species seem to have restrictive habitat requirements limiting them, almost exclusively, to moist, well-shaded rock outcrops, on which they build cribellate lampshade-shaped webs, and are often found in the vicinity of streams (Fergusson 1972; Huff and Coyle 1992). In addition, *Hypochilus* only seem to be found in these types of habitats at elevations between 2000 ft and 4500 ft (Fergusson 1972). *Hypochilus* habitat has been described in a similar manner by several authors, (Marx 1888; Petrunkevitch 1932; Gertsch 1958; Hoffman 1963; Shear 1970; Fergusson 1972; Catley 1994). Humidity is one environmental factor that is thought to be important in limiting the distribution of *Hypochilus* species to moist rocky forest habitats (Fergusson 1972; Catley 1994).

Hypochilidae dates back as early as the Jurassic, when the environment was more moist and warm and before ballooning behaviors became highly selected for, according to the phylogeny of Penney (2004). Catley's (1994) phylogeny of *Hypochilus* species supports the scenario that up to the Miocene-Pliocene period, *Hypochilus* were widely distributed across North America and that a plausible scenario resulting in their disjunct distribution was the demise of the Arcto-Tertiary vegetation across central North America. It is likely that the deciduous forests that once supported a link between eastern and western populations would have been too cool and dry after the event and would not have been able to maintain continuous populations (Catley 1994; Hedin 2001).

Connectivity of suitable habitat may be crucial to the ability of *Hypochilus* to colonize new habitats and increase gene flow between populations, yet *Hypochilus* are thought to be dispersal limited because they are non-ballooning species that are confined to specific rock habitats, which are often fragmented or patchy in distribution (Huff and Coyle 1992; Catley 1994; Hedin 2001; Hedin and Wood 2002). Of the three allopatric species that occupy Western North Carolina (*H. pococki, H. coylei,* and *H. sheari*) (Huff and Coyle 1992; Catley 1994; Corkern 2009), the latter two species are listed as "significantly rare" according to the N.C. Natural Heritage Program List of the Rare Animal Species of North Carolina (LeGrand et al. 2008), which indicates that these species are considered to be vulnerable and likely to go extinct. It is likely that the fragmentation of continuous suitable habitat, caused by destruction and disruption from development and urbanization, has contributed to a decline in their distribution (Corkern 2009). Since all *Hypochilus* species are ecologically and morphologically similar, the threats faced by one species today might in time affect other species as well.

Gene Flow in Hypochilus spp.

Hedin and Wood (2002) found that demes within a population of a single species, *H. thorelli*, were highly divergent, and that gene flow was limited by space and time. The analyses were done using mtDNA samples, collected mostly from adult females, which strongly suggested that female-based gene flow was limited (Hedin and Wood 2002). This suggests that males are largely responsible for gene flow between populations, but in order to determine this, more samples would need to be taken (Hedin and Wood 2002).

It has been suggested by several authors that males make long distance migrations during the breeding season in search of females, and that males might be the main source of gene flow between populations while the females stay relatively stationary (Fergusson 1972; Huff and Coyle 1992; Eberhard et al. 1993). Eberhard and colleagues (1993) recorded a male *Hypochilus pococki* covering a linear distance of 10.6 meters in 48 hours, which could suggest a long distance movement, but more data are needed in order to determine the average distance of male dispersal. However, despite the lack of supporting evidence, sex-biased dispersal, especially male-biased dispersal, is fairly common among spider species; thus, it is possible that such a process could have been selected for in *Hypochilus*.

Sex-Biased Dispersal

In general, dispersal is thought to be largely driven by the availability of natural resources required by the physiological requirements of an individual, which can differ at different life stages and between sexes (Ramenofsky and Wingfield 2007; Bowler and Benton 2009). This differentiation of dispersal behavior where natal dispersal or sex-biased dispersal takes place, is seen in many spider species, as well as many other taxa, and is generally considered to also be largely driven by inbreeding avoidance mechanisms (Waser 1985; Perrin and Mazalov 2000).

Sex-biased dispersal in spiders may be either male or female based, depending on the species. The fishing spider, *Dolomedes triton* Walckenaer, exhibits female-biased dispersal (Kreiter and Wise 2001). Females of this species were shown to have a higher rate of dispersal compared to males and juveniles, which was likely the result of an increase in female foraging behavior, due to the greater energy requirements needed for egg production during breeding season (Kreiter and Wise 2001). Male-biased dispersal may be more common because, in most species, males will leave their webs and stop feeding (or feed very little) after they molt to maturity, to search for female mates, making them no longer limited by food or web-site availability, but by mate availability (Thomas and Jepson 1999). This might lead males of some species out of "suitable habitat" because for breeding males, the presence of once essential resources within a habitat, might become less important than finding a suitable mate (Thomas and Jepson 1999). If the females of the same species stay relatively stationary during the breeding season, the majority of dispersal would be due to male migration, thus making dispersal male-biased; as may be the case for *Hypochilus* species.

Potential for Web Tenacity

Hedin and Wood (2002) found that females of *H. thorelli* were shown to have relatively little gene flow between populations, suggesting that despite the distance of male migration, females are likely to move very little during the breeding season. However, there is still very little known about female movement including the distance females travel, the causes for desertion of a web, and the mechanisms used when selecting habitat and web-site locations. Since *Hypochilus* are limited to a specific type of habitat that is often fragmented and patchy, it does seem plausible that natural selection would have favored behavior that increases web tenacity and decreases the frequency of web re-locating, however there are currently no studies that directly test this hypothesis in *Hypochilus.*

A factor that might inform such speculation is silk production. *Hypochilus* produce cribellate silk webs, which are more metabolically costly to produce than the adhesive capture threads produced by orb weavers (Opell 1998). Because of this great investment, *Hypochilus* may be more likely to have high web-site tenacity. In addition, studies have shown that spiders that build more costly webs, such as sheet webs and funnel webs, relocate less frequently than spiders that build less costly webs, such as orb weavers (Janetos 1982; Tanaka 1989). Species that build cheaper webs appear to have a lower cost of re-locating and a lower threshold for the tolerance of food availability that causes an individual to leave a web, compared to species that build more expensive webs (Janetos 1982). Because *Hypochilus* build expensive cribellate lampshade webs, which are more similar to sheet webs than orb webs, they are likely to sustain a higher cost of re-locating than that of an orb weaver.

Mechanisms in Web-Site Selection

When *Hypochilus* spiders do re-locate, perhaps there are certain mechanisms used in the habitat search and web-site selection processes that aid in reducing the cost. *Hypochilus* live in aggregates, in which webs are built close to each other, often touching, and have been found to be arranged in a clustered spatial pattern (Hodge and Storfer-Isser 1997). When constructing webs, *Hypochilus* often attach support lines to silk from other webs to use as anchors. Hodge and Storfer-Isser (1997) suggest that the presence of silk of other spiders might be the main attribute selected for by *H. thorelli* when choosing web-sites as apposed to the presence of other habitat features. The authors suggested that, the presence of silk might be indicated as suitable web attachment formations to emigrating spiders searching for a web-site with suitable surrounding support structures. Using silk encounter to select web-site locations can result in the formation of aggregates because conspecifics may be attracted to the silk of one another. Individuals that select web-sites near conspecifics are inevitably likely to occupy habitat that is optimal because it is currently inhabited by other individuals. Hodge and Storfer-Isser (1997) also found *Hypochilus* to sometimes exhibit a behavior where they usurp webs of conspecifics. Perhaps it is a less costly means of moving to a new web-site, however it is not very well studied and the frequency to which individuals exhibit this behavior is not known.

Focus of this Study

More studies are needed to further examine female and male *Hypochilus* dispersal behavior. Clearly, studies elucidating gene flow between populations, especially of males, would shed light on the question of whether *Hypochilus* exhibits male-biased dispersal, which is important to the overall knowledge and understanding of dispersal within the species. But because dispersal is a complicated process and is influenced by a multitude of different factors, it is best understood when studied from multiple levels (Dingle and Drake 2007). Since natural selection acts on the individual, studies that focus on how and why individuals use and move through their environment are important to the understanding of the functions and mechanisms for dispersal (Dingle and Drake 2007).

In order to better understand dispersal in *Hypochilus,* movement within each sex and age class must be thoroughly examined. Due to reasons of feasibility, this study focuses on movement of adult female *Hypochilus pococki.* Individuals were tracked and observed within designated areas over a period of time. Web use, web placement, and distances traveled by individuals were examined. This study tests the hypothesis that females rarely move, and that when they do move, they are more likely to move within a small area rather than to move far distances. In addition, it was hypothesized that spiders would be more likely to move to an already existing web than to build a new web and that webs would consistently be found built next to or very near to other webs. The following questions were addressed: Are spiders more likely to remain in the same web than to re-locate? If and when spiders do re-locate, how far and where do they move? Are re-locating spiders more likely to utilize webs of other spiders than to build new webs? Are webs consistently placed near other webs resulting in a clustered pattern?

NATURAL HISTORY OF *HYPOCHILUS*

Species Distribution

See Introduction for species distributions.

Habitat

See Introduction for description of habitat.

Web Design

Hypochilus species build cribellate webs that are shaped like upside down lampshades, with the narrower base attached to the substrate (usually rock surface) and the walls extending out in a broad cone shape (Figure 1). The spider rests in the center of the base of the web. The main components of the web include the cribellate cone-shaped walls, the non sticky tangle just at the top of the cone, and the non sticky guy lines that extend from the walls, attaching to various objects surrounding the web for support. The web structure of *H. gertschi* is described in detail by Shear (1970) and can be related to all other *Hypochilus* species. Shear (1970) also recognizes that web size is proportional to the size of the spider that occupies it.

Life Cycle

Hypochilus typically have a two-year life cycle, where spiderlings hatch in the spring and summer and mature at the end of the second summer (Coyle 1985). Mature males and females are abundant between August and October (Fergusson 1972; Eberhard et al. 1993). Mature males and females presumably die at the end of the second summer. It is unknown whether *Hypochilus* can live a third year, however there is one documented observation of mature females in the spring (Fergusson 1972).

As spiderlings emerge from the egg sac, they remain in a cluster on the adjacent substrate (*H. thorelli*: Fergusson 1972; *H. pococki*: personal observation). *Hypochilus* have not been observed to balloon, but spiderlings are often found scattered about the rock habitat in small lampshade webs, similar to adult webs (Fergusson 1972; personal observation). Based on his observations of *H. thorelli*, Fergusson (1972) suggested that dispersal away from the natal site most likely occurs by gradually spreading out over the substrate away from the egg sac, but actual dispersal mechanisms are not well understood. Juvenile spiders were observed to leave their webs after molting and find a new web site location (*H. pococki*: personal observation), but it is unknown as to whether this constitutes significant dispersal distance from one location to another over a period of time.

Within each rock habitat, *Hypochilus* live in aggregates, usually of two age classes (first year and second year individuals) (*H. thorelli*: Fergusson 1972), although some populations have been observed to only exhibit one cohort per year, alternating each year between juveniles or adults (*H. pococki*: personal observation). During the first year of life, spiders feed and grow and then overwinter, presumably in rock crevices before emerging the next spring (Fergusson 1972), but virtually nothing is known about overwintering strategies. During their second year spiders continue to feed and grow, reaching sexual maturity at the end of the summer.

Reproductive Biology

When males approach sexual maturity they build a molting web, which is similar to a regular web at the base but the sides extend up and meet at the top, enclosing the spider inside of the web (as described by Fergusson 1972). After this final molt, which takes place inside the enclosed web, the male leaves the web, stops feeding, and begins the search for suitable females (Fergusson 1972). Mature females continue to feed and occupy webs (Fergusson 1972). Mating takes place between August and early October (personal observation).

After mating, the female leaves the web and lays an egg sac, which is fixed to the rock substrate and camouflaged with moss and debris (as described by Fergusson 1972). Catley (1993) describes the egg structure and construction. Fergusson (1972) and Coyle (1985) noted that egg sacs are deposited in the fall. Catley (1993) reported egg-laying 20 days after copulation in the lab. However, during the course of the present study, some females were found laying egg sacs only days after earlier observations of the same females that were found occupying webs with males in the post-mating guarding position (personal observation).

Females may mate more than once within a breeding season, although this is not well documented (personal observation). Sometimes the same female was found with a different male on separate occasions and sometimes a female would be found back in a web after it was previously been found laying an egg sac. It is possible that *H. thorelli* females are able to store sperm, but it is not known for how long (Coyle et al. 1983). Since females have a cul-de-sac spermatheae, it may be argued that they are likely to exhibit last male preference (Elgar 1998), although this assumption has been contested by Uhl (2000), who showed that male preference cannot be predicted solely based on the number of openings of the female genital tract. Males have been seen guarding females (Fergusson 1972; Huff and Coyle 1992; Catley 1993) and since male *Hypochilus* have been shown not to associate with penultimate females (Eberhard et al. 1993), this behavior is considered to be a post copulatory behavior, which may be indicative of last male preference (Elgar 1998).

Mating Behavior

Fergusson (1972) and Catley (1993) describe the encounter between a male and female before, during, and after copulation in a lab situation. First, when the male encounters the silk of a female's web, he will use the first pair of his long legs to "tap" or "tug" the web (Fergusson 1972; Catley 1993). The female may try to attack the male, causing him to back away, but if there is no response from the female, then the male may move in a little closer (Fergusson 1972). Fergusson (1972) observed a male to enter a female's web after a successful "tapping" attempt that did not result in the female threatening to attack. Catley (1993) observed one female to leave her web and approach a male in a threatening manner after he exhibited repeated web-tugging, however this male did not back away, but rather began stroking the female with his legs. This stroking behavior caused the female to become receptive and easily manipulated by the male (Catley 1993). In both situations, the female assumed an "acceptance posture" where her opisthosoma was lifted up, while her prosoma remained parallel to the substrate (Fergusson 1972; Catley 1993). The male positioned himself facing the female with his ventral side resting against the substrate and his dorsal side adjacent to the ventral side of the female's prosoma (Fergusson 1972; Catley 1993). Catley (1993) observed the male to insert the palps alternately into the female's genital opening. After mating, the male assumes the "guarding-posture," where he rests closely to the female, often touching (Catley 1993).

Catley's (1993) account includes video documentation. A video documented observation of a male and female *H. pococki* copulating in the field was shot during a preliminary observation period for the present study (personal observation). The female was found feeding before the male began "tapping" on the web. Then the male entered the web. The female appeared to stop feeding while copulation took place, but then resumed feeding afterwards. During copulation, the male and female assumed the same positions described by Fergusson (1972) and Catley (1993). The male inserted his palps alternately one at a time, as Catley (1993) also observed.

Predatory Behavior

Hypochilus is considered to be a generalist sit-and-wait predator because the web functions to capture a variety of different prey organisms (saltitory, cursorial, flying) (Fergusson 1972). Prey are captured in the sticky cribellate lampshade parts of the web (Shear 1970; Fergusson 1972). Shear (1970) describes *H. gertschi* capture of prey in detail, and Fergusson (1972) describes *H. thorelli* prey capture in a very similar manner. *Hypochilus* does not wrap its prey, but rather bites repeatedly to subdue the prey, cutting it out of the web with its chelicerae and bringing it back to center of the web to feed (Shear 1970; Fergusson 1972). Feeding can take up to two hours (Shear 1970). When done feeding, the spider drops the prey remains out of web (Fergusson 1972).

Main prey items observed in *H. gertschi* webs were species of Diptera (Shear 1970). Fergusson (1972) has reported collecting a variety of prey remains from *H. thorelli* webs including, but not limited to species of: Tipulidae, Formicidae, Gryllacrididae, Ptilodactylidae, Cerambycidae, Lampyridae, Cicadellidae; Coleoptera, Trichoptera, Lepidoptera; Opiliones, and Araneae (Gnaphosidae, Lycosidae, *Hypochilus,* *Antrodiaetus*). He notes that the most common were opilionids and tipulids, which were extremely abundant in the habitat. Huff and Coyle (1992) found similar prey items in webs of *H. sheari*, *H. coylei*, and *H. pococki*, but that the primary prey items found were gryllacridid crickets and cursorial spiders (lycosids, gnaphosids, pisaurids). The small lampshade webs of juveniles inevitably capture much smaller prey items that are likely to consist of a slightly different variety of smaller macroinvertebrates than those of adults. For example, *H. pococki* juveniles that were newly emerged in the spring from overwintering and were still quite small were observed to feed on pseudoscorpions (personal observation), which would not likely be a sufficient meal for an adult, but would be for a juvenile and would be easily captured in a small web.

Defensive Escape Behavior

Two levels of defensive escape behavior have been described in at least two species of *Hypochilus*, *H. gertschi* (Shear 1970), and *H. thorelli* (Fergusson 1972), in response to a “mild” and “heavy” threat. These behaviors have also been observed in *H. pococki* (personal observation) and are likely to occur in other species as well. In response to a “mild threat,” when frame lines are tapped, the spider oscillates its body. If the threat continues, the spider will move to the side of the web and ultimately climb out over the top of the web or cut a hole in the web and crawl out (Shear 1970; Fergusson 1972). When the spider exhibits this behavior, it will often rest just outside of the web (personal observation) before returning about 20 minutes later (Shear 1970). In response to a “heavy threat,” for example if the spider is touched, the individual will “jump” out of the web with the legs drawn up over its prosoma, landing on the ground directly underneath the web (Shear 1970; Fergusson 1972).

During this study, *H. pococki* were observed to exhibit another defensive escape behavior that has not been previously described, in which an individual would “jump” out of its web, but get caught in the tangle portion just above the mouth of the web instead of dropping all the way to the ground (personal observation). When this occurred, the spider would usually return to the web after a period of time without disturbance. It would seem that with this behavior, the spider is able to return back to its web fairly quickly and easily and it may not result in any damage to the web as there may be with the “run-out” behavior.

Figure 1. Lampshade web of *Hypochilus pococki*.

METHODS

Study Site and Plot Selection

The study site was located in Canton, North Carolina in the Pisgah National Forest along the State Highway 215 near the Sunburst Campground. The roadside along much of this portion of the highway provides habitat for *Hypochilus pococki*, consisting of long stretches of exposed damp and shaded rock faces. A total of five plots of rock face, where *H. pococki* populations were present, were chosen within a two-mile stretch. All plots were either contiguous or within close proximity to one another. The location of each plot was carefully selected to ensure that at least five meters of continuous rock space was accessible, with little to no vegetation blocking the base, and located far enough from the edge of the road to avoid traffic. Plots were labeled A-E and measured to be 4 m high by 5 - 7.5 m long (7 m for plots A and B, 7.5 m for plot C, and 5 m for plots D and E). Plot lengths were measured along the ground at the base of the rock and each meter within a plot was marked off with a flag.

Plots were visited at varying intervals between August and October 2010, with the total number of visits to each plot varying according to the degree of use by spiders; as more abundant plots were visited more frequently (A=15, B=9, C=19, D=12, and E=6). Plot B was added but subsequently dropped because the number of spiders became too low to provide informative data. Plot E was added later so it received fewer visits and fewer observations overall.

Field Data Collection

On the first visit after a plot was selected and measured, initial locations of individual adult *H. pococki* and webs within each plot were recorded. Each web was assigned a number. Web locations were recorded as x and y coordinates, which were determined by measuring (in centimeters) the horizontal distance (x) from the web center to the starting edge of the plot and vertical distance (y) from the center of the web to the base of the rock directly perpendicular. The occupancy and intactness were recorded and each web base diameter measured in millimeters (web base diameter was not included in data analyses). If the web was occupied, the mark of the spider present in the web was recorded (see section on marking spiders). The state of intactness was categorized as intact, partially intact, or destroyed, which is also known as a “web scar” where the circular base of the web is still visible, but the web is no longer intact. Male molting webs were also noted.

On the first visit to each plot, all of the individual adult male and female *H. pococki* on the rock were marked and their initial locations were recorded. Spider locations were expressed as x and y coordinates in the same manner as the web locations, described above. Each spider was collected carefully, especially if occupying a web so as to not destroy the web, and was measured using digital calipers in millimeters (Tibia I, Tibia IV, and total body length were measured). (These morphometric measurements were taken for additional information, but were not used in data analyses.) Then the spider was marked (as described below) and carefully placed back in the exact spot or web in which it was initially found. If the spider was found in a web, the web number was also recorded.

During each visit data were collected for all webs and spiders (new and existing). If a new web was found, the web base was measured, given a new number, and its location recorded. Data collected for both existing webs and new webs included intactness and occupancy. If occupied, the individual in the web was recorded. When unmarked spiders were found, their location and web number were recorded. Spiders were removed, marked and placed back in their original locations. If a plot had not been visited for up to about two weeks and webs no longer matched initial data, a new inventory of all spiders and webs was completed. Web identification numbers were not repeated.

Spider Marking

Marking was used to track the movement of individuals. Mark/recapture studies, in which individual movements are observed, can reveal a great deal about a species natural history, but there are limitations to studying organisms this way in the field. Due to purposes of feasibility, this study focuses on adult *H. pococki* spiders only, and in particular, adult females. Juveniles were not practical candidates for this study due to the difficulty in marking such small individuals and the difficulty of tracking and re-marking each spider after a molt. Males are also more difficult to track because they do not stay in webs. Adult females are more easily tracked because they have undergone their final molt and so will not shed their marked exoskeleton and are generally found in webs.

Marking was done using enamel paint, which has been used successfully in past studies to mark spiders on the opisthosoma or prosoma (Aspey 1976) and legs (Bel-Venner and Venner 2006) with seemingly little or no side effects. For this study, legs were marked allowing spiders to be marked uniquely so individual spiders could be tracked over the course of the study. A small amount of paint was placed on the femur of one or two of an individual’s legs, giving each spider a different mark that was distinguished by the color of paint and by the combination of legs that were marked. Different colors were used for each plot, but only one color was used for each individual.

Data Analyses:

(a) Spider Presence in Plots

If females were not relocating very frequently, their abundance within each plot would be expected to remain relatively consistent for each visit over the course of the study and the same individuals likely would be present at each visit. In order to examine this, the total number of spiders within each plot was counted during each visit and the presence of all previously marked spiders and any unmarked spiders was recorded. When previously marked spiders were found again within the same plot, they were considered “recaptures,” but if they were not present, they were considered to be “not found.” When unmarked spiders were found, they were considered “new spiders.” Frequencies of “recaptures,” spiders “not found,” and “new spiders” were tabulated using pivot tables. Significant difference between frequencies of “recaptures” and spiders “not found” were tested using a chi square test.

(b) Web-Occupancy Transitions by Spiders

The location and web data were analyzed to determine whether spiders were more often found occupying webs than not occupying webs and whether spiders were more likely to be found occupying the same web than occupying a new or preexisting web. Each observation was assigned a category, which described a spider’s current state of web occupancy compared to the last time it was observed. Categories included: initial web (the web in which a spider was found during the first visit), same web (the same web a spider was found to occupy as in the previous visit), new web (a web that was not present during the previous visits), previously existing web (a web that had been present during the previous visit, but had either been unoccupied or occupied by a different spider), and out of a web (a spider found within the plot, but was not occupying a web). A pivot table was used to cross-tabulate the number of times spiders transitioned from one category during one visit to another category on the following visit. Significant differences between frequencies of different web-occupancy transitions were tested using a chi square test.

(c) Frequency of Web Occupancy and Type of Occupant

To determine if webs were more likely to remain occupied by the same spider than unoccupied, or occupied by a different spider on consecutive visits, web occupancy and occupant type was examined on each visit. Each web observation was given a category describing its occupant compared to the last observation (either unoccupied, occupied by the same spider as the previous visit, or occupied by a different spider). Using pivot tables, the categories were cross-tabulated in order to calculate the number of times each web was found to transition from being occupied to being unoccupied, or occupied by the same spider or a different spider as the previous visit. Significant differences between the frequencies of different transitions to occur were tested using chi square tests.

(d) Observed Distances of Spider Movement

Spiders recaptured in the same plot as previous visits but in different locations were considered to have “moved.” The linear distance a spider moved during one movement event (from one visit to the next) was called a "step-length." All spider location points were entered into Arc GIS 10 for analysis and visual representation. Points were referenced to UTM NAD 83 zone 17 with the (0, 0) point of the plot considered the (x, y) origin of the UTM zone. Centimeter values were then treated as meters, which did not change the distance calculations in any way. For each time a spider moved, the distance, turn angle, and bearing between each consecutive point was calculated using the supplemental software, Geospatial Modeling Environment (GME), using the "movement pathmetrics" program. Using the information calculated by GME, the following distances moved by spiders were described: 1) Sum of step-length distances per individual in each plot over the entire course of the study; 2) The total linear distance from where a spider was initially found to the last point it was found; and 3) The average step-length distance traveled per spider.

(e) Patterns of Movement: Using Correlated Random Walk as Comparison Model

To determine if the distance a spider traveled per movement event was significantly different from that expected by chance, the actual mean distances traveled by spiders were compared to 1000 mean distances created using a correlated random walk using the "Simple Correlated Random Walk" (CRW) simulator program in GME. The points generated by CRW were based on step-length and turn-angle distributions calculated from the actual data using the "movement pathmetrics" function as described above. Only data from individuals observed to move more than one time were included for this analysis. For each spider used, 1000 iterations of 10 consecutive random steps were generated, each beginning at the same starting points actual individuals were found. The 10 steps for each iteration were averaged, resulting in 1000 mean step-lengths per individual. Means generated from the CRW were used for comparison of the actual data to determine whether individual spiders had a tendency to travel more or less compared to chance. This was calculated using a nonparametric percentile comparison (Shepard et al. 2008).

(f) Patterns of Spatial Arrangement of Webs: Cluster Analysis

The tendency of individual spiders to build webs within aggregates in significantly clustered arrangements was analyzed using the “Average Nearest Neighbor” Spatial Statistics Tool in Arc GIS 10. This analysis compared the average nearest neighbor distances between webs present in plots during each visit to expected nearest neighbor values calculated by the program based on the plot area. This determined whether webs within each plot were significantly clustered on each visit.

RESULTS

Spider Presence in Plots

Over the course of the study a combined total of 89 individual females were captured and marked from all plots. Spider abundance within each plot did not remain constant from one visit to the next and the general trend was for abundance to decrease over time (Figure 2). However, overall, spiders were more likely to reoccur within the same plot on the following visit than to be not found at all (most P values ≤ 0.05; Table 1). And for most plots (A, B, C, and D) the average proportion of recaptured spiders found per visit was greater than the average proportion of new spiders found per visit (Figure 3). Plot E had a slightly greater average proportion of new spiders than recaptured spiders (Figure 3), however plot E also had a shorter observation period compared to other plots, which could have resulted in more initial spider findings and fewer observations of recaptured spiders.

Web-Occupancy Transitions by Spiders

On consecutive visits, spiders in webs were found to continue to occupy a web significantly more frequently than to not occupy a web ($\chi^2=159.2$, $P<0.001$; Figure 4). In addition, spiders remaining in the same webs on consecutive visits were found significantly more often than spiders that moved to different webs ($\chi^2=81.2$, $P<0.001$; Figure 4). Spiders occupying different webs were either in a new web that was not present during the previous visit, or a previously existing web that was present during the following visit, but was either unoccupied or occupied by a different spider. Frequencies of spiders found in different webs did not differ significantly between those found in a new web and spiders occupying a previously existing web (χ^2=1.68, P=0.194; Figure 4).

Frequency of Web Occupancy and Type of Occupant

The average proportion of occupied webs was greater than unoccupied webs in all plots except plot E, in which there was very little difference between the proportion of occupied and unoccupied webs (Figure 5). For all plots combined, webs that were found occupied during visits were more likely to remain occupied on the following visit than to be found unoccupied (χ^2=21.0673, P<0.001; Figure 6). Occupied webs were more likely to be found occupied by the same spider than by a different spider (χ^2=83.71, P<0.001; Figure 6).

Observed Distances of Spider Movement

When considering all spiders combined (n=89), 33 individuals moved more than once over the course of the study (Table 2). Step-length totals for each individual differed significantly from the respective linear distance totals for each individual (the distance between the initial point at which a spider was first observed and the last point at which it was observed during the course of the study) (*t*=5.031, P<0.001; Table 3). This indicates that those spiders that moved did not move continually in a linear direction. The difference generally increased as the number of movement events observed per individual increased (Figure 7). This indicates that a spider could have moved from point to point several times within the plot increasing its total distance moved, but may not have moved very far from the first point to last point at which it was found.

Patterns of Movement: Using Correlated Random Walk as Comparison Model

For 18 of the 33 individuals that moved more than once during the study the average distance traveled per movement did not significantly differ from what was expected by chance (P values > 0.05; Table 4). Of the remaining 15 individuals that traveled an average step-length that significantly differed from what was expected by chance, there were only 3 individuals that moved a greater average step-length than predicted compared to the 12 individuals that moved an average step-length that was less than predicted (P values ≤ 0.05; Table 4).

Patterns of Spatial Arrangement of Webs: Cluster Analysis

Overall, webs were more likely to be found in a random pattern (on 37 visits, P values > 0.05; Table 5) than in a non-random, clustered pattern (on 14 visits, P values ≤ 0.05; Table 5). Some plots clustered more times than others, for example, Plot D was not found to be clustered during any visits.

Table 1. Comparison of the proportion of spiders recaptured versus not found in plots on each consecutive visit. Significant differences between observed and expected values were tested using a chi-square test (*P ≤ 0.05).

Plot	Observed		Expected		Total	df	Chi Sq	P value
	Recaptured	Not Found	Recaptured	Not Found				
A	52	37	44.5	44.5	89	1	2.53	0.112
B	24	11	17.5	17.5	35	1	4.83	0.028*
C	117	44	80.5	80.5	161	1	33.10	< 0.001*
D	48	24	36	36	72	1	8.00	0.005*
E	10	16	13	13	26	1	1.38	0.239
Total	251	132	191.5	191.5	383	1	36.98	< 0.001*

Table 2. Total step-length and linear distances (cm) and total movement events out of total recapture visits for each individual that moved more than once over the course of the study.

Plot	Spider	Total Step-Length Dist. (cm)	Linear Dist. (cm)	Total Movement Events	Total Visits Recaptured
A	1	665.26	199.32	2	3
A	3	391.42	295.45	3	6
A	4	263.92	186.13	4	8
A	7	508.84	13.89	3	8
A	10	495.76	166.48	3	10
A	11	752.68	222.79	5	6
A	13	118.07	0.00	2	4
A	15	182.72	113.03	4	11
A	17	78.92	73.57	3	5
A	19	155.32	150.89	2	4
A	21	563.29	562.62	2	6
A	24	623.96	52.47	5	9
B	1	334.67	300.15	2	6
B	3	329.97	224.34	2	8
B	5	1083.65	230.83	4	7
B	7	117.66	77.41	3	5
C	3	126.46	32.06	3	14
C	6	643.12	643.05	2	4
C	9	772.81	189.21	6	13
C	10	989.75	123.44	7	15
C	12	718.85	0.00	4	7
C	17	1208.41	328.32	6	12
C	20	180.48	166.48	3	6
C	22	812.60	542.49	3	8
C	25	120.87	91.83	2	10
C	26	533.10	374.72	2	10
C	27	158.91	88.96	2	5
D	7	309.69	305.74	2	7
D	9	558.45	176.14	4	9
D	18	125.40	76.32	2	9
E	2	440.27	333.31	3	5
E	6	170.60	81.01	3	5
E	8	278.98	181.04	2	3

Table 3. Paired one-tailed t-test comparing two distances for each of the 33 individuals that moved more than once during the study. The total step-length distance (distance per movment event) traveled by each individual was compared to the linear distance traveled by the same individual (distance between starting location and ending location points). The difference was said to be significant if P ≤ 0.05.

Mean Difference	**t**	**df**	**p-value**
248.83	5.031	32	< 0.001

Table 4. Summary of data generated from a Correlated Random Walk of 1000 iterations of 10 step-lengths (cm) for each individual that moved more than once. The probability of the observed average (cm) was determined by the proportion of the distribution of the predicted values that were found at or above the observed value (if greater than the predicted median) or at or below the observed value (if below the predicted median). Observed values falling outside 90% of the predicted distribution around the median were significantly different from expected (*P ≤ 0.05).

Plot	Spider	Predicted Values (cm)		Observed Avg. (cm)	Prob ≤ or ≥ observed
		Median	Range		
A	1	169.19	37.00 - 382.65	332.63	0.010*
A	3	175.93	38.00 - 420.44	130.41	0.214
A	4	166.49	14.86 - 362.22	65.98	0.0190*
A	7	168.99	26.38 - 364.81	169.61	0.496
A	10	163.70	30.73 - 352.63	165.25	0.495
A	11	169.06	24.83 - 373.32	150.54	0.375
A	13	170.11	24.62 - 380.54	59.03	0.017*
A	15	168.55	43.43 - 338.45	45.68	0.001*
A	17	174.77	37.79 - 379.66	26.31	< 0.001*
A	19	167.83	44.58 - 419.56	77.66	0.034*
A	21	174.17	33.83 - 433.99	281.65	0.051
A	24	170.14	24.97 - 425.68	124.79	0.212
B	1	174.37	43.53 - 370.24	167.33	0.454
B	3	172.70	37.60 - 374.57	164.99	0.445

B	5	163.61	46.71 - 349.97	270.91	0.038*
B	7	172.89	44.49 - 346.93	39.22	< 0.001*
C	3	175.50	24.11 - 412.56	30.07	0.001*
C	6	176.25	36.063 - 402.30	321.56	0.016*
C	9	180.43	41.51 - 382.26	128.80	0.199
C	10	172.61	38.93 - 434.79	194.37	0.380
C	12	183.83	37.41 - 393.69	179.71	0.472
C	17	179.57	34.93 - 406.05	201.40	0.360
C	20	173.37	34.20 - 397.92	60.16	0.009*
C	22	174.44	32.30 - 387.34	270.87	0.064
C	25	170.90	30.05 - 367.07	60.44	0.008*
C	26	173.05	44.00- 379.02	266.55	0.070
C	27	175.53	33.32 - 437.78	79.45	0.027*
D	7	128.36	29.02 - 230.82	154.85	0.206
D	9	125.80	35.45 - 222.37	139.61	0.353
D	18	125.39	40.89 - 217.49	62.70	0.022*
E	2	116.10	29.66 – 212.30	146.76	0.189
E	6	114.44	18.32 - 233.82	56.87	0.026*
E	8	113.98	29.14 - 225.03	139.50	0.219

Table 5. The probability that spider webs were arranged in a clustered spatial arrangement. Probabilities were based on the z-score calculated from the observed mean nearest neighbor distance and the expected mean nearest neighbor distance (cm) (*P ≤ 0.05 considered significant).

Plot	**Visit**	**Obs Mean Dist (cm)**	**Exp Mean Dist (cm)**	**Nearest Neighbor Ratio**	**z-score**	**P-value**
A	1	28.28	79.78	0.35	-4.10	< 0.001*
	2	38.17	118.32	0.32	-2.90	0.004*
	3	57.53	70.71	0.81	-1.33	0.182
	4	41.34	68.31	0.60	-2.92	0.003*
	5	68.42	83.67	0.82	-1.10	0.270
	6	59.69	88.19	0.68	-1.85	0.064
	7	105.13	108.01	0.97	-0.13	0.900
	8	81.80	108.01	0.76	-1.14	0.255
	9	105.21	100.00	1.05	0.26	0.792
	10	101.39	108.01	0.94	-0.29	0.774
	11	88.86	88.19	1.01	0.04	0.965
	12	162.33	132.29	1.23	0.87	0.385
	13	161.56	152.75	1.06	0.19	0.849
B	1	31.55	60.70	0.52	-4.01	< 0.001*
	2	43.77	93.54	0.47	-2.88	0.004*
	3	93.21	118.32	0.79	-0.91	0.364
	4	78.44	93.54	0.84	-0.87	0.383

	5	140.37	118.32	1.19	0.80	0.425
	6	49.61	132.29	0.38	-2.39	0.017*
C	1	38.85	68.47	0.57	-3.31	< 0.001*
	2	81.14	96.82	0.84	-0.88	0.381
	3	30.41	111.80	0.27	-3.41	< 0.001*
	4	53.84	86.60	0.62	-2.29	0.022*
	5	41.31	75.96	0.54	-3.15	0.002*
	6	50.82	96.82	0.52	-2.57	0.010*
	7	130.87	122.47	1.07	0.29	0.770
	8	80.53	86.60	0.93	-0.42	0.671
	9	75.71	96.82	0.78	-1.18	0.238
	10	79.29	91.29	0.87	-0.75	0.451
	11	96.92	91.29	1.06	0.35	0.723
	12	91.02	96.82	0.94	-0.32	0.750
	13	54.21	86.60	0.63	-2.26	0.024*
	14	44.67	91.29	0.49	-2.93	0.003*
	15	60.21	86.60	0.70	-1.84	0.065
	16	60.21	86.60	0.70	-1.84	0.065
	17	74.01	91.29	0.81	-1.09	0.277
	18	72.66	91.29	0.80	-1.17	0.242
D	1	59.18	62.02	0.95	-0.32	0.752
	2	50.15	55.90	0.90	-0.79	0.431
	3	47.00	62.02	0.76	-1.67	0.095
	4	44.75	59.76	0.75	-1.80	0.072
	5	62.06	67.42	0.92	-0.50	0.614
	6	77.28	70.71	1.09	0.56	0.574

	7	75.76	79.06	0.96	-0.23	0.822
	8	80.40	91.29	0.89	-0.56	0.580
	9	68.25	70.71	0.97	-0.21	0.833
	10	68.25	70.71	0.97	-0.21	0.833
E	1	38.34	67.42	0.57	-2.74	0.006*
	2	66.62	84.52	0.79	-1.07	0.284
	3	74.01	91.29	0.81	-0.89	0.375
	4	113.18	111.80	1.01	0.05	0.963

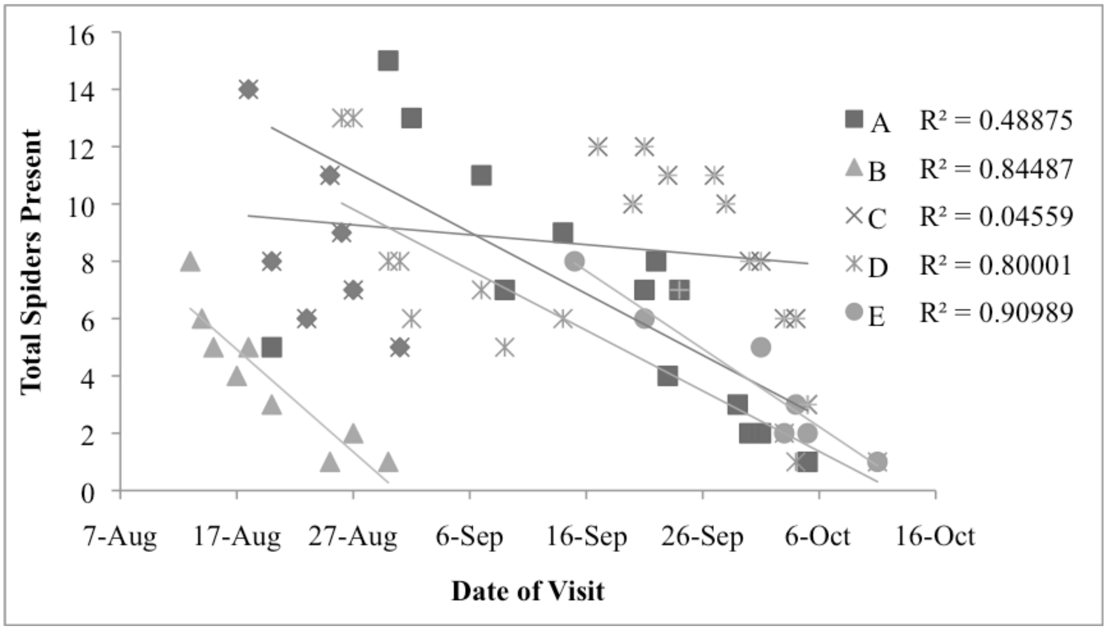

Figure 2. Spider abundance. Total number of spiders present in plots A, B, C, D, and E during each visit between mid-August and the beginning of October 2010.

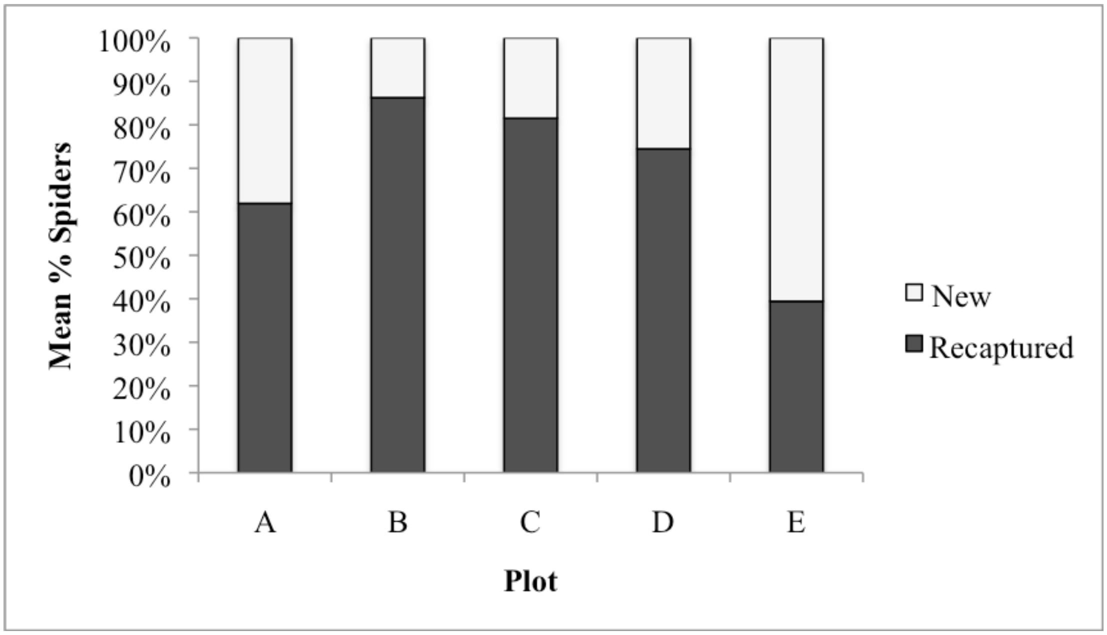

Figure 3. The mean percentage of new and recaptured spiders in plots (A, B, C, D and E) over the course of the study.

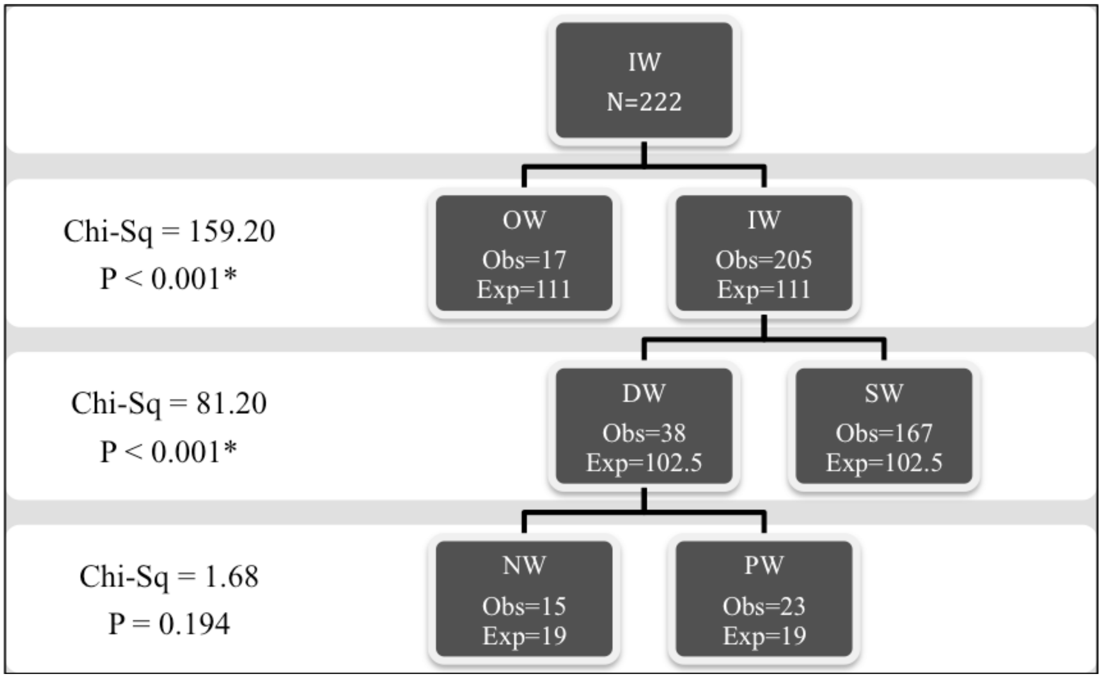

Figure 4. Frequencies of transitions in web-occupancy by spiders. Spiders in webs (IW) either remained in webs (IW) or were out of a web (OW) on the following visit. Those remaining in webs were either in the same web (SW) or were found in a different web (DW), which was either a newly found web (NW) or a previously existing web (PW). Significant differences between observed and expected values were tested using chi-square tests (*$P \leq 0.05$).

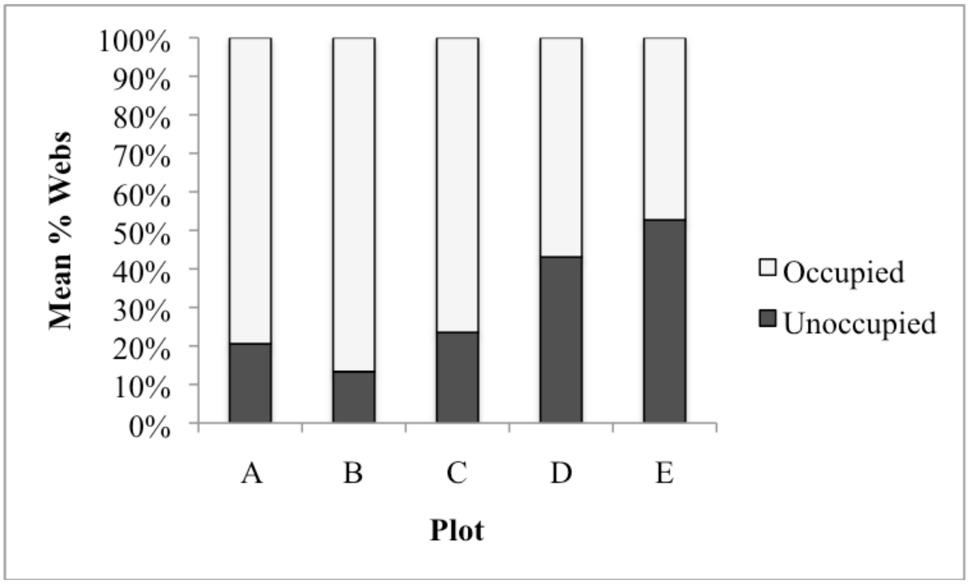

Figure 5. Mean percentage of occupied and unoccupied webs at each plot over the course of the study.

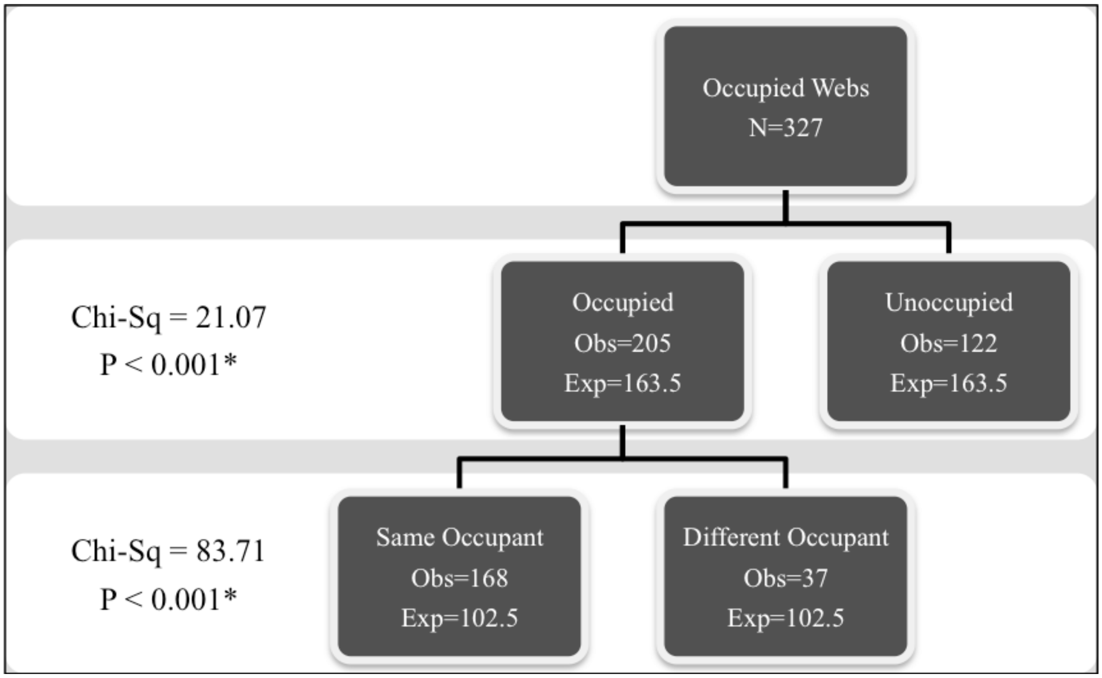

Figure 6. Frequencies of occupied webs to remain occupied or to become unoccupied on the following visit. Occupants in webs were either the same as the previous visit or were different individuals. Significant differences between observed and expected values were tested using chi-square tests (*P ≤ 0.05).

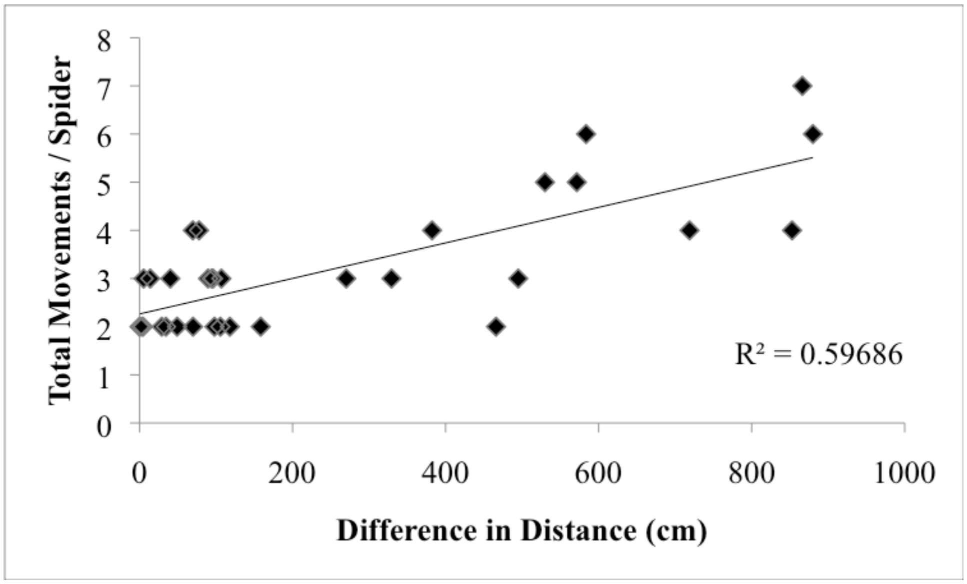

Figure 7. Linear relationship between the difference in step-length and linear distance totals per individual and the total number of movement events made per spider.

DISCUSSION

The adult female *Hypochilus pococki* that were marked and observed in this study generally persisted within the same plots upon consecutive visits. Moreover, most exhibited a greater tendency to occupy the same web than to either occupy a different web or to be outside of a web. These results demonstrate an overall propensity for web tenacity rather than movement. However, spiders did not remain completely stationary during the study. Some individuals presumably had moved into or out of plots, but most displaced individuals re-located within the same plot. Re-locating individuals either occupied a newly build web or moved to an already existing web built by a conspecific, but individuals did not show a greater tendency to exhibit either behavior. As new webs were built within plots and others became unoccupied and destroyed over the course of the study, the placement of new and existing webs within plots did not always result in a clustered spatial arrangement on every visit.

Movement Between vs. Within Plots

When observed as individuals, spiders most often remained within the same plots from visit to visit. However, spider abundance per visit changed within each plot over the course of the study, indicating that the individuals' presence in plots fluctuated between visits. Contributing to this fluctuation, unmarked spiders, which had not been previously found, were occasionally found within plots during visits and not every marked spider was always found on every proceeding visit. These inconsistencies in abundance and presence of individuals in plots over visits indicate that some movement occurred beyond plot boundaries. However, it is also possible that mortality was the cause of some spiders not being found.

Although it is possible that movement out of plots occurred, movement beyond plot boundaries was not measured, therefore the distance traveled by individuals re-locating out of plots could not be determined. However, overall there were more individuals recaptured than there were new or not found spiders, suggesting that if movement beyond plot boundaries did occur between visits, it was less common than remaining within the same web or moving within the plot boundaries between visits. Spiders that were recaptured were more likely to remain in a web from visit to visit than to re-locate.

Recaptured spiders that did move (33 individuals out of the 89 marked) did not move in a continual linear direction each time a movement event occurred. Therefore, very little overall distance was gained from the initial location points of each individual to their respective end location points. Most of these spiders moved an average step-length distance (distance per movement event) that was within an expected distance range. Only a few spiders moved a greater average distance than the expected range, but several spiders moved a shorter average distance than expected. Therefore, more individuals are likely to re-locate within a shorter distance rather than a longer distance. These results support the hypothesis that females rarely move, and movement that does occur, is most often within a short distance within microhabitat (defined by plot boundaries for this study).

Re-Locating within a Microhabitat

H. pococki individuals traveling short distances within microhabitat boundaries may have lower risks associated with re-locating than individuals traveling farther distances. Propensity to travel shorter distances within the microhabitat could be selected for, as it could decrease the time an individual might spend searching for new suitable microhabitat and adequate space for web construction. As a result, an individual could reserve some of the energetic costs spent actively searching and spend more time foraging in a web, where there is more protection from predation and desiccation.

Using presence of silk when selecting web-sites may contribute to the efficiency of re-locating within a microhabitat. Individuals that choose web-sites based on presence of silk (mainly of conspecifics), would inevitably build webs near other individuals, resulting in an aggregation. Individuals building a web within an existing aggregate are likely to benefit from choosing a productive web-site within microhabitat that is also within suitable environmental parameters. In addition, an individual may be able to reduce some of the metabolic cost of producing silk by incorporating some silk of other webs into their own construction. It has been suggested that the aggregating species, *Gasteracantha minax* Thorell, is able to increase foraging efficiency as a result of decreasing silk production by building webs within an aggregate and attaching their webs to other webs (Lloyd and Elgar 1997).

Individuals could also decrease silk production and time spent searching for adequate web space when re-locating by taking over the web of a conspecific. Some individuals were found to usurp the web of a conspecific, however overall, re-locating spiders did not exhibit a significantly greater tendency to either occupy already existing webs or to build new webs. Therefore, while taking over a web could be beneficial in certain situations, it may not always be more beneficial than building a new web. Comparing the costs and benefits of web take-over versus building a new web could be explored in future studies.

While individuals may be attracted to silk when searching for web-sites, there may be other physical attributes that individuals are capable of perceiving and selecting for when deciding where to build a web. If presence of silk were the only attribute selected for, then spiders in plots would be expected to always build webs adjacent to other webs. This was not found to be the case in this study. Webs were not found to be consistently clustered at all plots on all visits suggesting there are additional factors involved in web-site selection.

It is possible that there were areas within each plot that were more desirable and better suited for building webs. Various aspects of the rock face topography result in different levels of web-building suitability. For example, a ledge on the rock could provide more attachment area for a web compared to a flatter portion of rock. In addition, rock faces may contain small areas of vegetation or areas where the substrate generally remains excessively wet, which may not be suitable for web building. The extent to which individuals are able to perceive these aspects are unknown and could be explored in future studies.

Factors Affecting Re-Locating

Riechert and Gillespie (1986) recognized two phases in dispersal of web-building spiders: an initial random search for suitable habitat, followed by an active search for suitable microhabitat that meets the individual's physiological requirements, provides adequate prey availability, and provides a safe and suitable web-building site. When searching for a suitable web-site, different species select different critical features, some of which may be assessable before building a web, but others may require a trial and error approach (Riechert and Gillespie 1986). Janetos (1986) points out that the "decision" to leave a web may be a response to an inadequate aspect of the web location that the individual was initially incapable of predicting. Ultimately, for a spider to be successful when relocating, the expected gain from re-locating must exceed the expected gain from not re-locating (Janetos 1982). Therefore, different responses, either remaining in or leaving a web when exposed to varying pressures, would be selected as a function of the ultimate gain from leaving versus the gain from staying. For this reason, the cause of web-desertion may be critical in determining whether a spider embarks on a search for new habitat or a search for a new web-site within microhabitat.

Movements by females in this study can be viewed as re-locations within the microhabitat, because individuals presumably did not have to travel through patches of unsuitable microhabitat in order to settle at a new web-site. Dispersal from a web to a new, unconnected habitat patch is often a behavioral response triggered by an inadequate aspect of habitat quality (Riechert and Gillespie 1986). However, when movement from a web results in a short-distance re-location within the same mircohabitat, the reason for re-locating may not be a result of inadequate habitat quality. Alternatively, reasons for short distance web-site re-locations could be the result of factors that directly affect an individual's ability to remain within a web. A direct disturbance, in which a spider is threatened by an encroaching predator, or when a web becomes severely destroyed, are factors that could cause a spider to leave a web. But because a threat may only be temporary, and a destroyed or damaged web can be re-built or repaired, movement far from the web may not be justified.

Web-Abandonment and Re-Location in Response to Disturbance

Re-locating females in this study could have been driven to move out of webs because they were disturbed. Spiders and their webs likely experienced some disturbance as a result of the spider marking process, despite efforts to carefully remove and place spiders back into their webs. This disturbance could have caused spiders to leave their webs more than otherwise would have occurred. However, it is possible that the behaviors exhibited by *Hypochilus* in response to disturbance allow them to easily return to webs or to re-locate to new webs without long searches.

Hypochilus exhibit three different responses to threat in which an individual leaves its web in some manner (see *Natural History* section for complete description). For two of the responses, a) the spider runs-out of its web and b) the spider jumps from the web center into tangle portion of its web, the spider returns to its web after the exit. But in the third response, the spider completely abandons the web by jumping out onto the ground beneath. Web-return may be possible after this abandonment, but it is possible that re-locations also occur. Silk encounter may be used in this process.

In Fergusson's (1972) description of this jumping behavior, he remarked that the spider remains motionless on the ground for about 5 to 15 minutes, and then most likely finds its way back to the web by simply crawling straight up the rock until it reaches the silk base of its web. However, it would seem that in utilizing this method of silk encounter to search for a web, the spider might not always end up back in the same web. The spider may be capable of using gravitational cues to orient its movement vertically, as suggested by Fergusson (1972), but this alone would not ensure that the spider's first encounter of silk would be its own web. Perhaps the spider often ends up simply re-situating itself back into the aggregate in a different location, or encountering the web of a conspecific, thus facilitating a web take-over.

Nonetheless, these threat responses *Hypochilus* exhibit may have been selected because they allow escape from threats of varying degrees and still enable the spider to return, either to the same web or to easily re-locate without traveling very far. Comparing the costs and benefits of different strategies of web abandonment in response to threats in *Hypochilus*, as well as comparing responses of different spider species may be interesting to explore in the future.

Web-Abandonment and Re-Location Following Mating

Females leave webs after mating to produce eggs and construct egg sacs. Since this study took place over the breeding season, this could have been one of the factors leading to movement of individuals from their webs. Evidence for this can be attributed to several observations during the study in which a female was found outside of a web either actively constructing or resting adjacent to a partially or fully constructed egg sac. Often times, these spiders had been found previously in a web, sometimes even with a male in the post-mating guarding position. On some occasions, females, found with egg sacs on one visit, were found in a web on the following visit, suggesting that females search for a suitable web-site again following egg-laying.

Gene Flow and Male Movement

The sedentary nature and limited movements of female *H. pococki* are evident through the results of this study. This further supports a previous study that examined genetic data that showed limited female gene flow between populations of the species *H. thorelli* (Hedin and Wood 2002). Due to a lack of genetic sampling of male *H. thorelli* within the same populations, no definite conclusions about male gene flow could be determined (Hedin and Wood 2002). Similarly, male movement was not measured in this study, and therefore, no conclusions can be drawn about male movement. However, it can be speculated that since empirical data from this study and genetic data from the previous study suggest females do not contribute a large portion of the gene flow between populations, males are probably responsible for maintaining sufficient gene flow to prevent reproductive isolation from occurring. However, it also may be important to consider the degree to which male gene flow exists.

It would not seem highly beneficial for adult females or males to travel to isolated areas, even if it were to constitute suitable habitat. If females are to travel to areas devoid of other females, then they may not have a very good chance of encountering males. Furthermore, in order for males to increase their chances of finding mates, they must travel to or within aggregates of females. Therefore, it may be possible that both males and females travel only short distances.

In addition, males may not be physically equipped to make long distance movements. Male body size is small compared to female body size, making them more prone to desiccation, as this was found to be the case in at least one other spider species, *Pirata sedentarius* Montgomery (DeVito and Formanowicz 2003). In addition, without the safety of a web, they are likely to experience a high risk of predation. It is possible that male individuals only migrate as far as would be required to prevent inbreeding depression.

Kokko and Ots (2006) suggest that there is a degree to which a particular species can tolerate inbreeding, above which would result in the evolution of inbreeding avoidance mechanisms. Perhaps *Hypochilus* species experience some degree of inbreeding tolerance. If the mating system is largely inbred, it could result in populations with limited genetic variability and decreased adaptability, but with increased specialization. It is possible that in inbred populations, deleterious recessive alleles can be largely bred out (Bilde et al. 2005) or advantageous recessive alleles can become fixed (Joly 2010), contributing to a species that has little morphological and ecological variation, but well suited for its particular habitat and lifestyle such as *Hypochilus*.

Inbreeding tolerance has been shown to lead to the altruistic behaviors of social spider species (Bilde et al. 2005), but has not been largely addressed in non-social species. It would also be interesting to investigate the possibility of this type of mating system in *Hypochilus* as well as in other non-social, limited dispersing spider species in future research.

Habitat Colonization and Movement by Juveniles

Although there may be certain benefits to traveling short distances within a microhabitat, individuals that continually re-locate within a microhabitat would not likely be able to easily colonize new habitat or connect to other breeding populations. While the costs of moving away from an aggregate or across unsuitable habitat potentially outweigh the benefits for adult females, and possibly males, it may be that this is not the case for juveniles.

Juveniles of other spider species have been found to disperse for a number of reasons including competition with siblings for space and resources (particularly after ecloding the egg sac), as well as when changes in physiological requirements occur as a result of growth (Riechert and Gillespie 1986). Some species, as in the case of *Latrodectus revivensis* Shulov, leave the web after one or two molts and move to a new site, where a larger web can be built that can support the increased body size and has the ability to capture optimally sized prey (Lubin et al. 1993). It is possible that this occurs in juvenile *Hypochilus*, as a few *H. pococki* spiders were observed to move from their web a few days after a molt and build a new web. However, there is no documented evidence of how far juvenile *Hypochilus* generally travel when re-locating.

Juveniles often have slightly different web-site requirements than adults of the same species (Riechert and Gillespie 1986). *Hypochilus* juveniles build much smaller webs than adults, and therefore require less space and fewer surrounding support structures in order to construct a web. This could potentially allow juveniles the ability to inhabit areas between large patches of suitable habitat that adults may not be able to occupy due to a lack of large enough suitable web-sites. It may be that juveniles are able to exploit areas that adults would not be able to and therefore, would be more likely to colonize new habitats.

Conclusions

This study shows *Hypochilus* individuals to be limited in their ability to disperse far distances and this is particularly evident in females. Females may move short distances for various reasons and may use cues such as silk encounter to find web-sites within close range of the aggregate. It may be that staying within the aggregate is adaptive for adult females and could potentially aid in the survival of populations by preventing movement to isolated areas or across unsuitable habitat. As a result, female gene flow between populations is limited. Males may also have limited movement, but limited female movement and gene flow strongly suggest that males contribute to the gene flow thus preventing reproductive isolation. Further observations and genetic sampling of males in the field would be needed to confirm this likely scenario. It may also be speculated that juveniles exhibit a greater ability to colonize new habitats than adults due to less restrictive requirements for web-construction.

Field observations of individuals in natural populations can be time consuming and difficult to implement, but sometimes are the only way to learn certain aspects of behavior and natural history. Although genetic sampling may be a more feasible method for studying dispersal, further research that observes and tracks individual’s movement (particularly juveniles and males), and examines factors that initiate movement as well as responses to different pressures, could contribute to greater understanding of dispersal in *Hypochilus* species. In addition, because *Hypochilus* species do have limited dispersal and specialized habitat requirements, it may be important to monitor their abundance and distribution and availability of suitable habitat.

Habitat fragmentation may be detrimental to *Hypochilus* populations. In limited dispersing species with limited gene flow between populations, habitat fragmentation can further contribute to decreased gene flow and genetic diversity within populations. In *Hypochilus*, what little gene flow that exists between populations is likely important in maintaining reproductive connectivity within each species between otherwise fragmented populations. If the habitat becomes too fragmented, the surrounding habitat too unsuitable, or the distance between suitable habitat patches too great, populations could become highly isolated. Further isolation could lead to reproductive isolation and increased chances of extinction because the ability of individuals to colonize new or previously occupied habitats becomes more difficult.

It is important to protect *Hypochilus* habitat to prevent extensive fragmentation created by destructive human activities, such as development, clear-cutting, widening of roads, and other activities, which can destroy or alter habitat such that it is no longer suitable. Two out of the three species in Western North Carolina, *H. coylei* and *H. sheari*, are listed as “significantly rare” in the N.C. List of the Rare Animal Species (LeGrand et al. 2008) due largely to the highly restricted geographical ranges each of these two species occupy (Huff and Coyle 1992; Catley 1994; Corkern 2009). Their distribution has likely been negatively effected by human activities. By understanding the dispersal of *Hypochilus* species, we can better understand how they use and move about in their habitats and the landscape. This knowledge can be used to better conserve key habitats and especially corridors between habitats to help ensure the survival and connectivity of the rarer and range-restricted species, and prevent the widespread species from becoming rare and highly isolated.

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