COMPARATIVE SAMPLING METHODS AND COMMUNITY COMPOSITION OF GRASSHOPPERS (ORTHOPTERA: ACRIDIDAE) IN NORTHERN BOBWHITE HABITAT

By

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Abstract: This research contributes to a larger body of work concerning the decline of Northern Bobwhite in Western Oklahoma. Populations of Northern Bobwhite have been declining since at least the 1960's. Previous research has demonstrated that arthropods are essential to the diet of these birds. This resource provides protein to egg-laying hens that aids in producing eggs of better quality and to brooding chicks that aids in development of feathers and flight muscles. Grasshoppers (Orthoptera: Acrididae) are among the preferred arthropod prey for these birds. The objectives of this study were to compare standard methods of grasshopper sampling with a novel method and to characterize the community of grasshoppers in Northern Bobwhite habitat. Relative abundance as determined by sweep net sampling and density of grasshoppers observed in ring sampling was compared with a novel method of sampling that simultaneously measured relative abundance and number of grasshoppers caught per minute. Relative abundance estimates were not comparable between sampling methods, and density and rate of grasshoppers caught were positively correlated. Coefficients of similarity were calculated to show how similar measurements for abundance and richness were between sweep net and the novel sampling method. Community composition data were taken from sweep net samples. Proportions of functional group cover (components of vegetative make-up) were sampled using modified Daubenmire frames simultaneous to sweep net sampling. Abundant grasshopper taxa changed between vegetation types. Grasshopper subfamilies were also positively correlated with different functional groups. Factor analysis data show that grass and forb cover (as determined by modified Daubenmire frame sampling) were more important than litter and bare ground cover in predicting subfamily distribution. Simpson's diversity indices showed that grasshopper diversity increased over time and that upland sites were more diverse than any other vegetation type. This study was able to determine the effectiveness of standard and novel sampling methods and characterize grasshopper communities in Northern Bobwhite habitat and provides implications for management and further study of this system.

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INTRODUCTION AND REVIEW OF LITERATURE

Introduction

Northern Bobwhite (*Colinus virginianus*) are popular game birds for the state of Oklahoma. Researchers have noted declines in the bird's population due to a lack of suitable habitat brought on by suboptimal land management (Brennan 1991, Kitts 2004, Lusk et al. 2006, Doxon and Carroll 2010). The absence of essential arthropod prey is thought to contribute to the substandard habitat and the ultimate decline of Northern Bobwhite. Arthropods provide egg-producing hens with protein so they can develop better-quality eggs. They also provide protein to Northern Bobwhite chicks so they can develop feathers and flight muscles at a higher rate (Wenninger & Inouye 2007). Among the arthropod prey for Northern Bobwhite are members of the insect orders Hymenoptera, Coleoptera, and Orthoptera (Butler et al. 2004, Doxon & Carroll 2010). This research focuses on short-horned grasshoppers (Orthoptera: Acrididae) as a critical forage taxa of Northern Bobwhite.

Previous studies on grasshoppers as Northern Bobwhite forage taxa often only considered to the ordinal taxonomic level (Butler et al. 2004, Doxon & Carroll 2010). However, biological differences that may influence spatial and temporal partitioning of habitat including overwintering stages, dietary differences or preferences, and oviposition space occur at the subfamilial level. There are six subfamilies in the family Acrididae: Acridinae, Cyrtacanthacridinae, Gomphocerinae, Leptysminae, Melanoplinae, and Oedipodinae. The

grasshoppers most frequently encountered in this research belonged to Gomphocerinae, Melanoplinae, and Oedipodinae. Gomphocerinae and Melanoplinae have demonstrated similar life-histories, mostly overwintering as eggs and emerging as nymphs in the spring. Oedipodinae typically overwinter as nymphs and become adults earlier in the spring (Pfadt 1994, Capinera et al. 2004). Because of this, Gomphocerinae and Melanoplinae have a greater potential to compete with each other for resources directly, like food and oviposition space. Though this may not be the direct cause for this behavior, Gomphocerinae and Melanoplinae do partition the use of those resources.

Often considered to be generalist herbivores, these two subfamilies exhibit different feeding strategies. Melanoplinae have larger recorded dietary niche breadths, recorded ranges of plant species from which they feed. They eat a larger variety of plants from multiple groups (grasses, forbs, etc.) and may be considered generalist herbivores in the traditional sense. Gomphocerinae have smaller recorded dietary niche breadths, specializing on mostly grasses (Joern 1979, Behmer and Joern 2008). Additionally, it has been observed that some species of Melanoplinae prefer to lay their egg pods deep into loose soil devoid of vegetation. Some species of Gomphocerinae prefer to lay their egg pods in harder-compacted soil closer to the surface (Branson 2005). Partitioning the use of different plants as a food source and different substrates for oviposition may mitigate direct competition between these grasshopper subfamilies. Understanding these differences may help elucidate the availability of grasshoppers as prey to Northern Bobwhite.

Differences in grasshopper life stages may also be relevant to Northern Bobwhite. Juvenile grasshoppers (nymphs) may be a more optimal source of food due to their smaller size and inability to fly. Adult grasshoppers are larger than nymphs and may be too big for chicks to prey upon. Most adult grasshopper species also have fully developed wings that can aid them in escaping predation. They have sharp spines on their hind tibia that may make them difficult to

handle or consume. Nymphs lack these defensive traits and may also be more abundant during key forage times for hens and chicks. The differences between grasshopper life stages may prove to be important features that dictate the preferred and more important prey for Northern Bobwhite and should be considered in research as well.

Because of how the life history strategies of these Acrididae subfamilies differ, research that focuses on grasshoppers within the context of being prey for Northern Bobwhite and considers these differences may provide more useful information relevant to bird decline. Perhaps, due to the timing of feeding by Northern Bobwhite, only one subfamily acts as a primary source of prey. Nymphs may be the more easily-acquired food source, preferred over the larger mature grasshoppers. Treating the different life stages and subfamilies as one large group and ignoring these differences may lead to insufficient information regarding grasshopper ecology, an important component to Northern Bobwhite survival.

This research focuses on comparative sampling techniques and community composition of Acrididae in Northern Bobwhite habitat. There are two objectives of this research: 1) compare estimates of relative abundance and density from two standard techniques of grasshopper sampling with a novel method that combines relative abundance sampling and density sampling (through estimating rate of grasshoppers captured); 2) characterize the community of Acrididae in Northern Bobwhite habitat by measuring relative abundance, dominant species, and species diversity.

Results from these studies will benefit Northern Bobwhite research in several ways. Grasshopper subfamily emergence of both nymphs and adults will be measured, revealing when different grasshopper life stages are most abundant and in what locations in Northern Bobwhite habitat. These data can be used in conjunction with data from Northern Bobwhite researchers to see if the birds are foraging when and where the grasshoppers are most abundant. The most

abundant grasshopper species will also be recorded during each sampling year. When and where those species occur will also be recorded. A limited number of species may be identified as being more abundant and therefore more important to Northern Bobwhite over others. Also, the measurements of multiple sampling methods will be compared to determine how effective each is at capturing grasshopper species richness and relative abundance. Through development and assessment of a novel sampling method, recommendations on different ways to sample grasshoppers may be made. This could inform land-owners on how to assess the quality of their land as Northern Bobwhite habitat.

A chapter devoted to each objective will follow the literature review. These chapters are formatted for publication and include an introduction, explanation of methods used, presentation of results, and a discussion of results.

Northern Bobwhite

Since at least the 1960s, Northern Bobwhite (*Colinus virginianus*, henceforth referred to as "quail") populations have been on the decline (Brennan 1991). In Oklahoma, these birds are a popular game bird that generates money through sales of hunting licenses and revenue spent by hunters. Their decline is attributed to the lack of suitable late successional habitat promoted by suboptimal land management (Kitts 2004, Lusk et al. 2006, Doxon & Carroll 2010). Some species of quail build nests at the bases of tall bunch-grasses and forbs (non-grass plants). Brood-rearing requires ground-level alleyways essential to mobility, and can be provided by weedy field borders or small grain fields in agricultural settings. Shrubs and other small woody plants provide essential "loafing" areas: areas that are well-protected from predators and harsh weather where quail can rest when not foraging. Tracts of thick grasses and shrubs give quail places to hide when confronted by predators. Because of these diverse vegetative features, late

successional habitats with native vegetation also provide egg-laying hens and quail chicks with crucial arthropod prey (Wenninger & Inouye 2007). Habitats overrun by invasive exotic plants will form dense sod mats and not allow for the structural heterogeneity required by these birds to nest, forage for prey, and loaf (Barnes et al. 2013).

Habitats with introduced or non-native plant species have resulted in a negative effect on bird and arthropod diversity, density, and abundance. When looking at the differences in South Texas rangeland bird communities between habitats with native vegetation and those with exotic vegetation, Flanders et al. (2006) determined that exotic vegetation did not support a diverse bird community. Total bird densities were significantly lower in exotic vegetation as were resident breeding species densities (Flanders et al. 2006). Quail abundance was also twice as high in native sites than in exotic ones. It is thought that this occurs because the sites with exotic vegetation also limit the availability of essential arthropod prey (Flanders et al. 2006). Several orders of arthropods were less abundant in exotic vegetation, providing fewer resources for the rangeland birds to consume (Flanders et al. 2006). By creating less hospitable habitat for arthropods, exotic vegetation is not desirable for quail habitat.

Invasive and exotic plants can also create large homogenous tracts of land that reduce the survivability of the birds greatly by creating structurally similar and undesirable nesting sites that decrease plant biodiversity and increase the likelihood of predation. In a study examining chestnut-collared longspurs (Passeriformes: Calcariidae) in Montana, it was determined that birds that established nests in patches of habitat that were infested with exotic crested wheatgrass were less likely to produce successful nests (Lloyd and Martin 2005). The exotic sites were dominated with 99% cover of crested wheatgrass, while native sites were comprised of seven different plant species. While the native sites were not preferred over exotic ones, the birds that chose native sites had a greater number of successful nests (Lloyd and Martin 2005). Predation was the biggest cause of mortality in both native and exotic sites, but it was also noted that nests in native

sites produced a larger number of eggs and those nestlings grew at a faster rate than nestlings in exotic sites (Lloyd and Martin 2005). Though not addressed in the study, the slower development rate of nestlings from exotic sites could be attributed to a lower diversity and availability of essential arthropods in the habitat, allowing for greater rates of predation in these sites. If this was the case, it would support the importance of arthropods in developing grassland bird diets.

For quail chicks, arthropods are an essential dietary requirement (Butler et al. 2004, Harveson et al. 2004, Doxon & Carroll 2010). They represent an excellent source of protein for both growing chicks and hens during egg-laying season (Wood et al. 1986, Moreby et al. 2006, Doxon & Carroll 2010). Chicks need the protein to grow feathers, muscle and ultimately fledge faster; egg-laying hens will eat 5 times as many arthropods as they would if not egg-laying season (Brennan & Hurst 1995, Doxon and Carroll 2010). Arthropods exist in abundance in the same ideal nesting and brood-rearing habitats used by quail. However, in order for the arthropods to be of any use to quail chicks, they must be accessible. Bare-ground alleyways that increase mobility and make foraging easy allow quail chicks to access insect prey items necessary for development (Doxon & Carroll 2007).

It has been determined that quail will eat a variety of arthropod species, including members of the orders Araneae, Hemiptera, Hymenoptera, Lepidoptera, Orthoptera, and Coleoptera (Butler et al. 2004, Doxon & Carroll 2010). Studies have been performed that show preferences of some orders over others by foraging chicks. Doxon & Carroll (2010) determined that the diet of the quail chicks in their study was composed primarily of Hymenoptera (50%) and Coleoptera (32%), with the next-most-desirable orders being Araneae and Lepidoptera, both at 4%. Butler et al. (2004) found that when presented with prey items from several arthropod orders, 96% of chicks studied ate Homoptera, Lepidoptera, Araneae and Orthoptera. One-hundred percent of the chicks euthanized after 30- and 40-minute digestion periods had Araneaen, Coleopteran, and Orthopteran diagnostic fragments in their gizzards (Butler et al. 2004). While

not the ultimate purpose of their study, the data suggest that quail chicks exhibit some preferences in arthropod prey selection. Feeding is most likely determined by how easily chicks can capture prey items (Palmer et al. 2001, Doxon & Carroll 2007), but if they can access all arthropod orders equally, prey preferences might begin to appear. As one order was not significantly consumed more than any other in these studies, true preferences are not supported. However, it is apparent that several different orders in these studies were consumed and an assumption can be made that if they can be acquired in the wild, they will be consumed there as well (Butler et al. 2004, Doxon & Carroll 2010).

In a study of the summer diets of quail, Brennan and Hurst (1995) observed that certain animal foods were more important for hens than others. These researchers determined that snails (a gastropod), short-horned grasshoppers, crickets, stinkbugs, spittlebugs, and beetles were eaten more frequently than other arthropods. Because this study controlled the accessibility of all prey, the fact that these prey were consistently eaten over others implies a preference by quail hens (Brennan & Hurst 1995).

Grasshoppers (Orthoptera: Acrididae) are a common member of arthropod communities upon which quail prey (Doxon and Carroll 2010). Grasshoppers have complex assemblages and are known to fit into several different diverse ecosystems, including grasslands, mountains, and mixed-grass prairies (Alexander & Hilliard, Jr. 1969, Otte 1981, Capinera et al. 2004). They are generally considered only to the ordinal taxonomic level in dietary studies (Butler et al. 2004, Doxon & Carroll 2010) but have the potential for important species-based relationships with quail that may have gone unrealized. Little effort has gone into understanding the species composition of these assemblages and how they respond to vegetative communities and microclimates that exist within potential quail breeding habitat.

Grasshoppers are good indicators of habitat quality (Niemala et al. 1993, Anderson et al. 2001, Gebeyehu & Samways 2003) and characterizing their assemblages and the vegetation in which they live are important steps toward developing sustainable quail management techniques. Particular grasshopper species can be highly sensitive to grazing by cattle (Gebeyehu & Samways 2003) or disturbances like mining (Anderson et al. 2001). By describing the species diversity and abundance of grasshopper assemblages in potential quail breeding habitats of varying quality and composition, it can be determined if any significant relationship between these factors exists. Eventually, if relationships between quail success and grasshopper diversity and abundance have been established, assessments of habitat can be made based on the presence or absence of certain grasshoppers and predictions of how quail will be affected can be made. For these predictions and those based on grasshopper sampling to be accurate, an understanding of the interactions between grasshopper assemblages and their habitats must be ascertained.

Acrididae

Acridid grasshoppers (Orthoptera: Acrididae) are herbivorous, paurometabolous insects known to use a multitude of vegetation types at all phylogenetic levels. For example, species from the subfamily Gomphocerinae (stridulating slantfaced grasshoppers) have been found in ecosystems ranging from boreal tundras to swamps (Otte 1981). Even intraspecifically there can be a wide range of ecosystem usage. *Chorthippus curtipennis* has been found ranging from tundras in Alaska to Southern California (Otte 1981), and *Dissosteira carolina,* a member of the Oedipodinae subfamily (band-winged grasshoppers), are recorded in every continental US state (Capinera et al. 2004). However, other acridids are more specific, making choices based on three broad, potentially interacting factors: thermoregulation through choice of vegetation structure, feeding choice and behavior, and predator avoidance through substrate/color morph pairings

(Williams 1954, Dempster 1955, Mulkern 1969, Otte and Joern 1976, Gillis 1982, Stoner and Joern 2004, Gilman et al. 2008).

Structure of vegetation in a microhabitat can affect the thermoregulatory abilities of grasshoppers. In general, grasshoppers are heat-seeking: they have a high optimal temperature. In a field study by Mulkern (1969) it was found that *Melanoplus* species oriented themselves onto the sunlit sides of wooden stakes. As the sun moved and the previously sunlit sides of the stake became shaded, the grasshoppers moved from those positions to stakes that were in the sunlight (Mulkern 1969). *Trimerotropis pallidipennis* has a similar reaction at certain times of the day. Before sunrise, individuals of this species stay at ground-level, often with their abdomens pressed against the substrate. As the day progresses, individuals move into sunlit areas. They warm and begin foraging and courting at approximately 0800 hours (Gilman et al. 2008). *Trimerotropis pallidipennis* lives in very hot, dry places where temperatures can become extreme. When this happens, individuals retreat to cooler microsites. These microsites are frequently off the ground, within or even on top of the vegetation. In relation to this species, Gilman et al. (2008) describe a trend temperature gradients that were lower the further up from the ground they measured. These differences reached as high as 10.9° C at 50 cm above the ground surface. Most of the foraging exhibited by *T. pallidipennis* is on the ground, implicating the existence of a tradeoff between thermoregulation and feeding.

This trend agrees with earlier studies on nymphal grasshopper movement to and from differing microhabitats performed by Dempster (1955). It was determined that the average ground level temperatures in these study plots were significantly greater than the air temperature 9 cm above the ground. This was true of three different types of microhabitat: bare ground, short grass, and tall grass (Dempster 1955). It was also determined that the average ground temperature was significantly higher than the average air temperature in microhabitats of differing quality (i.e. green short grass and dry short grass). The nymphal grasshoppers studied

moved out of hot, dry microhabitats into those with less extreme temperatures; they moved (at the ground level) from short grass to tall grass and from dry short grass to green short grass (Dempster 1955).

In addition to having an effect on thermoregulatory behavior of grasshoppers, the vegetative structure of a microhabitat may affect certain feeding behaviors. In a laboratory study, Williams (1954) determined that individuals of the species *Chorthippus albomarginatus* ate grass oriented vertically with more frequency than grass oriented horizontally. *Gomphocerippus rufus* and *Chorthippus paralellus* adults also showed some preference for vertical lines mimicking vegetation structure over other differently oriented lines. Cards depicting lines oriented in varying ways (i.e. vertical, horizontal, angled, etc.) were placed on one side of a tank and the number of individuals that settled on any given part was counted. Most individuals of both species settled on and frequently attempted to chew, the side of the tank at the vertical lines. To Williams, this indicated a preference for vertically-oriented vegetation and led to an assumption that vegetation oriented this way elicits biting behavior, making it the preferred orientation for food resources (Williams 1954).

In a study examining how different factors at the local, landscape, and management level influenced arthropod assemblages in areas where habitat fragmentation occurred, Stoner and Joern (2004) were able to illustrate that different taxa were more influenced by specific factors. They divided the assemblages into four functional groups, represented by four different groups of taxa: Orthoptera (generalist herbivores), Curculionidae (specialist herbivores), Coccinellidae (predators), and Lepidoptera (specialist larvae/generalist adults). Each of these taxa theoretically represented all other taxa that fit into these functional groups but were not used in this study.

The only factors that were predicted to have an influence on Orthoptera directly were plant community composition and plant biomass (translated to "food availability"). These two

factors were hypothesized to be directly influenced by land management and the geography of the surrounding area (i.e. area, size, and shape of neighboring fragments) which, in turn, would indirectly influence Orthoptera. This prediction turned out to be mostly true. Strong influences due to changes in the plant community composition on Orthoptera were observed. Land management was found to have a stronger direct influence on plant community composition than the local geography. Habitat fragmentation may have less influence on generalist feeders than predicted because, by definition, a generalist may use multiple food resources. While adequate amounts of edible resources are required for generalists to survive (as represented by plant community composition and plant biomass in this study), the factors that affect the growth of specific edible resources are less important. The plant community needs to be made up of edible resources, but that criterion is met very easily for a generalist herbivore (Stoner & Joern 2004).

It is commonly understood that grasshoppers engage in "general herbivory". They can and will eat most of the plants they encounter. But exploration of this term and how it relates to grasshoppers reveals a more complex relationship between these insects and their food. There are actually three distinct types of feeding that grasshoppers can display: monophagy, oligophagy, and polyphagy (Chapman 1990). For grasshoppers, monophagy is defined as eating from only one plant genus. There are several documented monophagous species of grasshopper but only one confirmed true monophage. Crop contents of the species *Bootettix argentatus* were analyzed and it was determined that the only plants present were from the *Larrea* genus (creosote brush). The grasshoppers are such good mimics of *Larrea* species that they live only in habitats comprised of these plants (Otte & Joern 1976). To forage for other food sources and leave the safety of the creosote greatly increases the risk of predation; it would be unlikely that they would survive foraging for additional resources. This is likely what limits their food source to the *Larrea* genus exclusively. Several grasshopper species are oligophagous: they only eat a small number of different plants from one family (Chapman 1990). *Hesperotettix viridis*, for example,

only eats members of the family Asteraceae (Grace et al. 2010). Most of the plants this species eats are snakeweeds, hence the common name "snakeweed grasshopper" (Capinera et al. 2004). Similarly, there are grasshopper species that eat a small number of plant species from different families. Certain populations of one species may be monophagous or oligophagous, but because of the differences in plant families from which each population feeds, the feeding behavior of that species is described as "disjunct oligophagy" (Chapman 1990). Polyphagous grasshopper species exhibit the kind of feeding behavior that most closely resembles general herbivory. These species can eat multiple types of plants from multiple families. Most polyphagous species eat both grasses and forbs, though few species that are primarily grass-eaters are polyphagous (Chapman 1990).

Members of the subfamily Gomphocerinae eat grass primarily (Otte 1981). Members of the subfamily Melanoplinae (the spurthroated grasshoppers), specifically members of the *Meanoplus* genus, eat forbs primarily. Oedipodinae species eat a mixture of both primarily (Joern and Lawlor 1980). Joern (1979) recorded the feeding patterns of several grasshopper species in six sites and determined "dietary niche breadths" for each. These data show that while some species have wide niche breadths, indicating a broad diet, even more species have narrow niche breadths, indicating specialized diets. Most Gomphocerinae had small niche breadths. Because they are primarily grass eaters and grass has predictable growth, having a broader diet (a larger niche breadth) is unnecessary. Having diets comprised mostly of forbs suggests that the Melanoplinae should have a smaller dietary range. If the forbs being consumed have chemical defenses, the grasshoppers that eat them should have developed specific defense mechanisms against these chemicals and their overall niche breadths should be narrow. In this study, however, Melanoplinae generally had larger niche breadths. Joern (1979) suggests, as an alternative, that the wider dietary niche breadth for these forb-eaters could be the defense

mechanism protecting them from forb toxins. If they eat small amounts of several forbs, the Melanoplinae can bypass the danger of accumulating forb toxin (Joern 1979).

Overall dietary flexibility becomes important when interspecific competition for food becomes a relevant concern. When having to compete for food, some species will find once-desirable resources less so, and shift their resource utilization gradient (Joern and Lawlor 1980). In a study looking at the masses of grasshopper adults in a tallgrass prairie habitat, Evans (1992) noted a lack of interspecific competition between *Phoetaliotes nebrascensis* and *Orphulella speciosa*. These species have largely overlapping dietary needs and habitat use. Interspecific competition would have manifested itself as reduced adult masses, indicating less food intake by nymphs and adults. The growth and development of *O. speciosa* was not significantly related to the presence or absence of *P. nebrascensis* (Evans 1992). Their masses were relatively consistent in either case. A possible explanation for this lack of competition could be that one or both species shifted their resource gradient to include food that the other found less palatable or simply was not using.

Dietary differences exist at the intraspecific level too, between nymphal instars and adults and between sexes (Franzke et al. 2010). The dietary breadth of early nymphal *Chorthippus parallelus* instars was wide and narrowed with age. Then, during the fourth nymphal instar, females ate more lipid- and protein-rich legumes than males. This occurs most likely because at that life-stage females required more lipids and proteins for egg-pod production (Bernays & Simpson 1990, Franzke et al. 2010). With this broader understanding of the feeding habits of acridid grasshoppers, an assumption can be made about the relationship between the vegetation of a given area and grasshopper presence. If the grasshopper subfamilies stay true to the dietary tendencies previously noted, then the areas associated with each will most likely be comprised primarily of those plant types (i.e. grasses for Gomphoceranae, forbs for Melanoplinae, etc.) (Otte & Joern 1976, Joern and Lawlor 1980). Regardless of what predominant plant type is present, a

homogenous vegetation composition should cause lower grasshopper species diversity. Vegetative monocultures would not allow for sympatric grasshopper species to shift food resources in times of competition. Otte (1976) determined in a study that in areas with a greater number of plant species present, a greater number of grasshopper species was also present. This was not true for rocky hillsides that had a great number of different plant species, most likely due to the lack of appropriate oviposition sites available for egg-laying females. But in areas of great plant heterogeneity, feeding niche breadths for grasshopper species were at their greatest (Otte 1976). If a greater number of plant species present makes for a wider array of potential food resources and greater feeding niche breadths allows for the ability for sympatric grasshopper species to partition resources in their habitat more easily, then it would be logical that in areas with heterogeneous vegetation, greater grasshopper species diversity would occur.

In different regions, avian predators can have differing effects on grasshopper assemblages. Bock et al. (1992) observed that the densities of grasshoppers in bird exclosures were significantly greater than the densities of grasshoppers in open areas. The microclimate and insectivorous invertebrate presence were not significantly different between open and closed areas, meaning that the only factor that had an effect on the grasshopper densities was the likelihood of bird predation (Bock et al. 1992). In Montana, however, bird predation actually increased grasshopper density. The larger bodied species were more frequently eaten, decreasing their abundance and allowing for the abundance of smaller bodied species to increase (Belovsky et al. 1990, Bock et al. 1992).

A study in Florida by Squitier and Capinera (2002) showed that grasshopper nymphs were encountered more frequently in areas predominated by grass, and that these grassy areas likely allowed for more successful predation by birds. Removal of non-grass plants (forbs) from roadsides is a common practice for controlling the populations of crop-damaging grasshoppers. Roadsides with more forbs contained a greater abundance of grasshoppers overall in comparison

with roadsides containing only grass. The authors described the forb-rich roadsides as providing a greater variety of food and greater protection from avian predation, indicating that larger numbers of grasshoppers could be supported by a greater variety of food sources and cover from birds (Squitier and Capinera 2002). They did note that there was no significant difference in the grasshopper species richness between roadsides containing a greater proportion of forbs and roadsides containing a greater proportion of grass. Forb-rich roadsides had 16 grasshopper species represented while grass-rich roadsides had 15. This contradicts some findings from vegetation and grasshopper community interactions in the Qilian Mountains in China. The invasion of pestiferous plants reduced the total plant species richness and diversity, which in turn reduced grasshopper species diversity (Tao et al. 2013). However, the study reported that depending on which weed was invading, grasshopper abundance either increased or decreased, likely due to differences in nutrition and effects on oviposition space and cover from bird predators that different weeds provided (Tao et al. 2013).

In certain ecosystems, grasshopper herbivory can have a negative impact on vegetative biodiversity. In Western North Dakota, invasive crested wheatgrass limits the colonization of land by native plants (Branson and Sword 2009). In a single-year study, grasshopper feeding reduced the native forb abundance, species richness, and diversity. In a three year study, native forb abundance was significantly decreased by grasshopper herbivory. Reducing the amount of area covered and biomass of native forbs allowed for crested wheatgrass to establish itself in grassland communities (Branson and Sword 2009). If exotic invasive plants remained unpalatable to grasshoppers and could establish themselves in grassland ecosystems, it is possible that arthropod and avian populations inhabiting those areas could also be negatively impacted (Flanders et al. 2006). However, studies have shown that some grasshoppers can be conditioned to eat, or even prefer to eat, invasive plants (Lankau et al. 2004, Fielding and Conn 2011). Grasshopper herbivory had stronger negative effects on the biomass of an invasive tallow tree,

Sapium sebiferum. In laboratory preference experiments, grasshoppers ate significantly more *S. sebiferum* than other native plants (Lankau et al. 2004). Similar preference studies done with grasshoppers and the invasive narrow leaf hawksbeard (*Crepis tectorum*) showed that this invasive plant was preferred over two native grasses (Fielding and Conn 2011). Also, grasshoppers conditioned to feed on *S. sebiferum* continued to eat it when transferred into mesocosms containing native plants and the invasive tallow tree (Lankau et al. 2004). So while herbivory on native plants can be dangerous to the preservation of native plant biodiversity, the danger can be mitigated by grasshoppers feeding on, and sometimes preferring to eat, invasive plants.

It seems reasonable to assume that predation is the driving force behind several forms of cryptic morphological adaptations. This is evident in several grasshopper species throughout the world. The African grasshopper *Mesopsis laticornis* has a long, thin body that blends in with the tall grasses it inhabits (Gandar, 1982). A North American analog is *Pseudopomala brachyptera*, the short-winged toothpick grasshopper. This species, too, mimics the tall, light-colored grasses it occupies (Capinera et al. 2004). Two other African grasshoppers, *Acrotylus diana* and *Chrotogonus hemipterus*, have flattened bodies and cryptic colorations that help them blend into open, sandy areas (Gandar 1982). Several North American Oedipodinae are similar in cryptic coloration and habitat choice, frequently found in sandy areas like the sides of roads (Capinera et al. 2004). Nymphs of many species are also commonly found in areas with a high percentage of vegetative cover (Gandar, 1982). *Parapodisma subastris* nymphs had a higher survival rate when utilizing areas comprised of plants with physical defenses (i.e. tougher leaves or the presence of trichomes) as opposed to utilizing areas with plants that use chemical defenses. The physical characteristics that prevent predators from interacting with the nymphs do not prevent the nymphs from eating the plant, as they have appropriate mouthparts for chewing the tough leaves (Miura & Ohsaki 2004).

Circotettix rabula rabula individuals in Colorado exist in two color morphs that match the predominant substrate colors of that region: red and gray-green (Gillis 1982). When substrate preferences were tested experimentally, individuals continued to position themselves on substrate that matched their body color. The data collected strongly support the hypothesis that this choice is active. Red individuals with gray-green rings painted around their eyes chose to position themselves on the gray-green substrate. Red individuals with a novel blue color painted around their eyes chose to position themselves on a matching blue substrate. It is thought that the individual is able to judge the color of the parts of its body it can see and choose a substrate that matches. This hypothesis is further supported by data showing grasshoppers that are visually impaired (with black paint applied to their compound eyes and ocelli) made no consistent choice in substrate color (Gillis, 1982).

Red individuals painted with gray-green masks showed strong preference for the gray-green substrate. However, gray-green individuals with red masks did not show a significant preference for either red or gray-green substrates. It is postulated that red individuals are under more pressure from predators because their color can only be matched by the red granite, whereas gray-green individuals may have more substrate choices on which they can position themselves and become inconspicuous in the wild, thus indicating why gray-green individuals may not select substrate that matches their coloration exactly (Gillis 1982).

In studies testing the substrate preference of different color morphs of *Tetrix undulata*, Ahnesjö and Forsman (2006) determined that differently colored individuals would move to a specific substrate consistently when faced with potential interaction with a predator. Experimentally, black individuals and striped individuals did not vary significantly in substrate preference when no predatory threat was perceived. When a predator was simulated (via disturbing the cover of the cage), each morph consistently chose one kind of substrate over the other with statistical significance. The black individuals chose a substrate comprised mostly of

dark, burned spruce needles and the striped individuals chose a striped substrate containing yellow spruce needles (Ahnesjö and Forsman 2006).

Substrate and color morph pairings go beyond serving as predator avoidance strategies. They also play an important role in thermoregulation. Individuals of *T. undulata* have specific body temperatures that are often reflective of their color morphs. Without the potential for an interaction with a predator, individuals utilized habitats with different substrates (Ahnesjö and Forsman 2006). The grasshoppers with a darker color tend to warm up faster than those with a lighter color and frequently chose to position themselves on moss, a cooler, moist substrate. Males of *T. undulata* are smaller than females and as such are more easily susceptible to desiccation. They consistently chose substrates that would help maintain the appropriate body temperature as the day progressed, preferring cooler substrates in the hotter parts of the day (Ahnesjö and Forsman 2006).

Because grasshopper biology is complex, research that treats these insects beyond the ordinal level must be conducted. Developing the appropriate sampling protocol requires review of literature focused on general arthropod sampling as well as that which focuses specifically on grasshopper sampling.

Sampling Methods

Methods for sampling arthropods differ greatly depending on the taxonomic grouping desired. The methods used for sampling foliage-dwelling arthropods differ from methods used for sampling those that are ground-dwelling, have the ability to fly, etc. (Onsager and Henry 1977, Southwood 1978, Banaszak 1980). Different methods can give estimates of varying metrics like density, richness, or abundance, so often times there are multiple methods for sampling arthropods within the same order or family. To gain a broader understanding of the

diversity of a particular group of arthropods, multiple sampling methods are often employed simultaneously (Onsager 1977, Onsager 2000, Moir et al. 2005, Stephen and Rao 2007, Westphal et al. 2008).

A common method used for estimating populations of ground-dwelling arthropods is the pitfall trap sampling method. This method is used frequently to capture ground beetles (Coleoptera: Carabidae) and spiders (Araneae), among others (Greenslade 1964, Southwood 1978, Varchola and Dunn 1999, Tyler 2008, Blubaugh et al. 2011, Gardiner et al. 2013). Though designs vary based on available materials, desired arthropod, or other aspects of the study, pitfall traps usually consist of a collecting device (typically a cup) buried in the ground so that the lip of the collecting device is flush with the surrounding substrate. Often times there are funnels placed into the cup to facilitate the capture of arthropods. The collecting device frequently contains a killing solution (ethanol, ethylene glycol, etc.) (Southwood 1978, Varchola and Dunn 1999), though baiting the collecting device with some desirable resource is also done (Walker Jr. and Hoback 2007). Depending on what material is placed in the collecting device, bias toward sampling certain taxa over others may be introduced and would need to be considered when processing pitfall trap samples (Southwood 1978). When employing this method of sampling, an estimate of arthropod activity density is obtained: the number of actively moving arthropods in a given area (Southwood 1978, Gardiner et al. 2013). Effective pitfall trapping depends on the activity of the ground-dwelling arthropod as well as its population size. In addition, the size of the collecting device (trap aperture) may influence the observed arthropods, with small apertures having a bias toward small ground-dwelling arthropods and large apertures having a bias for large ground-dwelling arthropods (Southwood 1978). There are several aspects that must be considered when designing an experiment using pitfall traps, but the flexibility and modifiability of pitfall traps make them a useful tool in arthropod sampling.

Bee sampling provides a good model for looking at multiple methods being available to estimate density, abundance, and diversity. An early study by Banaszak (1980) looked at comparing three sampling methods for bee abundance and diversity: 1) glance survey method, where five quadrats measuring 1 m^2 were sampled at random twenty times within a two-hour timespan; 2) quick trap method, where a battery-operated sucking apparatus suspended 2 m in height and then lowered by a crane into vegetation and onto randomly chosen surfaces; 3) belts, where numbers of bees were counted as an observer walked along a 200 m long, 1 m wide swath of land at a speed of 10 m per minute. It was determined that the quadrats in the glance survey method accounted for almost twice as many bees as collected in the quick trap method (Banaszak 1980). The belt method was determined to be the best of all three because not only did it allow for reliable, consistent information on bee abundance, but it allowed for actual numbers of pollinating insects to be sampled by one person in 15 minutes, a relatively short amount of time compared to other sampling methods (Banaszak 1980).

More recent comparative sampling studies of bee populations have been performed with vane traps, sweep nets, and vacuums. Stephen and Rao (2007) set up blue and yellow cross vane traps in sunflower fields to determine if either was better at sampling for native bees. They set up posts with one blue and one yellow cross vane trap on each at the midpoints of the north, east, south, and west perimeters of each of the sunflower fields sampled. Cross vane traps are containers that open at the top and fitted with different colored funnels. Arising from the funnels are two plastic walls that bisect the opening twice, separating it into quarters. Bees fly into these walls and drop into the collecting device. It was determined that blue vane traps collected significantly more ($p < 0.0001$) individuals and captured a greater diversity of bee species than yellow vane traps, with five times as many individuals and twice as many species observed in the blue traps than the yellow traps (Stephen and Rao 2007). Blue traps also collected every species yellow traps collected with the exception of one: *Hyaleus calvus*. The positions of the traps in the

field showed significant differences in numbers of individuals and species observed: eastern traps had significantly more bees and bee species than other traps, though the reasoning behind this was unclear (Stephen and Rao 2007).

Quantitative differences between sweet net sampling and vacuum sampling were also determined. Sweep nets and vacuum sampling were similar in the number of bees and bee species observed, though both were significantly different from blue vane traps. Three times as many bees were observed in blue vane traps than in sweep nets or vacuums ($p = 0.011$) and more species were collected in the blue vane traps ($p = 0.001$) (Stephen and Rao 2007). Sweep nets and vacuum sampling did collect more *Apis mellifera* than the blue vane traps, indicating that they may be more biased toward collecting some species than others, though the reasoning behind this observation is also unclear (Stephen and Rao 2007).

Bee sampling literature also provides insight into the need for using multiple methods simultaneously to capture more accurately a greater biodiversity. A large scale study looking at bee diversity in several European habitats was performed comparing six different sampling methods: 1) observation plots; 2) standardized transect walks, where collection and observations occurred as the observer walked in one direction; 3) variable transect walks, where active searching for bees was performed by observers; 4) pan traps, where clusters of three shallow collecting bowls (one blue, one yellow, and one white to account for the varying levels of attractiveness each color may have on different bee groups) were placed 15 m apart and raised to vegetative height; 5) trap nests with reed internodes, where a series of reeds are bundled together to simulate nesting substrate; 6) trap nests with paper tube internodes, in which a series of paper tubes are bundled together to simulate nesting substrate (Westphal et al. 2008). These sampling methods were tested in different agricultural habitats throughout Europe, including oilseed rape fields and cantaloupe fields, and seminatural habitats like calcareous grasslands.

The pan traps were determined to be the most efficient method for capturing bee species richness and had the greatest sampling coverage (Westphal et al. 2008). When looking at the complementarity of sampling methods in agricultural settings, it was determined that standardized transect walks and observation plots had 90% species overlap, indicating that it is unnecessary to perform both when trying to capture the diversity of bee species in a given habitat. Pan traps and observational plots had the greatest dissimilarity in species composition, indicating that using both methods concomitantly could yield a more complete understanding of bee diversity (Westphal et al. 2008). In seminatural habitats, trap nests collected a group of species dissimilar to other trapping methods, likely due to the fact that the traps are designed to target cavity-nesting bees. One species of cavity-nesting bee, *Osmia rufa*, made up 62% and 73% of the trap nests with reed internodes and paper tube internodes respectively but 1% in all other trapping methods (Westphal et al. 2008). This study shows how complementarity of multiple sampling methods may give a broader, more complete understanding and estimation of bee communities than using just one method. Although this study only focused on bee sampling, it exemplifies why testing multiple methods of sampling is importantand serves as a good model to examine how sampling for other arthropod taxa should occur.

Capturing the biodiversity of Hemiptera, for example, is benefitted by sampling method complementarity. In a study by Moir et al. (2005), seven methods of sampling were compared: 1) beating, where a rod is used to literally beat a plant and dislodge Hemiptera into a collecting tray; 2) chemical knockdown, where insecticides are used to kill Hemiptera that are then collected; 3) sweeping, which involves using a net to sweep vegetation and remove Hemiptera collected with an aspirator or forceps; 4) branch clipping, where branches are removed from plants and all of the Hemiptera are collected; 5) collection by hand; 6) collection by vacuum sampling; 7) collection by sticky cards (Moir et al. 2005). Each method was assessed for efficiency at different sites in

Western Australia and at an individual plant level. Complementarity of the sampling methods was assessed by using species accumulation curves and ordinations.

The species accumulation curves for the techniques combined were steeper than those generated for individual methods, meaning that the combined methods caught more richness in a shorter amount of time. The species compositions observed using individual methods differed from the species compositions observed using multiple methods (Moir et al. 2005). When the species accumulations of different combinations of sampling methods were compared, the combinations that generated the steepest curves were the most complementary and considered to be the most desirable. Using beating and vacuum sampling produced the steepest curve at the site level and chemical knockdown and beating gave the steepest curve at the individual plant level (Moir et al. 2005).

Ordinations revealed similarities between the different suites of species observed by each method. Sticky cards were significantly different from all other methods of sampling, catching greater proportions of Psyllidae and other Sternorrhyncha (Moir et al, 2005). Because the combination of beating and vacuum sampling yielded a steep species accumulation curve, it was expected that the suite of species observed by each method individually would be different. Ordinations revealed this to be the case, with beat samples consisting mostly of Heteroptera and no Auchenorrhyncha and vacuum samples consisting of almost equal parts Heteroptera and Auchenorrhyncha (Moir et al. 2005). At an individual plant level, branch clipping collected only immobile Sternorrhyncha. Vacuum sampling and chemical knockdown collected many of the same species, indicating that, for capturing species diversity, they are not likely the best methods to use simultaneously. The authors conclude that no one sampling method can be used to obtain a complete look at Hemiptera biodiversity and make suggestions regarding which methods work best together. They also note that all of these methods were used to sample foliage-dwelling Hemiptera on understory plants and missing from their samples were representative species of

Gelastocoridae and Cydnidae, ground-dwelling Hemiptera (Moir et al. 2005). When attempting to capture the diversity of an arthropod taxon that includes species that live in multiple strata of a habitat, using sampling methods that incorporate those strata is critical. This has been exhibited in studies performed on ground-dwelling and foliage-dwelling Hemiptera (Moir et al. 2005) and social and cavity-nesting bees (Westphal et al. 2008), and likely can extend into sampling for any arthropod taxa, including grasshoppers.

Sampling for grasshoppers is typically done two ways: density ring sampling, which provides estimates of grasshopper density (Onsager 1977, Onsager & Henry, 1977) and sweep net sampling, which provides estimates of grasshopper relative abundance (Berry et al. 2000, Gardiner et al. 2005). These are frequently done concomitantly in a habitat to get a more complete picture of the grasshopper assemblage.

Density ring sampling involves observing and counting grasshoppers in a small area by an observer or observers. Onsager (1977) compared five different versions of this methodology: the night cage method, in which cages that enclosed an area of 4 ft^2 were placed on the ground at night when grasshoppers were inactive and visited in the morning to count grasshoppers inside; the cage sampler, where a cylindrical cage is forced down on the ground and any grasshoppers inside are counted; the net sampler, similar to the cage sampler except a net is used instead of a cylindrical cage; visual estimates, where a small a rea on the ground is estimated, though not delineated by cage or other boundary, and grasshoppers are counted inside; the pointer method, which is identical to the visual estimate only a long pointer is implemented to disturb the vegetation and cause otherwise unseen grasshoppers to jump and be included in the counts (Onsager 1977). Each method was not without its drawbacks, but it was determined that any method that involved creating a border or delineation around an area in which grasshoppers would be counted produced the most accurate and precise estimates of grasshopper density (Onsager 1977). However, it was also found that those methods were impractical, time

consuming, or limiting with regards to the kinds of vegetation in which those methods could be used. Night cages require observers to set up cages at inconvenient hours and then returning to those cages shortly thereafter the following morning (Onsager 1977). Cage and net samplers did not account for prematurely disturbed grasshoppers escaping the desired sampling area undetected, thus rendering the density estimate inaccurate. Tall and thick vegetation may also prevent the cage or net from completely enclosing an area and allow grasshoppers to pass underneath the sampling device, remaining uncounted (Onsager 1977). These limitations led to the conclusion that the visual estimates and pointer method would be favored because they are inexpensive, quick, and can be done anywhere (Onsager 1977).

Because it was clear that providing some delineation of the area from which grasshoppers should be counted caused precision and accuracy to increase in other density sampling methods, efforts to add a tangible border to the pointer method were made (Onsager and Henry 1977). This was achieved by including wire rings 0.1 m^2 in area to the methodology. In a study attempting to refine this density estimation method, Onsager and Henry (1977) established 8 transects of 50 rings. The rings were spaced 8 m apart from each other within each transect. The transects remained intact for the duration of the study and were counted by two or three individuals at an irregular interval of 1-3 days (Onsager and Henry 1977). Comparisons were made between an "expert" observer, who had performed the pointer method of density estimates for over 10 seasons, a "trainée", who had limited training performing the pointer method, and a "novice", who had no training in sampling insects. The "expert" observed an average of 20.8 grasshoppers/m^2 and the "trainée" observed an average of 19.9 grasshoppers/m^2 (Onsager and Henry 1977). The discrepancy between the two was less than 2.5% and was considered to be a precise result. The difference between the average densities estimated by the "expert" and the "novice" were significant, but because 22 of the 26 frequency distributions generated from the comparisons were Poisson (Onsager 1977), the methods were not considered imprecise (Onsager

and Henry 1977). It was concluded that the ring method generated comparable accuracy and precision observed in other methods that involved delineating a sampling border while continuing to be a fast and inexpensive method (Onsager and Henry 1977).

Using sweep nets is a standard method of sampling used to get estimates of grasshopper relative abundance (Gardiner et al. 2005). A net is used to sweep through and over the tops of vegetation to catch any grasshoppers present. Much variation exists between the number of sweeps taken in any one study, but typically between 100 and 200 sweeps are performed (Berry et al. 2000, Branson 2005, Gardiner et al. 2005). This method is used to acquire relative abundance of grasshopper species or subfamilies by figuring out the proportion of each taxonomic grouping from the total catch. These data may be used to calculate species or subfamily density by multiplying total grasshopper density (Onsager and Henry 1977) and the relative abundance (Onsager 2000, Branson 2005). For example, a relative abundance of species A of 50% in a location with an overall grasshopper density of 10 grasshoppers per m^2 would mean that the density of species A is 5 grasshoppers per m^2. The sweep net method contains a large amount of variation in terms of how it is employed and how data may be used, but its plasticity, simplicity, and low cost are what make it one of the most commonly used methods in research (Gardiner et al. 2005).

Southwood (1978) points out that estimates of relative abundance are difficult to interpret. There are several factors that influence the estimates including changes in the true population size, the susceptibility of the "phase" the individuals within the population are in to be caught, climate, the effectiveness of the method at finding the taxon desired, and the bias inherent in different observers performing the same method of sampling (Southwood 1978, Gardiner et al. 2005). Because of these challenges, relative estimates can be somewhat limited in what they uncover about a biological system. They can be useful in indicating the availability of a taxon given the climatic and phenological parameters when sampled or be used to calculate

estimates of total populations, but cannot be used to make statements about the total population (Southwood 1978). When performing a sweep net sampling regime, it is important to standardize as many parameters as possible in an attempt to reduce bias, but it is also important to note that bias cannot be completely eliminated and should be taken into account whenever data from such an experiment are analyzed.

CHAPTER II

SAMPLING METHODOLOGY COMPARISON

Introduction

Grasshoppers are an important part of the grassland ecosystem. They are integral in nutrient cycling, returning a larger percentage of nutrients to the system than cattle in some regions (Gandar 1982). They can be considered "wasteful eaters", often dropping uneaten fragments of plants to the ground. This, coupled with introducing nitrogen into the system through frass production, aids in returning nutrients to the soil and enhancing organic matter content. They are also important prey items for small mammals, birds, and other arthropods (Capinera et al. 2004). They provide essential nutrients in the form of protein to Northern Bobwhite and other birds during egg-laying and to their chicks during brooding (Woodard et al. 1977, Brennan and Hurst 1995, Doxon and Carroll 2010). Many grasshopper species are pests as well, contributing to crop loss in many regions (Capinera and Sechrist 1982, Capinera et al. 2004, Badenhausser et al. 2007). For these reasons, grasshopper sampling methodology has been studied extensively. Through these studies, sampling methodology has been refined down to two standard methods: density ring estimates and sweep net sampling (Onsager 1977, Onsager and Henry 1977, Gardiner et al. 2005).

Density ring sampling involves enumerating the grasshoppers detected within an aluminum ring 0.1 m^2 in area by an observer or observers. Onsager (1977) compared five different versions of this methodology: the night cage method, the cage sampler, the net sampler,

visual estimates, and the pointer method. Each method was not without their drawbacks, but it was determined that any method that involved creating a border or delineation around an area where grasshoppers could be counted (like the night cage, cage sampler, and net sampler methods) produced the most accurate and precise estimates of grasshopper density. However, it was also found that those methods were impractical, time consuming, or limiting with regards to the kinds of vegetation where those methods could be used (Onsager 1977). These limitations led to the conclusion that the visual estimates and pointer method would be favored because they are inexpensive, quick, and can be done anywhere (Onsager 1977). Efforts to add a tangible border to the pointer method were achieved by the addition of aluminum rings. By laying out aluminum rings 0.1 m^2 in area in a transect or other preferred arrangement, the portion of ground in which grasshoppers were to be counted was easier to see, increasing the precision and accuracy of the visual and pointer methods while maintaining their high speed and low cost (Onsager and Henry 1977). It has emerged as the standard method, being used frequently in contemporary studies that involve grasshopper density (Belovsky and Slade 2000, Joern 2004, Branson 2005, Joern 2005, de Wysiecki et al. 2011).

Sweep net sampling is the standard method used to acquire estimates of grasshopper relative abundance (Gardiner et al. 2005). A net is swept through and over the tops of vegetation to catch any grasshoppers present. There is much variation between the number of sweeps taken in any one study, but typically between 100 and 200 sweeps are performed (Berry et al. 2000, Branson 2005, Gardiner et al. 2005). This method is used to acquire relative abundance of grasshopper species, genera, or subfamilies by figuring out the proportion of each taxonomic grouping from the total catch. These data may be used to calculate species or subfamily density by multiplying total grasshopper density (Onsager and Henry 1977) and the relative abundance (Onsager 2000, Branson 2005). For example, a relative abundance of species A of 50% in a location with an overall grasshopper density of 10 grasshoppers per m^2 would mean that the

density of species A is 5 grasshoppers per m^2. The sweep net method contains a large amount of variation in terms of how it is employed and how the data may be used, but its plasticity, simplicity, and low cost are what make it one of the most commonly used methods in research (Gardiner et al. 2005).

Southwood (1978) points out that estimates of relative abundance are difficult to interpret. There are several factors that influence the estimates including changes in the true population size, the susceptibility of the "phase" the individuals of the population are in to be caught, climate, the effectiveness of the method at finding the taxon desired, and the bias inherent in different observers performing the same method of sampling (Southwood 1978, Gardiner et al. 2005). Because of these challenges, relative estimates can be somewhat limited in what they uncover about a biological system. They can be useful in indicating the availability of a taxon given the climatic and phonological parameters when sampled or be used to calculate estimates of total populations, but cannot be used to make statements about the total population (Southwood 1978). Despite its limitations, it is a useful and easily obtainable parameter to assess grasshopper populations.

Our objective was to develop a novel sampling method that measures both the relative abundance of grasshopper species and the rate of grasshoppers caught per minute simultaneously. It was expected that relative abundance estimates as determined by this novel method would be comparable to the relative abundance estimates determined by the standard sweep net sampling method and that the rate of grasshoppers caught per minute would be comparable to the density of grasshoppers observed in the standard density ring count method. By combining the two standard methods into one, grasshopper sampling could become even easier and less time consuming, with implications for a standardized method to be used by people concerned with monitoring beneficial or detrimental grasshoppers.

Methods

Study site. Our research took place on the McFarland Unit of the Beaver River Wildlife Management Area in Beaver County, OK (Fig. 1). The Beaver River Wildlife Management Area covers approximately 17,700 hectares of land. It consists of four vegetation types that occur in a gradient that runs perpendicular to the Beaver River (Storer and Blanca 2011). The first and closest to the river is a riparian zone consisting mostly of salt cedar (*Tamarix* spp.). The second vegetation type is a mixed grass lowland. The vegetation type furthest from the river is a sandy upland consisting mostly of sagebrush (*Artemisia* species) and sand plum (*Prunus angustifolia*). The last vegetation type occurs between the lowland and upland and is a transitional zone between the two (called an ecotone) (Storer and Blanca 2011). Each vegetation type has differing proportions of vegetative cover and bare ground that could potentially influence grasshopper population dynamics. Six transects were established that ran perpendicular to the Beaver River and passed through all four vegetation types. A central point (centroid) was established in each vegetation type for each transect. These centroids were marked with 4-foot-long pieces of reinforcing bar encased in five-foot-long polyvinyl chloride pipe. Using the centroids as a starting point, a compass was then used to randomly acquire an azimuth where each individual sampling effort could be inititated. The study design was a split plot with repeated measures.

Grasshopper sampling. The standard method for sampling the relative abundance of each grasshopper species used was sweep net sampling (Gardiner et al. 2005). The southwest corner of one 10 m X 10 m sweep net sampling arena was established twenty meters from the centroid in each vegetation type. Two additional 10 m X 10 m arenas were established at least 15 m apart. These arenas remained undisturbed for at least 30 minutes before being sampled. When enough time passed, fifty sweeps were made within each arena. In 2012, the corners of these arenas were marked with wooden stakes. In 2013, the corners of the arenas were not marked with

stakes to reduce the amount of time sampling would take and decrease the impact of the sampler on grasshoppers being sampled. Each arena was sampled by walking in an "X" pattern across the area, as vegetation and terrain would allow. One sweep is equivalent to moving a net no less than 90° in front of the sampler's body on and over the tops of vegetation and is performed concomitantly with one step. The net had a diameter of 38.5 cm. The sweep net was emptied into a plastic storage bag, frozen, and returned to the lab for later sorting and identification. Adults were identified to species and nymphs were identified to subfamily and instar (Otte 1981, Pfadt 1994, Capinera et al. 2004).

The standard approach for sampling total grasshopper densities was the density ring method (Onsager 1977, Onsager and Henry 1977). Ten aluminum rings with an area of 0.1 m^2 each were placed 10 m apart along a transect within each vegetation zone that was at least 20 m from all other sampling efforts occurring at that time. These rings remained undisturbed for at least 30 minutes. When enough time had passed, the sampler approached the first ring slowly, being sure they could clearly see if they caused any grasshoppers to jump in or out of the ring. Grasshoppers seen jumping into the ring were not counted. Grasshoppers seen leaving the ring upon the sampler's approach were counted. The sampler counted the number of grasshoppers seen in or on the ring. The ring was disturbed using a meter stick and any previously unseen grasshoppers that jumped out or otherwise detected were also counted. This process was repeated for each ring in the transect and for each centroid in the study site. The rings were collected by the sampler upon completion of the observation and counting. The total number of grasshoppers in each 0.1 m^2 ring is equal to the density of grasshoppers per m^2 (Onsager 1977, Onsager and Henry 1977)

Simultaneous to these sampling efforts, a novel method of grasshopper sampling was evaluated. The novel method of sampling grasshoppers was deemed the "By Any Means Necessary" method (BAMN). Within each vegetation zone but not interfering with density ring

sampling and sweep net arenas, a sampler timed themselves to see how long it took to collect twenty grasshoppers. Wearing two timers, the collector entered the field acquiring grasshoppers opportunistically, either by hand or with an aerial net. One timer was started at the beginning of the sampling effort and recorded total time taken to collect twenty grasshoppers. The second timer was started when the sampler caught grasshoppers in their hands or net and transferred them into a 50 mL vial containing 80% ethanol. The timer was stopped when the grasshoppers were transferred or if they escaped from the sampler. This timer was used to collect "handling time," the total time spent handling the grasshoppers by the sampler. Any grasshoppers that escaped from the sampler were recorded as "escapes". Sampling ended when 20 grasshoppers were successfully collected or when 20 minutes had elapsed. In 2013, the total time, the handling time, and the number of escapes were recorded when the collector caught 10 grasshoppers successfully as well as when they caught 20. The vials were returned to the lab and relative abundance of adult grasshopper species and nymphal grasshopper subfamilies was determined by identifying individual grasshoppers morphologically. The rate of grasshoppers caught per minute was determined by dividing the total number of grasshoppers caught by the total amount of time in minutes taken to collect them.

During summer 2012 and 2013, relative abundance estimates, overall grasshopper density, and BAMN sampling efforts were performed at each centroid five times (May 19 – May 22, June 12 – June 16, June 28 – July 7, July 19 – July 26, August 7 – August 15) and seven times (May 11 – May 16, May 25 – May 30, June 8 – June 13, June 22 – June 27, July 6 – July 11, July 21 – July 28, August 3 – August 7) respectively. Each range of dates is referred to as a "sampling event." Sampling occurred between 1000 hrs and 1600 hrs or when temperatures were $\geq$ 25° C in an attempt to standardize conditions when grasshoppers were sampled (Southwood 1978, Gardiner et al. 2005).

Statistical analysis. Comparisons of relative abundance between sweep net sampling and BAMN sampling were analyzed using analysis of variance with repeated measures. An autoregressive period 1 covariance structure was used to model the intratransect variation across time (SAS version 9.3, SAS Institute, Cary, NC, 2001). This analysis was also performed for comparisons between densities of grasshoppers observed and rates of grasshoppers caught per minute using the BAMN method. Correlations between densities of grasshoppers and rates of grasshoppers caught per minute were determined by calculating Pearson correlation coefficients using Microsoft Excel (Microsoft 2010).

Sørenson's coefficient of similarity (C_S) was calculated to determine the similarity of species richness observed between sweep net sampling and BAMN sampling. It is calculated using the formula:

$$C_S = 2j/(a+b)$$

where j was the number of common species observed in both sampling methods, a was the number of species observed in sweep net sampling, and b was the number of species observed in BAMN. This formula will produce a value between 0 and 1 which represents a percentage of similarity between the two sampling methods. A modified Sørenson's coefficient of similarity (C_N) was also calculated to determine the similarity of abundance observed between sweep net sampling and BAMN sampling. The same formula was used, only j represented the total abundance of common species observed in both sampling methods, a was the total abundance of species observed in sweep net sampling, and b was the total abundance of species observed in BAMN.

The Berger-Parker dominance index (d) was calculated to determine how dominant the most abundant species observed was in a sample. It is calculated using the following formula:

$$d = N_{max}/N_T$$

N_{max} is the number of individuals of the most abundant species present and N_T is the total number of individuals for every species. The formula gives a value between 0 and 1 and can be expressed as a percentage. Values approaching 1 signify the level of domination by the most abundant species.

Results

In the summers of 2012 and 2013, grasshoppers from the following four subfamilies were collected: Cyrtacanthacridinae, Gomphocerinae, Melanoplinae, and Oedipodinae. One species of Cyrtacanthacridinae was collected (*Schistocerca lineata*), nineteen species of Gomphocerinae were collected, sixteen species of Melanoplinae were collected, and twelve species of Oedipodinae were collected (Table 1). Of the nineteen Gomphocerinae species collected, two were caught exclusively by the sweep net method (*Mermiria picta* and *Psoloessa deliculata*) and two were caught exclusively by the BAMN method (*Aulocora elliotti* and *Pseudopomala brachyptera*). Of the sixteen Melanoplinae species collected, three were caught exclusively by the sweep net method (*Melanoplus bivittatus, M. femurrubrum,* and *M. sanguinipes*) and one was caught exclusively by the BAMN method (*Melanoplus packerdii*). Of the twelve Oedipodinae species collected, six were caught exclusively by the BAMN method (*Arphia simplex*, *Circotettix rabula*, *Chortophaga viridifasciata*, *Hippopedon capito*, *Psinidia fenestralis*, and *Spharagemon bolli*).

Relative abundance estimates from sweep net sampling and BAMN sampling of four grasshopper taxa were compared: Gomphocerinae nymphs, Melanoplinae nymphs, *Paropomala wyomingensis* adults, and *Melanoplus bowditchi* adults (Figs. 2 - 5). Comparisons between relative abundances from the first three sampling events of 2012 were performed. During the initial sampling event, for Gomphocerinae nymphs, one significant difference between relative abundances ($p < 0.05$) was observed in the ecotone vegetation type. Three similar relative

abundance comparisons ($p > 0.85$) were observed, one during the first sampling event in the lowland vegetation type and two during the third sampling event in the ecotone and upland vegetation types (Fig. 2). For Melanoplinae nymphs, two significant differences between relative abundances were observed, one during the first sampling event in the ecotone vegetation type and one during the second sampling event in the riparian vegetation type (Fig. 3). One similar relative abundance comparison was observed during the third sampling event in the upland vegetation type (Fig. 3). For *Paropomala wyomingensis* adults, there were no significantly different comparisons in relative abundance between sampling methods. Two similar relative abundance comparisons were observed, one during the second sampling event in the upland vegetation type and one during the third sampling event in the ecotone vegetation type (Fig. 4). For *Melanoplus bowditchi* adults, two significant differences in relative abundance were observed during the second sampling event in the ecotone and upland vegetation types (Fig. 5). Two similar relative abundance comparisons were also observed, one during the second sampling event in the lowland vegetation type and one during the third sampling event in the lowland vegetation type (Fig. 5). During the first sampling event, for both *P. wyomingensis* and *M. bowditchi*, there were no adults present and only adults were identified to species.

Differences between mean rates of grasshoppers caught per minute during each of the 2012 sampling events in each of the vegetation types (Fig. 6) resulted in a variable pattern of significance compared to mean grasshopper densities observed during those same sampling events (Fig. 7). During all sampling events, the ecotone had the highest rate of grasshoppers caught per minute (Fig. 8). The only significant differences observed were during the third and fourth sampling events ($p < 0.05$). During the third sampling event, the rate of capture observed in the ecotone was significantly greater than the rate observed in the riparian vegetation type, though neither was different from the lowland or upland vegetation types (Fig. 8). During the fourth sampling event the rate of capture observed in the ecotone was significantly greater than in

all other locations (Fig. 8). The rate observed in the upland was significantly greater than the rate observed in the riparian vegetation type, though neither rates of capture observed in the upland or riparian vegetation types were significantly different from the rate observed in the lowland. During all five sampling events, densities observed from the density rings in the ecotone and upland vegetation types were not significantly different from each other, but significantly greater ($p < 0.05$) than the densities observed in the riparian and lowland vegetation types (Fig. 9). Significant positive correlations were observed between densities of grasshoppers observed in the density rings and rates of grasshoppers caught per minute in 2012 ($r = 0.3775$, $t = 4.428$, $p < 0.0001$) and 2013 ($r = 0.5649$, $t = 8.793$, $p < 0.0001$) (Fig. 9).

Coefficients of similarity between sweep net and BAMN sampling are reported in table 2. The lowest Sørenson's coefficient of similarity (C_S) calculated was from 2013 in the upland vegetation type ($C_S = 0.581$). The lowest modified Sørenson's coefficient of similarity (C_N) was from 2012 in the riparian vegetation type ($C_N = 0.566$), with the BAMN sampling method catching a greater number of grasshoppers than the sweep net method. The highest C_S calculated was from 2013 in the riparian vegetation type ($C_S = 0.809$). In both instances, the BAMN sampling method captured greater species richness than the sweep net sampling method. The highest C_N obtained was from 2012 in the upland vegetation type ($C_N = 0.905$), with the sweep net method catching a greater number of grasshoppers than the BAMN sampling method.

The Berger-Parker dominance index (d) was calculated for both sampling methods using data from 2012, 2013, and a combined 2012 and 2013 dataset (Table 3). In 2012, *Melanoplus bowditchi* was the most dominant species of grasshopper in both sampling methods (sweep nets: $d = 0.331$, BAMN: $d = 0.212$). In 2013, *Ageneotettix deorum* was the most abundant species of grasshopper in both sampling methods (sweep nets: $d = 0.180$, BAMN: $d = 0.145$). *Melanoplus bowditchi* was the most dominant species in the combined dataset (sweep nets: $d = 0.221$, BAMN: $d = 0.164$).

Discussion

Based on the research performed, BAMN sampling should not be used to replace sweep net sampling or density ring observations. Relative abundance estimates and rates of grasshoppers caught were too dissimilar from relative abundance observed in sweep net sampling and densities observed in density rings. Having standard sampling methods aids in streamlining collection efforts by researchers and if done by multiple researchers in different locations can help garner comparable information between regions, furthering the body of knowledge of the taxa in question. However, using one standard method may inadvertently limit the scope of information collected and underestimate species richness and biodiversity of target taxa in a given area. When comparing the diversity of species caught using the sweep net method with those caught using the BAMN method, it was revealed that the BAMN method caught a greater number of unique species (Table 1). Nine species of grasshopper were only caught by the BAMN method, six of which belonged to the Oedipodinae subfamily. This may be due to the nature of the sampling method and the biology of those grasshopper species. In general, Oedipodinae are stronger flyers and tend to fly greater distances when threatened than other grasshopper subfamilies. Because of this, active searching and "hunting" (the nature of the BAMN method) may be a more effective method of catching them as opposed to non-directed, passively-directed sampling (sweep net sampling). This has been demonstrated with other insect taxa where multiple methods of sampling are used. Studies with bees show different methods catch different numbers and species of bees, depending on the biology of the bee species (Stephen and Rao 2007). Despite the benefits of standardizing grasshopper sampling methods, it is apparent that employing multiple methods gives a more complete picture of biodiversity and species richness within a particular area.

The Berger-Parker dominance index calculations revealed that sweep net samples were more often dominated by the most abundant grasshopper taxon than BAMN samples, but there

was no difference between sampling types. For the 2012 data and the combined 2012 and 2013 data, *Melanoplus bowditchi* was the dominant grasshopper species. In 2013, *Ageneotettix deorum* was the dominant species. *Melanoplus bowditchi* is in the subfamily Melanoplinae and *Ageneotettix deorum* is in the subfamily Gomphocerinae; their dominance in different years is likely due to climate that created more optimal conditions for one subfamily over the other.

Gomphocerinae and Melanoplinae differ in several ways. They have different dietary preferences (Joern 1979, Behmer and Joern 2008), different optimal oviposition conditions (Russell and Detling 2003, Branson 2005), and some species are cryptically different. Studies analyzing the crop contents of several grasshoppers of multiple species have shown that Gomphocerinae tend to specialize on grasses while Melanoplinae tend to be generalists, eating a mix of grasses and forbs (Joern 1979, Behmer and Joern 2008). Gomphocerinae also generally prefer to lay their egg pods at a shallower depth in harder, more compact soil than Melanoplinae. Melanoplinae prefer to lay their egg pods deeper in loose, sandy soil. Differences in thermoregulatory requirements are likely the driving force behind this behavioral difference (Russell and Detling 2003, Branson 2005). There are some species of Gomphocerinae that cryptically resemble grass, so climatic conditions or land management that provide more grass might yield a greater abundance of those grasshoppers. It's not possible to say which of these differences is being exploited by the grasshoppers between years, but it is likely that one or a combination of several are responsible for the observed changes in dominant species.

The coefficients of similarity revealed that the BAMN method of sampling caught a greater abundance of grasshoppers and a greater number of species than sweep net sampling in all vegetation types with the exception of the ecotone. It is unclear why this is the case, but it is important to note that certain sampling methods may be better suited at capturing grasshoppers in certain vegetation types over others. In this instance, the BAMN method captured a greater richness of grasshoppers in three of the four vegetation types. Just because it captured a greater

number of grasshopper individuals, however, does not make it better than the sweep net method at determining relative abundance. It is important to note that the abundance of grasshoppers caught using BAMN was limited by design, allowing a maximum of twenty grasshoppers caught per site. The C_N value is really only a measurement of how close the sweep net abundance was to twenty individuals. To assess the quality of the relative abundance estimates made by the BAMN method, comparisons between those and the relative abundance as estimated by the sweep net method were made.

Sweep net sampling is considered the standard method by which grasshopper relative abundance is measured (Gardiner et al. 2005). To determine if the novel BAMN method made comparable relative abundance estimates, comparisons to those determined by the sweep net method were made. Forty-eight different grasshopper species were collected, so comparisons between the relative abundance estimates of only the four most abundant grasshopper taxa were made: Gomphocerinae nymphs, Melanoplinae nymphs, *Paropomala wyomingensis* adults, and *Melanoplus bowditchi* adults (Fig. 2, 3, 4, 5). With each taxon there are "comparisons of interest" (comparisons with p-values over 0.85), which indicate seasonal and locational points where both sampling methods captured a similar relative abundance. Significant differences ($p < 0.05$) were also noted. Of the four taxa, only *Paropomala wyomingensis* adults had no significant differences in their comparisons. This may be due to the fact that there was a greater amount of variation within single sampling methods, greatly reducing the likelihood of statistically significant differences.

Seven of the eight "comparisons of interest" were found between relative abundance estimates that were less than 5% of the total catch. This is likely just an artifact of the low relative abundance estimate. Between the relative abundance comparisons that yielded a $p > 0.85$ and a $p < 0.05$, there was no pattern or consistent relationship that could be identified. Because of

these data, it is likely that the BAMN method does not accurately estimate and may not be the best method to determine grasshopper relative abundance.

When comparing the rates of grasshoppers caught with the densities observed in the density rings, it was expected that a relationship between the two different metrics would be uncovered. This was not the case. The densities increased as sampling occurred away from the riparian vegetation type with significant differences only occurring between the two vegetation types closest to the Beaver River (riparian and lowland) and the two furthest from the Beaver river (ecotone and upland) (Fig. 7). The maximum rates of grasshoppers caught occurred in the ecotone vegetation type, then slowed in the adjacent lowland and upland, and slowed even more in the riparian vegetation type. Within the various vegetation types, only rates measured during the third and fourth sampling events were significantly different ($p < 0.05$, Fig. 6). While correlations between rate of capture and overall density were significantly positive in both 2012 and 2013 (Fig. 8, 9) and support the expectation that such a correlation existed, the data do not indicate that rate of grasshoppers caught can be directly converted into density of grasshoppers per m^2. The strongest reason for this is that the grasshoppers caught using BAMN may not have been observed and counted using density ring sampling. Though many of the grasshoppers caught using the BAMN method were actively sought out, meaning they were observed and chased until captured, there could have been some grasshoppers caught accidentally as well, likely as collateral from grasshoppers being pursued in tall or thick vegetation. If the collector pursued a grasshopper in the lowland vegetation type, for example, and their net passed through a stand of grass, it is likely that they caught not only the grasshopper they were attempting to catch, but also other grasshoppers. This differs from the density ring method because even though the area within the previously laid out rings was disturbed with a probe in an attempt to scare up any previously unseen grasshoppers, if the grasshopper did not move or make itself apparent in any way, it went undetected. If the areas of the density rings were enclosed and grasshoppers within

were enumerated, similar numbers between rate and density might have been measured, but because the nature of the two sampling methods pursue grasshoppers differently, a more precise relationship than the one demonstrated may not exist.

Additionally, there may be some component of the vegetation types that was not measured that made them more ideal for grasshoppers to be caught by the BAMN method or observed in the density rings. The rates of grasshoppers caught in the lowland and upland vegetation types were not significantly different but the densities of grasshoppers observed in the lowland and upland were, so whatever factors drive the rate of capture did not have the same effect on density.

This comparative study has revealed that the standard methods for grasshopper sampling and the novel BAMN method are slightly comparable. Coefficients of similarity indicate no less than 61% similarity between sweep net sampling and BAMN when estimating richness and no less than 66% similarity when estimating abundance. A strong positive correlation between the overall density of grasshoppers observed in density ring counts and rate of grasshoppers caught using the BAMN method was also revealed.

Despite these similarities, several dissimilarities were also observed. The BAMN method caught a different suite of species than the sweep net method, capturing several unique Oedipodinae species the sweep net method did not. This is likely because the Oedipodinae are easier to catch when being actively hunted, as was done using the BAMN method, as opposed to being passively sampled, as with the sweep net sampling method. Relative abundance estimates measured by the standard sweep net samples were not similar to relative abundance estimates measured by the BAMN method. If sweep net sampling is accepted as the standard for estimating grasshopper relative abundance, then the novel BAMN method would have to generate similar estimates to be considered comparable. Because it did not, it can be asserted that BAMN

is not a suitable replacement for sweep net sampling as a means to estimate relative abundance. Rates of grasshoppers caught were highest in the ecotone vegetation type and not always significantly different from each other between vegetation types. In contrast, densities of grasshoppers observed were highest in both the ecotone and upland vegetation types during every sampling event. Despite being positively correlated, these dissimilar patterns of significance indicated that the rates of grasshoppers caught by the BAMN method were not analogous to the densities observed in density rings. Lastly, though the same species was identified as the dominant species within the same years between sampling methods, the Berger-Parker dominance index indicated that sweep net samples were more dominated by the most abundant species. This is likely an artifact of how both sampling methods are performed, but is telling about the nature of the results produced from each method. If the total catch from the BAMN method is less dominated by one particular species, results of relative abundance may be skewed. Because the BAMN method is novel, the results from sweep net sampling are considered to be the more accurate in their estimation of relative abundance. However, future studies could be performed to see how often such a pattern of dominance is observed and would need to be performed to determine if the BAMN method is better at accurately estimating relative abundance than the sweep net method. However, using the BAMN method in conjunction with sweep net sampling can give a broader view of the grasshopper biodiversity of a given area. Because several species of grasshopper were caught only when using BAMN sampling, it should be noted in future studies that sweep net sampling does not provide a complete catalog of all grasshopper species present.

CHAPTER III

GRASSHOPPER COMMUNITY COMPOSITION

Introduction

Since at least the 1960s, Northern Bobwhite (*Colinus virginianus*, henceforth referred to as "quail") populations have been on the decline (Brennan, 1991). In Oklahoma, these birds are popular game that brings money into the state through sales of hunting licenses and revenue generated by hunters. Their decline is attributed to the lack of suitable late successional habitat brought on by suboptimal land management (Kitts 2004, Lusk et al. 2006, Doxon & Carroll 2010). Quail build nests at the bases of tall bunch-grasses and forbs. Brood-rearing requires ground-level alleyways essential for mobility, and can be provided by weedy field borders or small grain fields. Shrubs and other small woody plants provide essential "loafing" areas: areas that are well-protected from predators and harsh weather where quail can rest when not foraging. Tracts of thick grasses and shrubs give quail places to hide when confronted by predators (National Resources Conservation Service 1999). Because of these diverse vegetative features, early successional habitats with native vegetation also provide egg-laying hens and quail chicks with crucial arthropod prey (Wenninger & Inouye 2007). Habitats overrun by invasive exotic plants will form dense sod mats and not allow for the structural heterogeneity required by these birds to nest, forage for prey, and loaf (Barnes et al. 2013).

Grasshoppers (Orthoptera: Acrididae) are a ubiquitous member of the arthropod communities upon which quail prey (Doxon and Carroll 2010). Grasshoppers have complex assemblages and are known to fit into several habitats, including grasslands, mountains, and mixed-grass prairies (Alexander & Hilliard, Jr. 1969, Otte 1981, Capinera et al. 2004). They are often considered only to the ordinal level in dietary studies (Butler et al. 2004, Doxon & Carroll 2010) but have the potential for important species-based relationships with quail that may have go unrealized. Little effort has gone into understanding the species that comprise these assemblages and how these assemblages respond to the vegetative communities and microclimates that exist within potential quail breeding habitat.

Though often considered "generalist herbivores," meaning they will eat any plant material they encounter, grasshopper feeding is actually more specific. Members of the subfamily Gomphocerinae primarily eat grass (Otte 1981). Members of the subfamily Melanoplinae (the spurthroated grasshoppers), specifically members of the Melanoplus genus, primarily eat forbs. Oedipodinae species eat a mixture of both (Joern and Lawlor 1980). Joern (1979) recorded the feeding patterns of several grasshopper species in six sites and determined "dietary niche breadths" for each. These data show that while some species have wide niche breadths, indicating a broad diet, even more species have narrow niche breadths, indicating specialized diets. Most Gomphocerinae had small niche breadths. Because they are primarily grass eaters and grass has predictable growth, having a broader diet (a larger niche breadth) is unnecessary. Having diets comprised mostly of forbs suggests that the Melanoplinae should have a smaller dietary range. If the forbs being consumed have chemical defenses, the grasshoppers that eat them should have developed specific defense mechanisms against these chemicals and their overall niche breadths should be narrow. In this study, however, Melanoplinae generally had larger niche breadths. Joern (1979) suggests, as an alternative, that the wider dietary niche breadth for these forb-eaters could be the defense mechanism protecting them from forb toxins.

If they eat small amounts of several forbs, the Melanoplinae can bypass the danger of accumulating forb toxin (Joern 1979).

Our objective was to characterize the Acrididae community in a western Oklahoma grassland that served as Northern Bobwhite habitat. We attempted to identify all of the present Acrididae species and track the emergence and decline of each subfamily. We also attempted to track the emergence and decline of the most abundant species present. We assessed the diversity of the Acrididae population using Simpson's diversity indices in each of four different vegetation types that made up the vegetative gradient in the habitat we sampled. We attempted to determine if certain species of grasshopper were more abundant in vegetation types that contained a greater proportion of the plants they preferred to eat. We anticipated that Gomphocerinae would be in greater abundance in vegetation types with a greater proportion of grass and Melanoplinae would be in greater abundance in vegetation types with a greater proportion of forbs.

Methods

Study site. Our research took place on the McFarland Unit of the Beaver River Wildlife Management Area in Beaver County, OK (Fig. 1). The Beaver River Wildlife Management Area covers approximately 17,700 hectares of land. It consists of four vegetation types that occur in a gradient that runs perpendicular to the Beaver River (Storer and Blanca 2011). The first and closest to the river is a riparian zone consisting mostly of salt cedar (*Tamarix* spp.). The second vegetation type is a mixed grass lowland. The vegetation type furthest from the river is a sandy upland consisting mostly of sagebrush (*Artemisia* species) and sand plum (*Prunus angustifolia*). The last vegetation type occurs between the lowland and upland and is a transitional zone between the two (called an ecotone) (Storer and Blanca 2011). Each vegetation type has differing proportions of vegetative cover and bare ground that could potentially influence grasshopper

population dynamics. Six transects were established that ran perpendicular to the Beaver River and passed through all four vegetation types. A central point (centroid) was established in each vegetation type for each transect. These centroids were marked with 4-foot-long pieces of reinforcing bar encased in five-foot-long polyvinyl chloride pipe. Using the centroids as a starting point, a compass was then used to randomly acquire an azimuth where each individual sampling effort could be inititated. The study design was a split plot with repeated measures.

Grasshopper sampling. The standard method for sampling the relative abundance of each grasshopper species used was sweep net sampling (Gardiner et al. 2005). The southwest corner of one 10 m X 10 m sweep net sampling arena was established twenty meters from the centroid in each vegetation type. Two additional 10 m X 10 m arenas were established at least 15 m apart. These arenas remained undisturbed for at least 30 minutes before being sampled. When enough time passed, fifty sweeps were made within each arena. In 2012, the corners of these arenas were marked with wooden stakes. In 2013, the corners of the arenas were not marked with stakes to reduce the amount of time sampling would take and decrease the impact of the sampler on grasshoppers being sampled. Each arena was sampled by walking in an "X" pattern across the area, as vegetation and terrain would allow. One sweep is equivalent to moving a net no less than 90° in front of the sampler's body on and over the tops of vegetation and is performed concomitantly with one step. The net had a diameter of 38.5 cm. The sweep net was emptied into a plastic storage bag, frozen, and returned to the lab for later sorting and identification. Adults were identified to species and nymphs were identified to subfamily and instar (Otte 1981, Pfadt 1994, Capinera et al. 2004).

During summer 2012 and 2013, relative abundance estimates, overall grasshopper density, and BAMN sampling efforts were performed at each centroid five times (May 19 – May 22, June 12 – June 16, June 28 – July 7, July 19 – July 26, August 7 – August 15) and seven times (May 11 – May 16, May 25 – May 30, June 8 – June 13, June 22 – June 27, July 6 – July 11, July

21 – July 28, August 3 – August 7) respectively. Each range of dates is referred to as a "sampling event." Sampling occurred between 1000 hrs and 1600 hrs or when temperatures were $\geq$ 25° C in an attempt to standardize conditions when grasshoppers were sampled (Southwood 1978, Gardiner et al. 2005).

Proportion of plant functional group cover. A 50 cm X 20 cm PVC rectangle was thrown within each vegetation type from each centroid to a random spot. The proportion (no greater than 100%) of five functional groups (bare ground, litter, grass, forb, and "other") that covered the area within the rectangle was visually estimated (modified from Daubenmire 1959). The "other" category constituted any non-grass or non-forb material (e.g. cow manure, cacti, etc.). This process was repeated ten times per centroid and the values were averaged to get a mean proportion of cover for each functional group in each vegetation type. Proportion of cover estimates were completed at the same time as grasshopper relative abundance estimates for each centroid during the same five sampling periods throughout the summer of 2012 and seven sampling periods throughout the summer of 2013.

Statistical analysis. A two-factor factorial ANOVA (SAS version 9.3, SAS Institute, Cary, NC, 2001) with repeated measures was performed to determine significance ($p < 0.05$) between the relative abundance of Gomphocerinae and Melanoplinae grasshoppers in each of the vegetation types during each of the sampling events in the summer of 2012. Additionally, interactions between the proportions of plant functional group cover and Gomphocerinae and Melanoplinae subfamily relative abundance were analyzed with Pearson correlation coefficients (SAS version 9.3, SAS Institute, Cary, NC, 2001). The proportions of plant functional group cover were then analyzed using factor analysis to reduce the correlated variables to their commonalities and express their effects on relative abundance as linear relationships. Factor analysis was used to understand how a large number of different explanatory variables (plant

functional group cover) acted on a response variable (Gomphocerinae and Melanoplinae relative abundance) in conjunction with each other.

The Berger-Parker dominance index (*d*) was calculated to determine how dominant the most abundant species observed is in a sample. It is calculated using the following formula:

$$d = N_{max}/N_T$$

N_{max} is the number of individuals of the most abundant species present and N_T is the total number of individuals for every species present. The formula gives a value between 0 and 1 and can be expressed as a percentage. This was calculated for each vegetation type in 2012 and 2013 (Southwood 1978).

Simpson's diversity index (λ) was calculated using the following formula:

$$\lambda = \sum_{i=1}^{s} n_i(n_i - 1)/n(n - 1)$$

Simpson's diversity index gives you the probability that any two individuals selected from a sample at random will belong to the same taxonomic distinction. It is a value represented between 0 and 1. As the value approaches 0, greater diversity is being reported; the probability of two individuals being removed from the total catch at random belonging to the same species is low. Simpson's diversity index was calculated for samples collected in each vegetation type during each sampling event in 2013. A two factor factorial ANOVA with repeated measures was also performed to determine significant differences ($p < 0.05$) between Simpson's diversity indices at different sampling events and vegetation types (SAS version 9.3, SAS Institute, Cary, NC, 2001).

Results

Grasshoppers from four subfamilies were collected in the summers of 2012 and 2013: Cyrtacanthacridinae, Gomphocerinae, Melanoplinae, and Oedipodinae. One species of Cyrtacanthacridinae was collected (*Schistocerca lineata*), seventeen species of Gomphocerinae were collected, fifteen species of Melanoplinae were collected, and six species of Oedipodinae were collected (Table 4).

In 2012 and 2013, Gomphocerinae were the most abundant grasshopper subfamily in the riparian vegetation type as nymphs and adults (Fig. 10, 11). In 2012, Gomphocerinae adults became more abundant than nymphs in the riparian vegetation type during the third sampling event (June 28 – July 7). Melanoplinae adults became more abundant than nymphs in the fourth sampling event (July 19 – July 26). In 2013, both Gomphocerinae and Melanoplinae adults became more abundant than nymphs in the fifth sampling event (July 6 – July 11). During 2012 and 2013, gomphocerinae nymphs were in greater abundance than Melanoplinae and Oedipodinae nymphs in the lowland vegetation type (Fig. 12, 13). In 2012, Gomphocerinae were the most abundant adults during all sampling events but in 2013, Melanoplinae were the most abundant adults during the sixth sampling event only (July 21 – July 28). In 2012, both Gomphocerinae and Melanoplinae adults became more abundant than nymphs in the lowland vegetation type during the third sampling event (June 28 – July 7). In 2013, both subfamilies were more abundant as adults than as nymphs during the fifth sampling event (July 6 – July 11). In 2012 and 2013 in both the ecotone and upland vegetation types, Melanoplinae adults and nymphs were the most abundant grasshopper subfamily (Fig. 14, 15, 16, 17). In 2012 in the ecotone, Melanoplinae adults became more abundant than nymphs during the second sampling event (June 12 – June 16) and Gomphocerinae adults became more abundant than nymphs during the third sampling event (June 28 – July 7). In 2013, Melanoplinae adults became more abundant during the fourth sampling event (June 22 – June 27) and Gomphocerinae adults became more

abundant during the fifth sampling event (July 6 – July 11). In 2012 in the upland vegetation type, Melanoplinae and Gomphocerinae adults became more abundant than nymphs during the third sampling event. In 2013, both became more abundant as adults during the fifth sampling event. The Oedipodinae abundance was low compared to the Gomphocerinae and Melanoplinae subfamilies and did not show consistent decreases of nymphal abundance and increases of adult abundance over time.

The Berger-Parker dominance index (d) was calculated using data from 2012, 2013, and a combined 2012 and 2013 dataset (Table 5). In 2012, *Melanoplus bowditchi* was the most dominant species of grasshopper (d = 0.331). In 2013, *Ageneotettix deorum* was the most abundant species of grasshopper (d = 0.180). *Melanoplus bowditchi* was the most dominant species in the combined dataset (d = 0.221).

The abundances of the two most dominant species were recorded to show when both become most abundant and in which vegetation type. In 2012 *Ageneotettix deorum* was most abundant in the lowland vegetation type during the fourth sampling event (July 19 – July 26) with 16 individuals being sampled (Fig. 18). In 2013, *A. deorum* was most abundant in the lowland vegetation type during the sixth sampling event (July 21 – July 28) with 37 individuals being sampled (Fig. 19). In 2012, *Melanoplus bowditchi* was most abundant in the ecotone vegetation type during the fourth sampling event (July 19 – July 26) with 99 individuals being sampled (Fig. 20). In 2013, *M. bowditchi* was most abundant in the upland vegetation type during the fifth sampling event (July 6 – July 11) and in the ecotone vegetation type during the sixth sampling event (July 21 – July 28), at both times with 25 individuals being sampled (Fig. 21).

Simpson's diversity indices were calculated for the grasshopper assemblages in each vegetation type during each sampling period. The general trend observed when analyzing differences between the mean Simpson's diversity associated with sampling events given

vegetation type was that the earliest sampling events had significantly larger diversity indices than the later sampling events (Fig. 22). The general trend observed when looking at the diversity indices associated with vegetation type given sampling event was that the grass lowland always had the lowest mean diversity index (and therefore the greatest diversity) during every sampling event (Fig. 23).

The mean proportions of cover of five different "plant functional groups" were estimated by the use of Daubenmire frames in each vegetation type from all sampling events during 2012 and 2013 (Fig. 24, Fig. 25). In 2012, the riparian and lowland vegetation types had greater proportions of litter and grass cover than forb and bare ground cover. The ecotone and upland vegetation types had greater proportions of bare ground, litter, and forb cover than grass cover. Riparian and lowland vegetation types had greater proportions of grass cover than ecotone and upland vegetation types. Ecotone and upland vegetation types had greater proportions of forb cover than riparian and lowland vegetation types (Fig. 24). In 2013, the riparian and lowland vegetation types had greater proportions of litter and grass cover than forb and bare ground cover. The ecotone and upland vegetation types had greater proportions of forb cover than bare ground, litter, and grass cover. Riparian and lowland vegetation types had greater proportions of grass cover than ecotone and upland vegetation types. Ecotone and upland vegetation types had greater proportions of forb cover than riparian and lowland vegetation types (Fig. 25).

The relative abundances of the five most abundant adult grasshopper taxa were determined from the sweep net samples performed during all sampling events in 2012 and 2013 (Table 6, Table 7). In 2012, *Paropomala wyomingensis* was the most abundant grasshopper in the riparian and lowland vegetation types. Females from the *Melanoplus* genus were the most abundant grasshoppers in the ecotone and upland vegetation types. Of the 5 most abundant grasshopper taxa in the riparian vegetation type, four were from the subfamily Gomphocerinae and one was from the subfamily Melanoplinae. Of the 5 most abundant grasshopper taxa in the

lowland vegetation type, three were from the subfamily Gomphocerinae and two were from the subfamily Melanoplinae. Of the five most abundant grasshopper taxa in the ecotone vegetation type, three were from the subfamily Melanoplinae and two were from the subfamily Gomphocerinae. Of the five most abundant grasshopper taxa in the upland vegetation type, three were from the subfamily Melanoplinae, one was from the subfamily Oedipodinae and one is from the subfamily Gomphocerinae (Table 6). In 2013, *Paropomala wyomingensis* was the most abundant grasshopper in the riparian vegetation type. Females from the *Melanoplus* genus were the most abundant grasshoppers in the lowland, ecotone and upland vegetation types. Of the 5 most abundant grasshopper taxa in the riparian vegetation type, three were from the subfamily Gomphocerinae and two were from the subfamily Melanoplinae. Of the 5 most abundant grasshopper taxa in the lowland vegetation type, three were from the subfamily Gomphocerinae and two were from the subfamily Melanoplinae. Of the five most abundant grasshopper taxa in the ecotone and upland vegetation types, three were from the subfamily Melanoplinae, one was from the subfamily Oedipodinae and two were from the subfamily Gomphocerinae (Table 6).

The two-factor ANOVA revealed several significant differences between the relative abundance estimates of Melanoplinae and Gomphocerinae (Fig. 26). In the riparian vegetation type, the relative abundance of Gomphocerinae was significantly greater than the relative abundance of Melanoplinae in the fourth ($p = 0.0146$) and fifth ($p = 0.0227$) sampling events. In the lowland vegetation type, Gomphocerinae relative abundance was significantly greater in the third ($p = 0.0003$), fourth ($p = 0.0006$), and fifth ($p = 0.0055$) sampling events. In the ecotone and upland vegetation types, Melanoplinae relative abundance was significantly higher at all sampling events with a $p < 0.001$, except for the fourth sampling event in the transitional vegetation type where $p = 0.0054$.

The relative abundance of Melanoplinae grasshoppers had significant correlations with four of the five plant functional group cover proportions. Bare ground ($r = 0.234$, $p = 0.01$) and

forb cover ($r = 0.645$, $p < 0.0001$) were both positively correlated with Melanoplinae relative abundance. Litter ($r = - 0.209$, $p = 0.0223$) and grass cover ($r = - 0.619$, $p < 0.0001$) were both negatively correlated with Melanoplinae relative abundance (Fig. 27). The relative abundance of Gomphocerinae grasshoppers was significantly correlated with only three of the five plant functional groups. Bare ground ($r = - 0.248$, $p = 0.0062$) and forb cover ($r = -0.605$, $p < 0.0001$) were both negatively correlated with Gomphocerinae relative abundance. Grass cover ($r = 0.622$, $p < 0.0001$) was positively correlated with Gomphocerinae relative abundance (Fig. 28). The "other" plant functional group showed no significant correlation with relative abundance of either subfamily. Of the shared significant correlations between relative abundance and proportion of plant functional group cover, those that were positively correlated for Melanoplinae were negatively correlated for Gomphocerinae and vice versa.

The factor analysis grouped the explanatory variables into two factors (Table 8). Factor 1 included bare ground cover, litter cover, forb cover, and grass cover. Factor 2 included grass cover, other cover, and species richness. The variables that have like signs in front of them (e.g. bare ground and forb cover) explain components of variation of the relative abundance of the grasshoppers in the same direction. The nature of the signs is relative and not to be interpreted as being only positive or only negative; if one variable has a positive sign and one effect, a variable with a negative sign has the opposite effect, even if that effect is a positive increase in one of the variables.

Discussion

Grasshopper nymphs were most abundant in the early sampling events with abundances tapering off later in the season. This is because the grasshoppers are maturing into adults. Peak abundances of Gomphocerinae and Melanoplinae nymphs occur in mid to late May. Peak adult abundances were typically lower than peak nymph abundances likely due to the fact that a

number of nymph grasshoppers died either by predation or other means. Though nymphal mortality rate was not measured, it is understood that, in general, many immature individuals of an arthropod taxa will die before reaching adulthood. Another reason fewer adult individuals were caught than nymphs could be because adults are more agile and have wings, making it easier for them to avoid being caught by sweep nets.

The Berger-Parker dominance index calculations revealed that for the 2012 data and the combined 2012 and 2013 data, *Melanoplus bowditchi* was the dominant grasshopper species. In 2013, *Ageneotettix deorum* was the dominant species. The difference in dominant taxon could be explained by differences in climatic conditions between years. *Melanoplus bowditchi* is in the subfamily Melanoplinae and *Ageneotettix deorum* is in the subfamily Gomphocerinae; their dominance in different years is likely due to climate that created more optimal conditions for one subfamily over the other.

Gomphocerinae were most abundant in riparian and lowland vegetation types and Melanoplinae were most abundant in ecotone and upland vegetation types. This occurred likely because both subfamilies differ in several ways. They have different dietary preferences (Joern 1979, Behmer and Joern 2008), different optimal oviposition conditions (Russell and Detling 2003, Branson 2005), and some species are differently cryptic. Studies analyzing the crop contents of several grasshopper individuals of multiple species of grasshopper have shown that Gomphocerinae tend to specialize on grasses while Melanoplinae tend to be generalists, eating a mix of grass and forbs (Joern 1979, Behmer and Joern 2008). Gomphocerinae also generally prefer to lay their egg pods at a shallower depth in harder, more compact soil than Melanoplinae. Melanoplinae prefer to lay their egg pods deeper in loose, sandy soil. Differences in thermoregulatory requirements are likely the driving force behind this behavioral difference (Russell and Detling 2003, Branson 2005). There are some species of Gomphocerinae that cryptically resemble grass, so climatic conditions that provide more grass might find a greater

abundance of those grasshoppers. It's not possible to say which of these differences are being exploited by the grasshoppers between years, but it is likely that one or a combination of several are responsible for the observed changes in dominant species.

Regardless of all contributing factors to why this kind of habitat partitioning occurs, it is likely that different subfamilies will be preyed upon preferentially by Northern Bobwhite depending on where they are foraging. If foraging occurs in riparian and lowland vegetation types, Gomphocerinae are more likely going to be preyed upon. If foraging occurs in ecotone and upland vegetation types, Melanoplinae are more likely going to be preyed upon. Unpublished data from Tanner et al. indicate that quail nests occur in greater abundance and are more successful in upland vegetation type sites (Table 9). Because of this, it is likely that the upland sites are providing optimal foraging for chicks by way of corridors for active hunting of invertebrate prey. This makes Melanoplinae the most likely eaten grasshopper subfamily by Northern Bobwhite. There are no data available regarding which vegetation types were being visited by hens that were acquiring protein prior to egg-laying, so there may not be a potential preference for Melanoplinae during those periods.

Sweep net sampling has revealed that Oedipodinae are not very abundant in any of the vegetation types during any of the sampling events. This may be because, generally speaking, the peak activity of Oedipodinae is at the temporal extremes of the sampling season performed. Oedipodinae overwinter as nymphs and are more abundant in late summer to fall. Those that overwinter at this time are adults earlier than Gomphocerinae or Melanoplinae (Pfadt 1994, Capinera et al 2004) in the year. Cyrtacanthacridinae were represented by only one species in the collected samples and were not very abundant in the summers of 2012 and 2013. In general their maturation was slightly asynchronous with the Gomphocerinae and Melanoplinae, appearing as nymphs in the middle of the summer and only showing an increase in abundance during the last sampling events of both 2012 and 2013.

These observations indicated that neither Oedipodinae nor Cyrtacanthacridinae are likely food sources for Northern Bobwhite. Not only is the abundance of both asynchronous with peak quail feeding times, but both subfamilies are characterized by strong flight behavior. Oedipodinae are cryptic against sandy substrate, preferring to find refuge in open areas rather than those dominated by vegetation (Capinera et al. 2004). Because of this, when threatened or otherwise molested they will fly away rather than seek refuge in dense vegetation cover. *Schistocerca lineata* is the only Cyrtacanthacridinae species represented in our samples. Grasshoppers in this genus are responsible for crop-destroying plagues that swarm over the African continent (Joern and Gaines 1990). These known flight behaviors may translate to successful avoidance of sweep net sampling efforts as well as avoidance of potential quail predators.

Simpson's diversity indices decreased over time, meaning that the diversity of the population in question increased. This was an expected result because during the earlier sampling events grasshopper species were not being recorded. The nymphs were only being identified to subfamily, of which there were only four. As time progressed and adults were starting to emerge, the diversity increased. During every sampling event, the grass lowland had the greatest diversity. This is likely because the Gomphocerinae were the most species-rich subfamily of grasshoppers, and because the grass lowland had a greater abundance of Gomphocerinae. Having more representative species in the Beaver River grasshopper community and being in greater abundance than any other subfamily in the grass lowland, it is likely that the Gomphocerinae are driving this increased diversity.

Previous studies have shown that plant community composition can affect the grasshopper biodiversity of a given habitat (Tao et al. 2013). Findings from vegetation and grasshopper community interactions in the Qilian Mountains in China have demonstrated that the invasion of weeds reduced the plant species richness and diversity, which in turn reduced

grasshopper species diversity (Tao et al. 2013). Unpublished data from Fishbein et al. collected simultaneously to when grasshoppers were sampled in this study and in the same locations indicated that this was not the case. Overall grasshopper taxa richness changed significantly in accordance with changes in plant species richness (Fig. 29), but when looking at taxa richness within subfamilies, there is no significant change in the richness (Fig. 30). This is observed despite significant changes in grass species richness (Fig. 31) and forb species richness (Fig. 32) as well as changes in the ratio between invasive and native plants species richness (Fig. 33). Because of the results presented regarding grasshopper diets differing between subfamilies and the importance of grass for Gomphocerinae and forb for Melanoplinae, it is important to consider the changes in richness of those subfamilies as the richness of their preferred dietary resource changes along the vegetation gradient. Because changes in taxa richness of specific host plant type had no effect on the richness of the grasshopper subfamilies, it is likely that the biodiversity of grasshoppers is not significantly influenced by plant species composition.

As predicted, we found significant differences in relative abundance between grasshopper subfamilies in our study across different vegetation types, with a greater relative abundance of Gomphocerinae in riparian and lowland areas and a greater abundance of Melanoplinae in upland regions. It has been previously observed that Gomphocerinae and Melanoplinae grasshoppers occupy habitats with different vegetation composition (Joern 1979). This habitat partitioning is often associated with dietary preferences: Gomphocerinae are considered to specialize on a few plant species, often grasses, and carry out their lifecycles in areas that are predominantly comprised of grasses while Melanoplinae are considered to be generalist feeders, eating a wider variety of plants and carrying out their lifecycles in areas that suit this preference (Joern 1979, Chapman 1990).

The relative abundance of Melanoplinae grasshoppers was positively correlated with the proportion of bare ground and forb coverage. A greater proportion of bare ground in the ecotone

and upland vegetation types can indicate more optimal oviposition space for the grasshoppers of this subfamily (Fig. 24, Fig. 25). Some Melanoplinae prefer to lay their eggs in loose, sandy soil, much like the dunes that comprise the upland and spill over into the hybrid vegetation types (Branson 2005).

Because Melanoplinae rely on non-grass plants for food resources (Joern 1979, Chapman 1990) the greater proportion of such plants in the ecotone and upland vegetation types likely explains the greater relative abundance of these grasshoppers in those areas. This is further supported by the strong negative correlation between Melanoplinae relative abundance and the proportion of grass cover (Fig. 27). These results indicate a potential rejection of grass as a food source and a preference for forb on the part of the Melanoplinae. Strengthening these indications are the opposite results of Gomphocerinae relative abundance and the proportions of forb and grass cover (Fig. 28). The Gomphocerinae are considered "specialists", eating mostly grass species in previous studies (Joern 1979, Chapman 1990). If food preference is the driving force behind the habitat partitioning along this vegetation gradient, then these results would be expected.

The shift from insignificant differences to significant differences in relative abundance between Melanoplinae and Gomphocerinae over time in the riparian and lowland vegetation types may be an illustration of competition for food resources between generalist and specialist grasshoppers. When generalist and specialist species inhabit the same area and share a resource upon which the specialist thrives, the specialists will ultimately out-compete the generalists and force them to switch to a different resource or move to an area with fewer specialists (Beckerman 2000). Many Melanoplinae species are generalists and many Gomphocerinae species are specialists (Chapman 1990). The subfamilies were not significantly different until later in the summer in riparian and lowland sites, areas that are predominantly grass-covered (Fig. 24, Fig. 25). It may be that the Gomphocerinae species present in the riparian and lowland out-competed

the Melanoplinae species for the grass as a dietary resource and force the Melanoplinae into the hybrid and upland sites over time (Beckerman 2000). Because the vegetation types change along a gradient and the hybrid and upland vegetation types were relatively close in proximity to the riparian and lowland vegetation types (separated by only hundreds of meters), there was a potential for the Melanoplinae to migrate up the gradient into places with more palatable food resources.

Based on the loadings in Factor 1 from the factor analysis (Table 8), it was determined that bare ground and forb cover worked in one direction on grasshopper relative abundance and litter and grass cover worked in the opposite direction. Because the forb cover and grass cover are of a similar value with opposite signs, their contributions to grasshopper relative abundance are similarly strong with opposite effects. Forb cover and grass cover have larger loading values so their effects contributed more to relative abundance than bare ground cover and litter cover. If bare ground cover and litter cover only contributed to oviposition space and escape space, their lower loading values indicated that those contributions were not as important in determining relative abundance of grasshoppers. Because previous studies have shown that Melanoplinae and Gomphocerinae have different dietary preferences (Melanoplinae preferring forb and Gomphocerinae preferring grass) and because our factor analysis showed that forb cover and grass cover contributed the most to grasshopper relative abundance (as indicated by larger factor loadings) and worked in opposite directions, it is likely that these variables worked on the dietary preferences of these grasshopper subfamilies and that those preferences dictated habitat portioning.

Factor 2 included grass cover, other cover, and species richness of grasshoppers observed (Table 8). Based on the signs of the factor loadings, "other cover" and "species richness" worked in one direction and grass cover worked in the opposite direction. The relevance of these loadings to Gomphocerinae and Melanoplinae relative abundance is not apparent with the data

collected for this study, and it may only contribute noise against which Factor 1 works. Variables that were not measured in this study may end up contributing to Factor 2 and could elucidate its significance. However, with the data collected we cannot interpret the significance of Factor 2.

After observing these patterns of habitat partitioning between the two most abundant subfamilies of Acrididae, we can make predictions as to what subfamily the most abundant taxa in each vegetation type will belong. Because the riparian and lowland vegetation types had a greater proportion of grass cover than forb cover (Fig. 24, Fig. 25) and it was determined that the relative abundance of Gomphocerinae was positively correlated with grass cover (Fig. 28), it can be expected that the most abundant taxa in those vegetation types would belong to the grass-eating Gomphocerinae subfamily. This was the case in 2012, as *Paropomala wyomingensis* and *Ageneotettix deorum* were the first and second most abundant (respectively) grasshopper species in the riparian and lowland vegetation types (Table 6). Conversely, because the ecotone and upland vegetation types were characterized by having greater proportions of forb cover than grass cover (Fig. 24, Fig. 25) and it was determined that the relative abundance of Melanoplinae was positively correlated with forb cover (Fig. 27), it can be expected that the most abundant taxa in those vegetation types would belong to the generalist and forb-eating Melanoplinae subfamily. Again, in 2012, this prediction was correct. Females from the genus *Melanoplus* and male *Melanoplus bowditchi* were the first and second most abundant (respectively) taxa in the ecotone and upland vegetation types (Table 6).

In 2013, the data are nearly identical with the exception of one of the vegetation types. As in 2012, *P. wyomingensis* and *A. deorum* were the first and second most abundant (respectively) species in the riparian vegetation type and *Melanoplus* females and *M. bowditchi* males were the first and second most abundant (respectively) species in the ecotone and upland vegetation types. *Melanoplus* females were also the most abundant taxa in the lowland vegetation type, being 2.8% more abundant than *Ageneotettix deorum* (Table 7). While this does

not follow the pattern of most abundant grasshopper taxa in 2012, it is likely being observed for the following reasons. First, there were seven different *Melanoplus* species observed in the lowland vegetation type in 2013. Because the females of these genera were treated as one taxon (due to the difficulty in identifying them to species morphologically) there is likely a greater diversity of species within that one taxonomic grouping. Females of seven different species could be contained within that one taxon and, were they identified to species, that grouping would be split up among those species. Second, two more sampling events occurred during 2013. Because these are relative abundances of the total grasshopper taxa abundance in every sampling event combined, the two additional sampling events could be responsible for differences in the community composition observed between years. There could also be differences in the community composition of grasshoppers between years due to abiotic factors not measured during this study. Measurements of temperature, soil moisture, and rainfall performed over several years concomitantly with grasshopper sampling could help elucidate the changes in community composition between vegetation types over time.

Our data have recorded how the Acrididae population of the Beaver River Wildlife Management are assembled and emerge. Thirty nine species were identified from four different subfamilies. The most abundant during the sampling season were the Gomphocerinae and Melanoplinae, emerging as nymphs in mid-May and peaking in abundance as adults in June. Oedipodinae and Cyrtacanthacridinae either have life cycles that are asynchronous with Gomphocerinae and Melanoplinae and not active when sampling occurred or species in both subfamilies avoided being caught by sweep nets and were underrepresented in the samples taken. Grasshopper nymphs were wingless and in greater abundance in adults, they may be the preferred life stage for quail to prey upon, indicating that the most grasshopper-prey-rich time for quail is mid- to late May. Oedipodinae nymphs are more abundant in September and though they may

be the appropriate size and life stage for quail to eat, they may be phenologically inaccessible making them a less important potential food source than Gomphocerinae or Melanoplinae.

The most dominating species were *Ageneotettix deorum* and *Melanoplus bowditchi*. Because these dominated the samples, it is possible that they were the most abundant in the area and were preyed upon with greater frequency by quail than any other grasshopper species. Implications could be made to monitor populations of these common grasshoppers as indicators of prey-rich habitat for dwindling quail populations. However, because both species dominated a different year (*Melanoplus bowditchi* in 2012 and *Ageneotettix deorum* in 2013), it may be that the dominating species changes annually. *Melanoplus deorum* is a Melanoplinae and *Ageneotettix deorum* is a Gomphocerinae, further implying that different subfamilies may dominate the habitat during different times and that at least the majority of the grasshopper community should be monitored for making implications about prey-rich or prey-poor habitats. Unpublished data from Tanner et al. show that Northern Bobwhite established more nests in the upland vegetation types than any other and that more of these nests were successful in terms of surviving chick broods (Table 9). Besides the Melanoplus females, *M. bowditchi* and *M. angustipennis* are the most abundant grasshopper species in the upland vegetation type. Due to their greater abundance, these grasshopper species may be more important in terms of serving as prey for Northern Bobwhite. It would impossible to say without analyzing the crop contents of the quail or their feces if these grasshopper species are in fact being eaten more than others, but their greater abundance in the upland vegetation types should not be ignored.

CHAPTER IV

SUMMARY

Since at least the 1960s, Northern Bobwhite (*Colinus virginianus*, henceforth referred to as "quail") populations have been on the decline (Brennan 1991). In Oklahoma, these birds are a popular game bird that generates money through sales of hunting licenses and revenue spent by hunters. Their decline is attributed to the lack of suitable late successional habitat promoted by suboptimal land management (Kitts 2004, Lusk et al. 2006, Doxon & Carroll 2010). Late successional habitats with native vegetation provide diverse vegetative features crucial to Northern Bobwhite success, as well as provide egg-laying hens and quail chicks with crucial arthropod prey (Wenninger & Inouye 2007). Habitats overrun by invasive exotic plants will form dense sod mats and not allow for the structural heterogeneity required by these birds to nest, forage for prey, and loaf (Barnes et al. 2013).

In a study of the summer diets of Northern Bobwhite, Brennan and Hurst (1995) observed that certain animal foods were more important than others for hens. They determined snails (a gastropod), short-horned grasshoppers, crickets, stinkbugs, spittlebugs, and beetles were eaten more frequently than other arthropods. This study did not examine the accessibility of arthropod prey, but the fact that these food items were consistently eaten over others implies a preference by Northern Bobwhite hens for them (Brennan & Hurst 1995).

Grasshoppers (Orthoptera: Acrididae) are a ubiquitous member of the arthropod communities upon which quail prey (Doxon and Carroll 2010). They are considered only to the

ordinal level in dietary studies (Butler et al. 2004, Doxon & Carroll 2010) but have the potential for important species-based relationships with quail that may have gone unrealized. Little effort has gone into understanding the species composition of these assemblages and how these assemblages respond to the vegetative communities and microclimates that exist within potential quail breeding habitat. By describing the species diversity and abundance of grasshopper assemblages in potential quail breeding areas of varying quality and composition, it can be determined if any significant relationship between these factors exists. Eventually, if such a relationship exists, assessments of habitat can be made based on the presence or absence of certain grasshoppers and predictions of how quail will be affected can be made. For these predictions and those based on grasshopper sampling to be accurate, an understanding of the interactions between grasshopper assemblages and their habitats must be ascertained.

It is commonly understood that grasshoppers engage in "generalist herbivory". They can and will eat most of the plants they encounter. But exploration of this term and how it relates to grasshoppers reveals a more complex relationship between these insects and their food. There are actually three distinct types of feeding that grasshoppers can display: monophagy, oligophagy, and polyphagy (Chapman 1990). Members of the subfamily Gomphocerinae primarily eat grass (Otte 1981). Members of the subfamily Melanoplinae (the spurthroated grasshoppers), specifically members of the *Meanoplus* genus, primarily eat forbs. Oedipodinae species primarily eat a mixture of both (Joern and Lawlor 1980). Joern (1979) recorded the feeding patterns of several grasshopper species in six sites and determined "dietary niche breadths" for each. These data show that while some species have wide niche breadths, indicating a broad diet, even more species have narrow niche breadths, indicating specialized diets. Most Gomphocerinae had small niche breadths. Because they are primarily grass eaters and grass has predictable growth, having a broader diet (a larger niche breadth) is unnecessary. Having diets comprised mostly of forbs suggests that the Melanoplinae should have a smaller dietary range. If the forbs being consumed

have chemical defenses, the grasshoppers that eat them should have developed specific defense mechanisms against these chemicals and their overall niche breadths should be narrow. In this study, however, Melanoplinae generally had larger niche breadths. Joern (1979) suggests, as an alternative, that the wider dietary niche breadth for these forb-eaters could be the defense mechanism protecting them from forb toxins. If they eat small amounts of several forbs, the Melanoplinae can bypass the danger of accumulating forb toxin (Joern 1979). With this broader understanding of the feeding habits of acridid grasshoppers, an assumption can be made about the relationship between the vegetation of a given habitat and the grasshopper presence. If the grasshopper subfamilies stay true to the dietary tendencies previously noted by Otte, Joern, and Lawlor, then the areas associated with each will most likely be comprised primarily of those plant types (i.e. grasses for Gomphoceranae, forbs for Melanoplinae, etc.) (Otte & Joern 1976, Joern and Lawlor 1980). Regardless of what predominant plant type is present, a homogenous vegetation composition should cause lower grasshopper species diversity.

Methods for sampling arthropods differ greatly depending on the taxonomic grouping desired. The methods used for sampling foliage-dwelling arthropods differ from methods used for sampling those that are ground-dwelling, have the ability to fly, etc. (Onsager and Henry 1977, Southwood 1978, Banaszak 1980). Different methods can give estimates of varying metrics like density, richness, or abundance, so often times there are multiple methods for sampling arthropods within the same order or family. To gain a broader understanding of the diversity of a particular group of arthropods, multiple sampling methods are often employed simultaneously (Onsager 1977, Onsager 2000, Moir et al. 2005, Stephen and Rao 2007, Westphal et al. 2008).

Sampling for grasshoppers is typically done two ways: density ring sampling, which provides estimates of grasshopper density (Onsager 1977, Onsager & Henry, 1977) and sweep net sampling, which provides estimates of grasshopper relative abundance (Berry et al. 2000,

Gardiner et al. 2005). These are frequently done concomitantly in a habitat to get a more complete picture of the grasshopper assemblage. Density ring sampling involves observing and counting grasshoppers in a small area by an observer or observers. Onsager (1977) compared five different versions of this methodology. Each method was not without its drawbacks, but it was determined that any method that involved creating a border or delineation around an area in which grasshoppers would be counted produced the most accurate and precise estimates of grasshopper density (Onsager 1977). However, it was also found that those methods were impractical, time consuming, or limiting with regards to the kinds of vegetation in which those methods could be used. It was concluded that the ring method generated comparable accuracy and precision observed in other methods that involved delineating a sampling border while continuing to be a fast and inexpensive method (Onsager and Henry 1977).

Using sweep nets is a standard method of sampling used to get estimates of grasshopper relative abundance (Gardiner et al. 2005). A net is used to sweep through and over the tops of vegetation to catch any grasshoppers present. This method is used to acquire relative abundance of grasshopper species or subfamilies by figuring out the proportion of each taxonomic grouping from the total catch. These data may be used to calculate species or subfamily density by multiplying total grasshopper density (Onsager and Henry 1977) and the relative abundance (Onsager 2000, Branson 2005).

Our first objective was to develop a novel sampling method that measured both the relative abundance of grasshoppers and a rate of grasshoppers caught per minute simultaneously and compare those measurements to those obtained from standard methods of measuring grasshopper relative abundance (sweep nets) and density (density rings). It was expected that relative abundance estimates as determined by this novel method would be comparable to the relative abundance estimates determined by the standard sweep net sampling method and that the rate of grasshoppers caught per minute would be comparable to the density of grasshoppers

observed in the standard density ring count method. By combining the two standard methods into one, grasshopper sampling could become even easier and less time consuming, with implications for a standardized method to be used by people concerned with monitoring beneficial or detrimental grasshoppers.

Our second objective was to characterize the Acrididae community in a Western Oklahoma grassland that served as Northern Bobwhite habitat. We attempted to identify all of the present Acrididae species and track the emergence and decline of each subfamily. We also attempted to track the emergence and decline of the most abundant species present in the habitat. We assessed the diversity of the Acrididae population using Simpson's diversity indices in each of four different vegetation types that made up the vegetation gradient in the habitat we sampled. We attempted to determine if certain species of grasshopper were more abundant in vegetation types that contained a greater proportion of the plants they preferred to eat. We anticipated that Gomphocerinae would be in greater abundance in vegetation types with a greater proportion of grass and Melanoplinae would be in greater abundance in vegetation types with a greater proportion of forbs.

Our research took place on the McFarland Unit of the Beaver River Wildlife Management Area in Beaver County, OK. The Beaver River Wildlife Management Area covers approximately 17,700 hectares of land. It consists of four vegetation types that occur in a gradient that runs perpendicular to the Beaver River: riparian, lowland, ecotone, and upland (Storer and Blanca 2011). Each vegetation type has differing proportions of vegetation cover and bare ground that could potentially influence grasshopper population dynamics. We established six transects that ran perpendicular to the Beaver River and passed through all four vegetation types that comprise the vegetation gradient. A central point (centroid) was established in each vegetation type in each transect. These centroids were marked with 4-foot-long pieces of reinforcing bar encased in five-foot-long polyvinyl chloride pipe. Using the centroids as a

starting point, a compass was then used to randomly acquire an azimuth from which each individual sampling effort could be set up. The study design was a split plot with repeated measures.

Density rings and sweep net samples were used to acquire estimates of grasshopper density and grasshopper relative abundance. Daubenmire frames were used to estimate the proportion of five functional groups (bare ground, litter, grass, forb, and "other") in each vegetation type in each transect (modified from Daubenmire 1959). For the first objective, a novel sampling method called "By Any Means Necessary" (BAMN) was also used. This method was developed to be a timed form of sampling, recording how long it took the collector to catch twenty grasshoppers, going no longer than twenty minutes. This provided the rate at which grasshoppers were caught per minute. Relative abundance estimates, overall grasshopper density, and BAMN sampling efforts were performed at each centroid five times during the summer of 2012 (May 19 – May 22, June 12 – June 16, June 28 – July 7, July 19 – July 26, August 7 – August 15) and seven times during the summer of 2013 (May 11 – May 16, May 25 – May 30, June 8 – June 13, June 22 – June 27, July 6 – July 11, July 21 – July 28, August 3 – August 7). Each range of dates is referred to as a "sampling event." Sampling occurred between 10:00 am and 4:00 pm or when the temperature was $\geq$ 25° C in an attempt to standardize conditions during which grasshoppers were sampled (Southwood 1978, Gardiner et al. 2005).

For the first objective, comparisons of relative abundances between sweep net sampling and BAMN sampling were analyzed using analysis of variance with repeated measures. An autoregressive period 1 covariance structure was used to model the intratransect variation across time (SAS version 9.3, SAS Institute, Cary, NC, 2001). This analysis was also performed for comparisons between densities of grasshoppers observed and rates of grasshoppers caught per minute using the BAMN method. Correlations between densities of grasshoppers and rates of grasshoppers caught per minute were determined by calculating Pearson correlation coefficients

using Microsoft Excel (Microsoft 2010). Sørenson's coefficient of similarity (C_S) was calculated to determine the similarity of species richness observed between sweep net sampling and BAMN sampling. The Berger-Parker dominance index (*d*) was calculated to determine how dominant the most abundant species observed is in a sample for each sampling method.

A total of 48 different grasshopper species were observed in the Beaver River WMA in 2012 and 2013: 1 Cyrtacanthacridinae, 19 Gomphocerinae, 16 Melanoplinae, and 12 Oedipodinae. Five species were caught exclusively by the sweep net sampling method and 9 species were caught exclusively by the BAMN sampling method. Relative abundance estimates of the eight most abundant grasshopper taxa were compared between sweep net sampling and BAMN sampling. The relative abundance estimates varied significantly ($p < 0.05$) between sampling method, time of year, and vegetation type within each species, so it was determined that these methods were not comparable. Density and rate were also compared within each vegetation type over time. The highest densities were observed in the ecotone and upland vegetation types. In every sampling event these were significantly higher ($p < 0.05$) than densities observed in riparian and lowland vegetation types. The rates of grasshoppers caught had a different pattern of significance. The ecotone had the highest rates of grasshoppers caught, followed by lowland and upland, then riparian vegetation types ($p < 0.05$). The rates were not significantly different during every sampling event either. These differences indicated to us that these measurements were not comparable and did not produce similar data. Pearson correlations revealed that the density and rate of grasshoppers caught were positively correlated, but understanding the nature of this relationship requires more research and analysis.

Coefficients of similarity revealed that the least similar comparison between species richness (C_S) as observed in BAMN and sweep net sampling was in the upland vegetation type during 2013 ($C_S = 0.581$) and that the least similar comparison between abundance (C_N) observed in BAMN and sweep net sampling was in the riparian vegetation type during 2012 ($C_N = 0.566$).

The highest C_S was found in the riparian vegetation type during 2013 ($C_S = 0.809$) and the highest C_N was found in the upland vegetation type during 2012 ($C_N = 0.905$).

It is apparent from this research that the novel BAMN method did not report similar measurements of relative abundance and density to the standard sweep net sampling and density rings. But differences in species composition of catches from both methods indicate that using multiple methods captures a greater diversity that would go unseen if only standard methods were applied.

For the second objective a two-factor factorial ANOVA (SAS version 9.3, SAS Institute, Cary, NC, 2001) with repeated measures was performed to determine significance ($p < 0.05$) between the relative abundance of Gomphocerinae and Melanoplinae grasshoppers in each of the vegetation types during each of the sampling events in the summer of 2012. Additionally, interactions between the proportions of plant functional group cover and Gomphocerinae and Melanoplinae subfamily relative abundance were analyzed with Pearson correlation coefficients (SAS version 9.3, SAS Institute, Cary, NC, 2001). The proportions of plant functional group cover were then analyzed using factor analysis to reduce the correlated variables to their commonalities and express their effects on relative abundance as linear relationships. Factor analysis was used to understand how a large number of different explanatory variables (plant functional group cover) acted on a response variable (Gomphocerinae and Melanoplinae relative abundance) in conjunction with each other.

Simpson's diversity index was also calculated to calculate the probability that any two individuals pulled out of a sample at random will belong to the same taxonomic distinction. A two factor factorial ANOVA with repeated measures was also performed to determine significant differences ($p < 0.05$) between Simpson's diversity indices at different sampling events and vegetation types (SAS version 9.3, SAS Institute, Cary, NC, 2001).

Simpson's diversity indices were calculated for the grasshopper assemblages in each vegetation type during each sampling period. The general trend observed when analyzing differences between the mean Simpson's diversity associated with sampling events given vegetation type was that the earliest sampling events had significantly larger diversity indices than the later sampling events. The general trend observed when looking at the diversity indices associated with vegetation type given sampling event was that the grass lowland always had the lowest mean diversity index (and therefore the greatest diversity) during every sampling event.

The two-factor ANOVA revealed several significant differences between the relative abundance estimates of Melanoplinae and Gomphocerinae. In the riparian vegetation type, the relative abundance of Gomphocerinae was significantly greater than the relative abundance of Melanoplinae in the fourth ($p = 0.0146$) and fifth ($p = 0.0227$) sampling events. In the lowland vegetation type, Gomphocerinae relative abundance was significantly greater in the third ($p = 0.0003$), fourth ($p = 0.0006$), and fifth ($p = 0.0055$) sampling events. In the ecotone and upland vegetation types, Melanoplinae relative abundance was significantly higher at all sampling events with a $p < 0.001$, except for the fourth sampling event in the transitional vegetation type where $p = 0.0054$.

The factor analysis revealed that grass cover and forb cover had a stronger influence of subfamily relative abundance than bare ground and litter cover. It also revealed that these factors worked in opposite directions, meaning that whatever forb cover contributed to relative abundance, grass cover contributed some opposite effect. Correlations revealed that Gomphocerinae relative abundance was positively correlated with grass cover and Melanoplinae relative abundance was correlated with forb cover. Because previous literature has indicated that Gomphocerinae prefer to eat grass and Melanoplinae prefer to eat forb, and because of the results of the correlations and factor analysis we performed, our data support the hypothesis that subfamily habitat distribution is mostly determined by feeding preferences. An identical study

that also analyzed the crop and/or gut contents of the grasshoppers sampled would be required to determine if ingestion of grass or forb by these grasshoppers was occurring to make stronger implications of how much diet contributes to grasshopper habitat partitioning. But our data show that grass and forb are more important in terms of figuring out what contributes to habitat partitioning than other functional groups (bare ground and litter).

Our data have recorded how the Acrididae population of the Beaver River Wildlife Management are assembled and emerge. Thirty nine species were identified from four different subfamilies. The most abundant during the sampling season were the Gomphocerinae and Melanoplinae, emerging as nymphs in mid-May and peaking in abundance as adults in June. Oedipodinae and Cyrtacanthacridinae either have life cycles that are asynchronous with Gomphocerinae and Melanoplinae and not active when sampling occurred or species in both subfamilies avoided being caught by sweep nets and were underrepresented in the samples taken. Because nymphs were wingless and in greater abundance in adults, they may be the preferred life stage for Northern Bobwhite to prey upon, indicating that the most prey-rich time for quail is mid- to late May.

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APPENDICES

Appendix A – Field Site

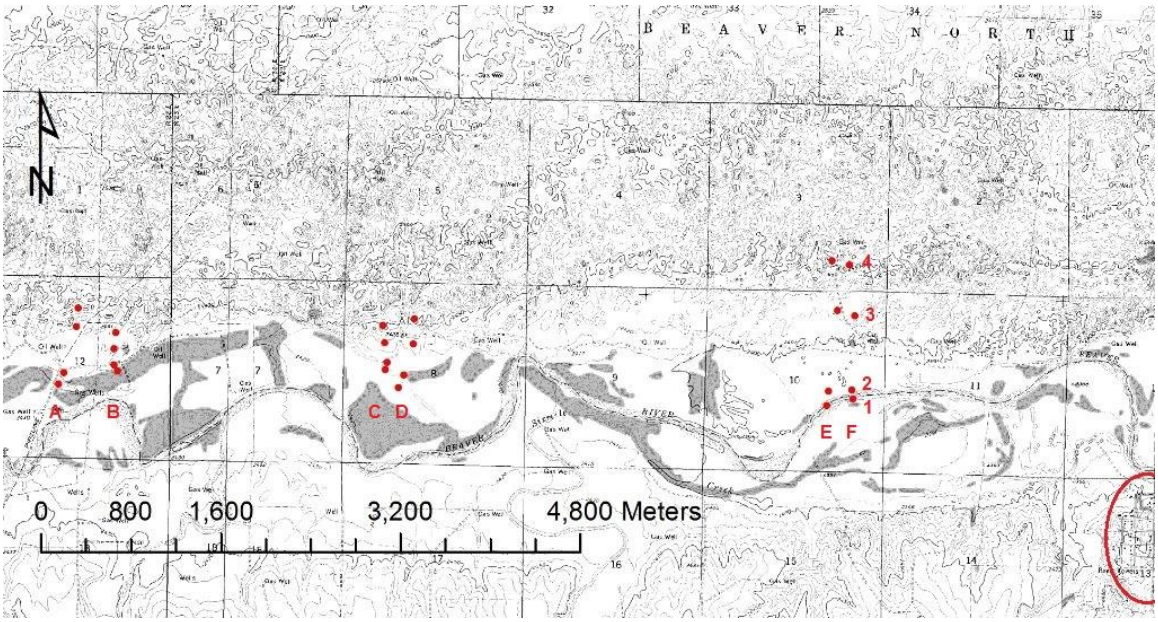

Figure 1: Beaver River Wildlife Management Area, Beaver County, OK (ArcGIS 10.1). Each red point on this map represents a centroid from which sampling efforts were performed. The six different transects are noted by letters (A-F) and the vegetation types are noted by number: 1 = riparian, 2 = lowland, 3 = ecotone, and 4 = upland. The town of Beaver, Oklahoma is circled in red for reference.

Appendix B –Tables

Gomphocerinae (19)
- *Acrolophitus hirtipes*
- *Ageneotettix deorum*
- *Amphitornus coloradus*
- *Aulocora elliotti**
- *Boopedon nubilum*
- *Cordillacris occipitalis*
- *Erittetix simplex*
- *Mermiria texana*
- *Mermiria bivittata*
- *Mermiria picta* †
- *Opeia obscura*
- *Orphulella pelidna*
- *Orphulella speciosa*
- *Paropomala wyomingensis*
- *Phlibostroma quadrimaculata*
- *Pseudopomala brachyptera**
- *Psoloessa deliculata* †
- *Psoloessa texana*
- *Syrbula admirabilis*

Melanoplinae (16)
- *Aeoloplides turnbulli*
- *Hesperotettix speciosus*
- *Hesperotettix viridis*
- *Melanoplus angustipennis*
- *Melanoplus bivittatus* †
- *Melanoplus bowditchi*
- *Melanoplus confusus*
- *Melanoplus differentialis*
- *Melanoplus femurrubrum* †
- *Melanoplus foedus*
- *Melanoplus gladstoni*
- *Melanoplus lakinus*
- *Melanoplus occidentalis*
- *Melanoplus packerdii**
- *Melanoplus sanguinipes* †
- *Phoetaliotes nebrascensis*

Oedipodinae (12)
- *Arphia conspersa*
- *Arphia simplex**
- *Circotettix rabula**
- *Chortophaga viridifasciata**
- *Hadrotettix trifasciatus*
- *Hippopedon capito**
- *Pardolophora sausseuri*
- *Psinidia fenestralis**
- *Spharagemon bolli**
- *Spharagemon cristatum*
- *Trachyrhachys kiowa*
- *Trimerotropis pallidipennis*

BAMN only *
Sweep net only †
Both methods

Table 1: All species of grasshopper (Orthoptera: Acrididae) caught using both sampling methods during the summers of 2012 and 2013 in the Beaver River Wildlife Management Area, Beaver County, Oklahoma. Species names followed by * were caught only in BAMN. Species names followed by † were caught only in sweep nets. Species names followed by no symbol were observed in both. The subfamily Cyrtacanthacridinae is omitted from this table because only one species was observed: *Schistocerca lineata*. Both sampling methods caught individuals of this species.

	2012		2013	
	C_S	**C_N**	C_S	**C_N**
Riparian	0.732	**0.566**	0.809	**0.671**
Lowland	0.739	**0.695**	0.704	**0.825**
Ecotone	0.690	**0.652**	0.757	**0.704**
Upland	0.769	**0.905**	0.581	**0.696**

Table 2: Sørenson's coefficients of similarity calculated between sweep net samples and BAMN sampling from 2012 and 2013. Sørenson's coefficient of similarity (C_S) is the similarity between species richness detected by sweep nets and BAMN sampling. Modified Sørenson's coefficient of similarity (C_N) is the similarity between abundance estimated by sweep nets and BAMN sampling. Values are unit-less and fall between 0 and 1. Values approaching 1 indicate increased similarity between the sampling methods in detecting richness or abundance.

Year	*d*		Dominating species
	Sweep Nets	BAMN	
2012	0.331	0.212	*Melanoplus bowditchi*
2013	0.180	0.145	*Ageneotettix deorum*
2012 & 2013	0.221	0.164	*Melanoplus bowditchi*

Table 3: Berger-Parker dominance indices for sweep net sampling and BAMN sampling in 2012 and 2013. Values are unit-less and fall between 0 and 1. Values approaching 1 indicate greater dominance by a species in question.

Gomphocerinae (17)

- *Acrolophitus hirtipes*
- *Ageneotettix deorum*
- *Amphitornus coloradus*
- *Boopedon nubilum*
- *Cordillacris occipitalis*
- *Erittetix simplex*
- *Mermiria texana*
- *Mermiria bivittata*
- *Mermiria picta*
- *Opeia obscura*
- *Orphulella pelidna*
- *Orphulella speciosa*
- *Paropomala wyomingensis*
- *Phlibostroma quadrimaculata*
- *Psoloessa deliculata*
- *Psoloessa texana*
- *Syrbula admirabilis*

Melanoplinae (15)

- *Aeoloplides turnbulli*
- *Hesperotettix speciosus*
- *Hesperotettix viridis*
- *Melanoplus angustipennis*
- *Melanoplus bivittatus*
- *Melanoplus bowditchi*
- *Melanoplus confusus*
- *Melanoplus differentialis*
- *Melanoplus femurrubrum*
- *Melanoplus foedus*
- *Melanoplus gladstoni*
- *Melanoplus lakinus*
- *Melanoplus occidentalis*
- *Melanoplus sanguinipes*
- *Phoetaliotes nebrascensis*

Oedipodinae (6)

- *Arphia conspersa*
- *Hadrotettix trifasciatus*
- *Pardolophora sausseuri*
- *Spharagemon cristatum*
- *Trachyrhachys kiowa*
- *Trimerotropis pallidipennis*

Table 4: All species of grasshopper (Orthoptera: Acrididae) caught using sweep net sampling during the summers of 2012 and 2013 in the Beaver River Wildlife Management Area, Beaver County, Oklahoma. The subfamily Cyrtacanthacridinae is omitted from this table because only one species was observed: *Schistocerca lineata*.

Year	*d*	Dominating species
2012	0.331	*Melanoplus bowditchi*
2013	0.180	*Ageneotettix deorum*
2012 & 2013	0.221	*Melanoplus bowditchi*

Table 5: Berger-Parker dominance indices for sweep net sampling in 2012 and 2013. Values are unit-less and fall between 0 and 1. Values approaching 1 indicate greater dominance by a species in question.

Riparian, 2012 (n = 127)	%	Lowland, 2012 (n = 201)	%
*Paropomala wyomingensis**	31.5	*Paropomala wyomingensis**	30.3
*Ageneotettix deorum**	23.6	*Ageneotettix deorum**	21.9
*Amphitornus coloradus**	7.9	*Melanoplus* spp. ♀♀ Δ	12.9
Melanoplus angustipennis Δ	7.9	*Amphitornus coloradus**	8.5
*Mermiria bivittata**	6.3	*Melanoplus angustipennis* Δ	6.5
Ecotone, 2012 (n = 676)	**%**	**Upland, 2012 (n = 444)**	**%**
Melanoplus spp. ♀♀ Δ	41.9	*Melanoplus* spp. ♀♀ Δ	54.5
Melanoplus bowditchi Δ	29.8	*Melanoplus bowditchi* Δ	16.9
Melanoplus angustipennis Δ	9.3	*Melanoplus angustipennis* Δ	12.2
*Paropomala wyomingensis**	5.9	*Spharagemon cristatum*	6.1
*Ageneotettix deorum**	3.7	*Mermiria bivittata**	3.2

* = Gomphocerinae, Δ = Melanoplinae, unmarked = Oedipodinae

Table 6: The relative abundance of the five most abundant grasshopper taxa observed in the Beaver River WMA in each vegetation type during all five sampling events in 2012.

Riparian, 2013 (n = 306)	%	Lowland, 2013 (n = 501)	%
*Paropomala wyomingensis**	23.2	*Melanoplus* spp. ♀♀ Δ	20.2
*Ageneotettix deorum**	22.5	*Ageneotettix deorum**	17.4
Melanoplus spp. ♀♀ Δ	13.1	*Paropomala wyomingensis**	12.2
Melanoplus angustipennis Δ	7.5	*Melanoplus angustipennis* Δ	9.8
*Mermiria bivittata**	6.2	*Mermiria bivittata**	9
Ecotone, 2013 (n = 436)	**%**	**Upland, 2013 (n = 250)**	**%**
Melanoplus spp. ♀♀ Δ	35.7	*Melanoplus* spp. ♀♀ Δ	39.6
Melanoplus bowditchi Δ	16.7	*Melanoplus bowditchi* Δ	13.6
Melanoplus angustipennis Δ	9.7	*Melanoplus angustipennis* Δ	12.8
Spharagemon cristatum	6.5	*Ageneotettix deorum**	6.8
*Ageneotettix deorum**	6	*Spharagemon cristatum*	6

* = Gomphocerinae, Δ = Melanoplinae, unmarked = Oedipodinae

Table 7: The relative abundance of the five most abundant grasshopper taxa observed in the Beaver River WMA in each vegetation type during all seven sampling events in 2013.

Explanatory Variables	Factor 1		Factor 2
Bare ground cover	- 0.28985	*	0.08653
Litter cover	0.25313	**	0.13048
Forb cover	- 0.35233	*	0.17455
Grass cover	0.35153	**	- 0.32162
Other cover	0.11869		0.62984
Species richness	0.15873		0.57869

Table 8: The loadings of the factor analysis for the proportion of plant functional group cover versus Gomphocerinae relative abundance and Melanoplinae relative abundance. Factor loadings with asterisks indicate that those variables are interacting significantly with both Gomphocerinae and Melanoplinae relative abundance. The same number of asterisks indicates the variables that have been reduced to a linear commonality and are explaining similar components of variation in relative abundance.

Appendix C - Figures

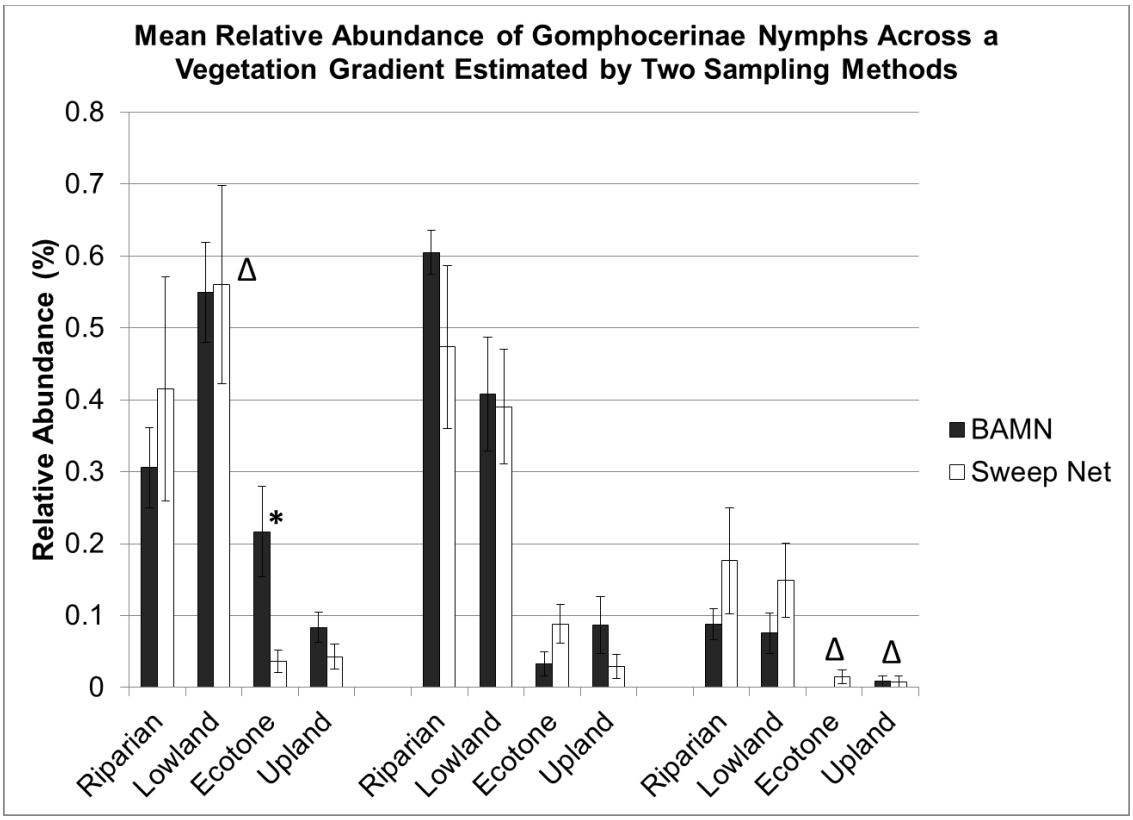

Figure 2: Comparisons between relative abundance estimates of Gomphocerinae nymphs taken using sweep net sampling and BAMN sampling across the vegetation gradient on the Beaver River Wildlife Management Area, Beaver County, Oklahoma during three sampling events in 2012. Triangles indicate statistical comparisons with $p > 0.85$. Asterisks indicate statistical comparisons with $p < 0.05$.

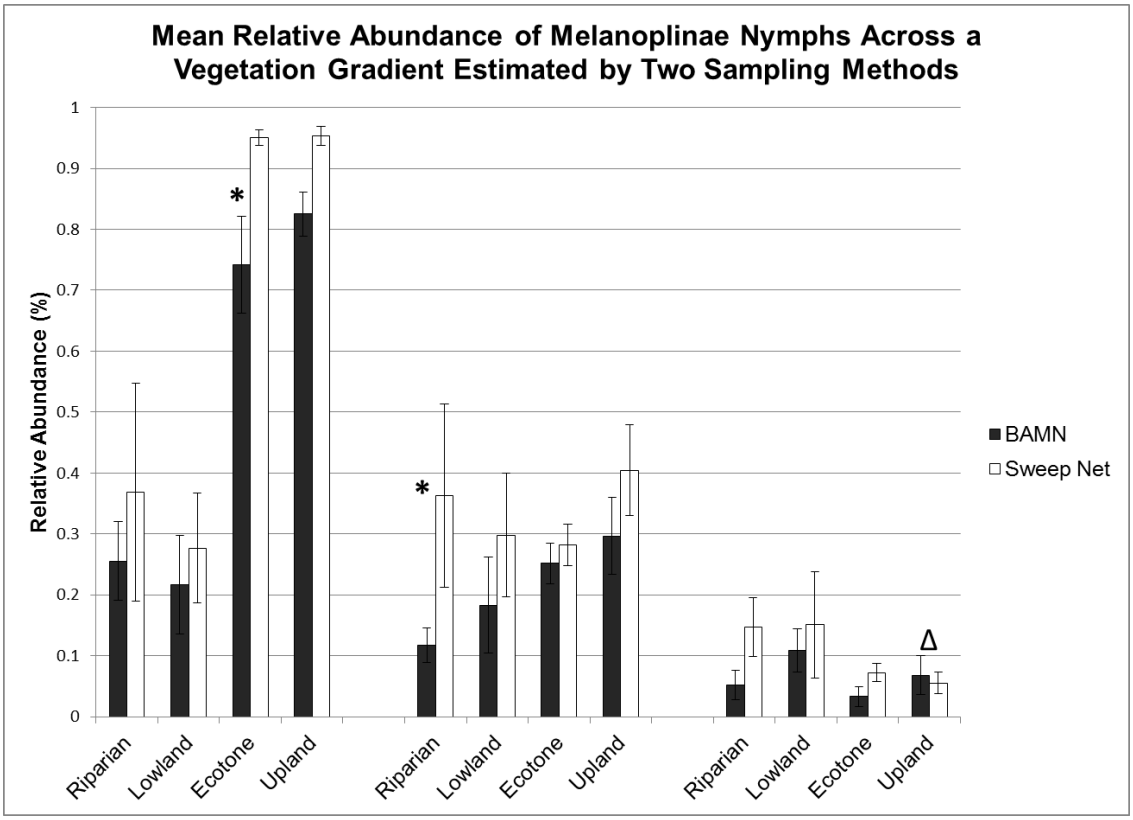

Figure 3: Comparisons between relative abundance estimates of Melanoplinae nymphs taken using sweep net sampling and BAMN sampling across the vegetation gradient on the Beaver River Wildlife Management Area, Beaver County, Oklahoma during three sampling events in 2012. Triangles indicate statistical comparisons with $p > 0.85$. Asterisks indicate statistical comparisons with $p < 0.05$.

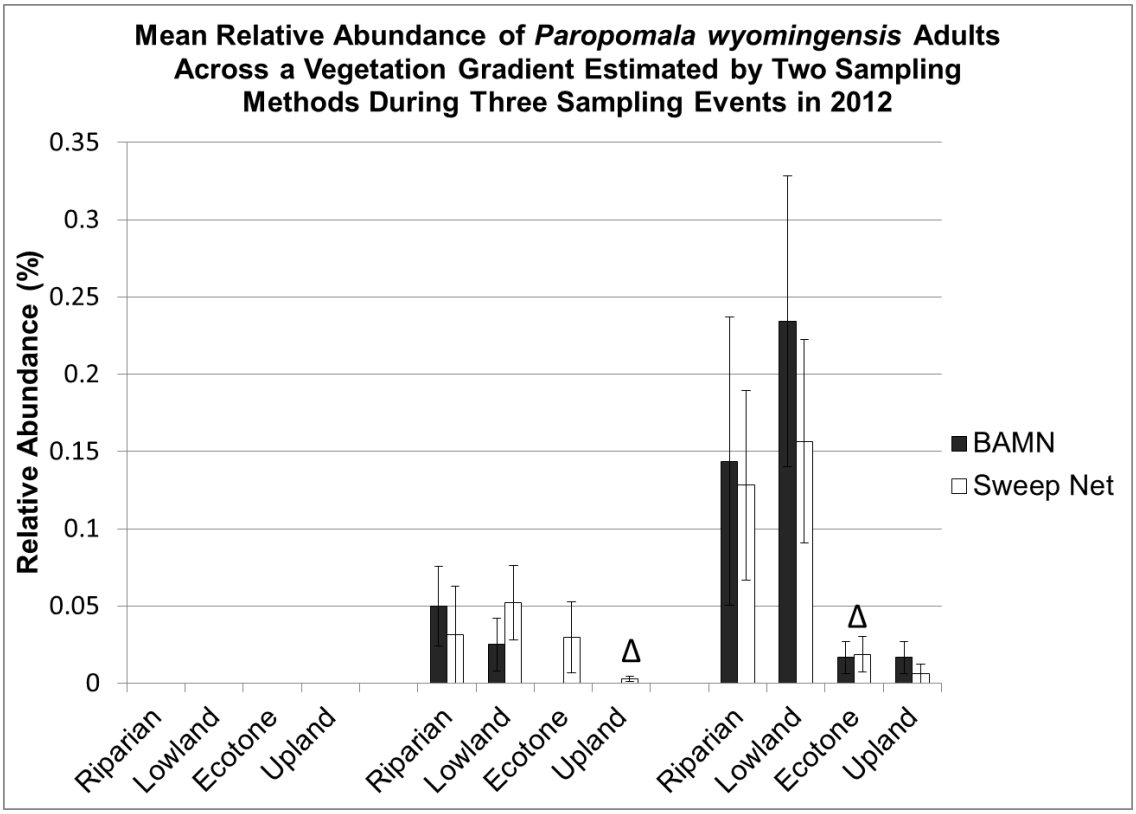

Figure 4: Comparisons between relative abundance estimates of *Paropomala wyomingensis* adults taken using sweep net sampling and BAMN sampling across the vegetation gradient on the Beaver River Wildlife Management Area, Beaver County, Oklahoma during three sampling events in 2012. Triangles indicate statistical comparisons with $p > 0.85$. Asterisks indicate statistical comparisons with $p < 0.05$.

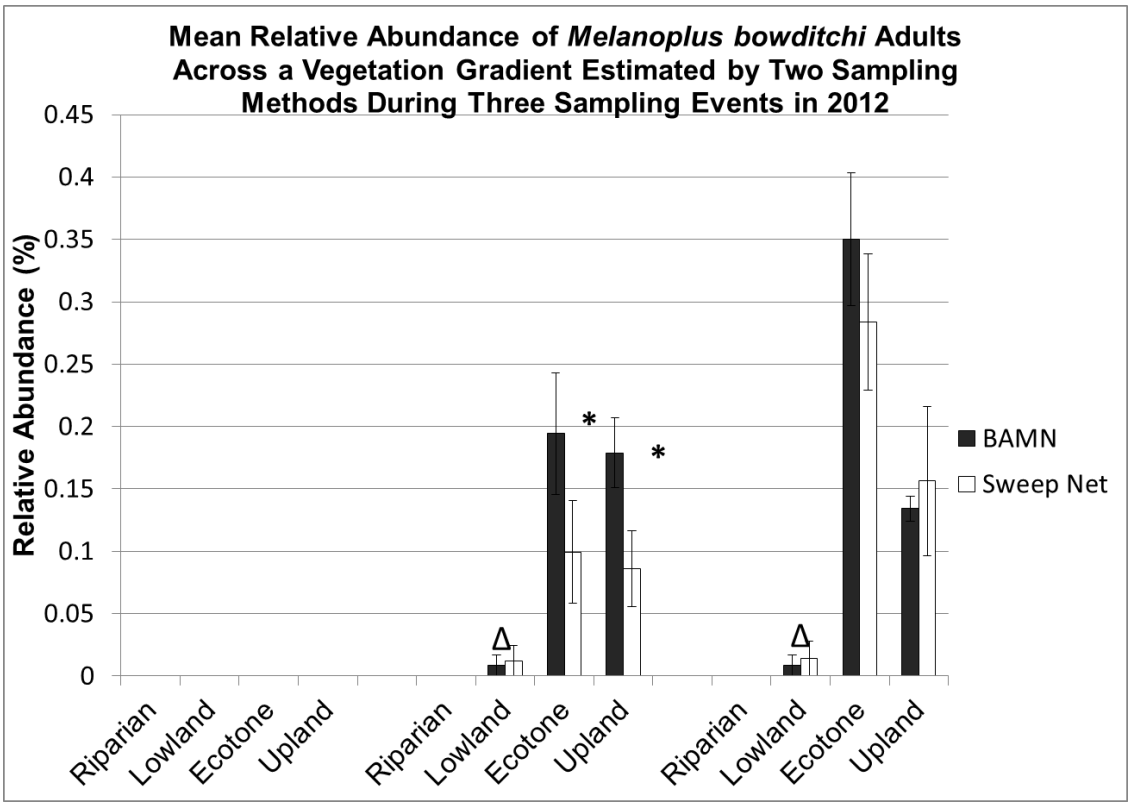

Figure 5: Comparisons between relative abundance estimates of *Melanoplus bowditchi* adults take using sweep net sampling and BAMN sampling across the vegetation gradient on the Beaver River Wildlife Management Area, Beaver County, Oklahoma during three sampling events in 2012. Triangles indicate statistical comparisons with $p > 0.85$. Asterisks indicate statistical comparisons with $p < 0.05$.

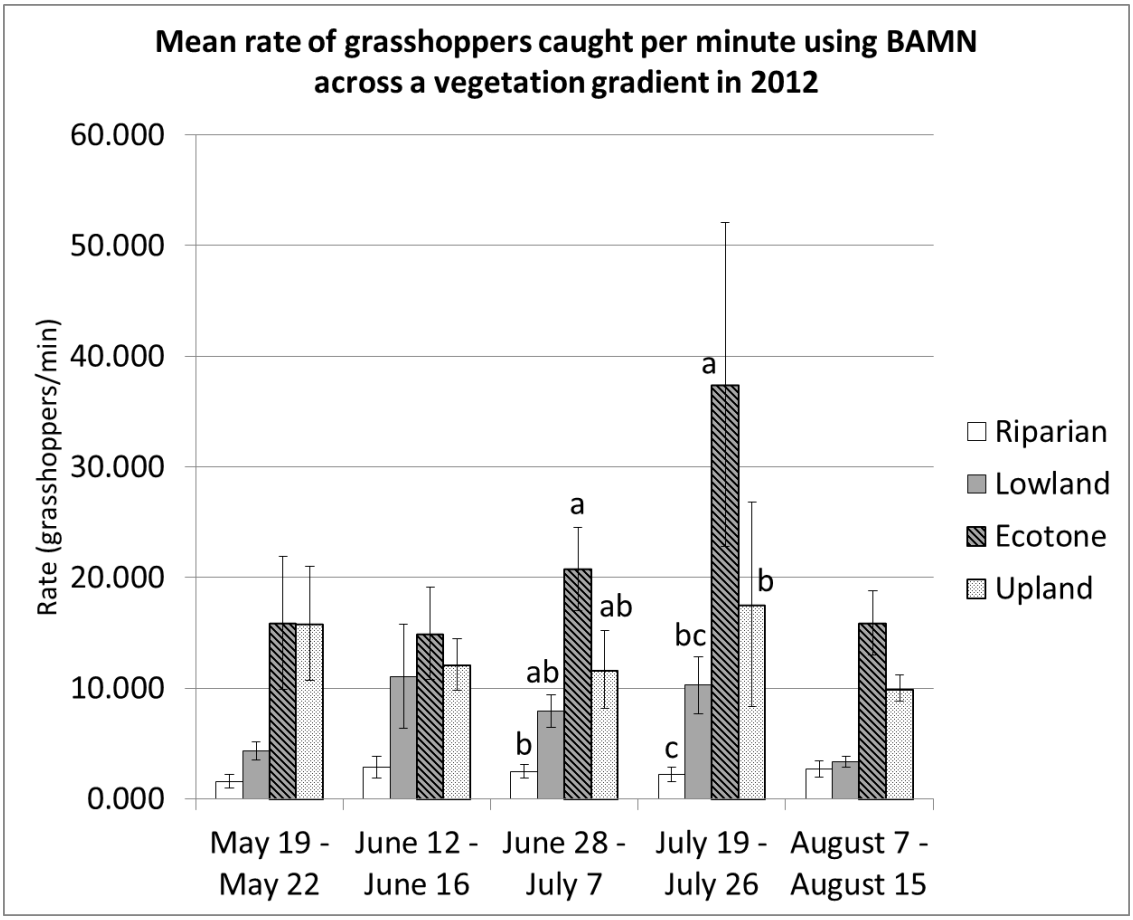

Figure 6: The mean rate of grasshoppers caught per minute as determined by BAMN sampling during five sampling events in 2012. Two means with the same letter within a sampling event are not significantly different ($p < 0.05$).

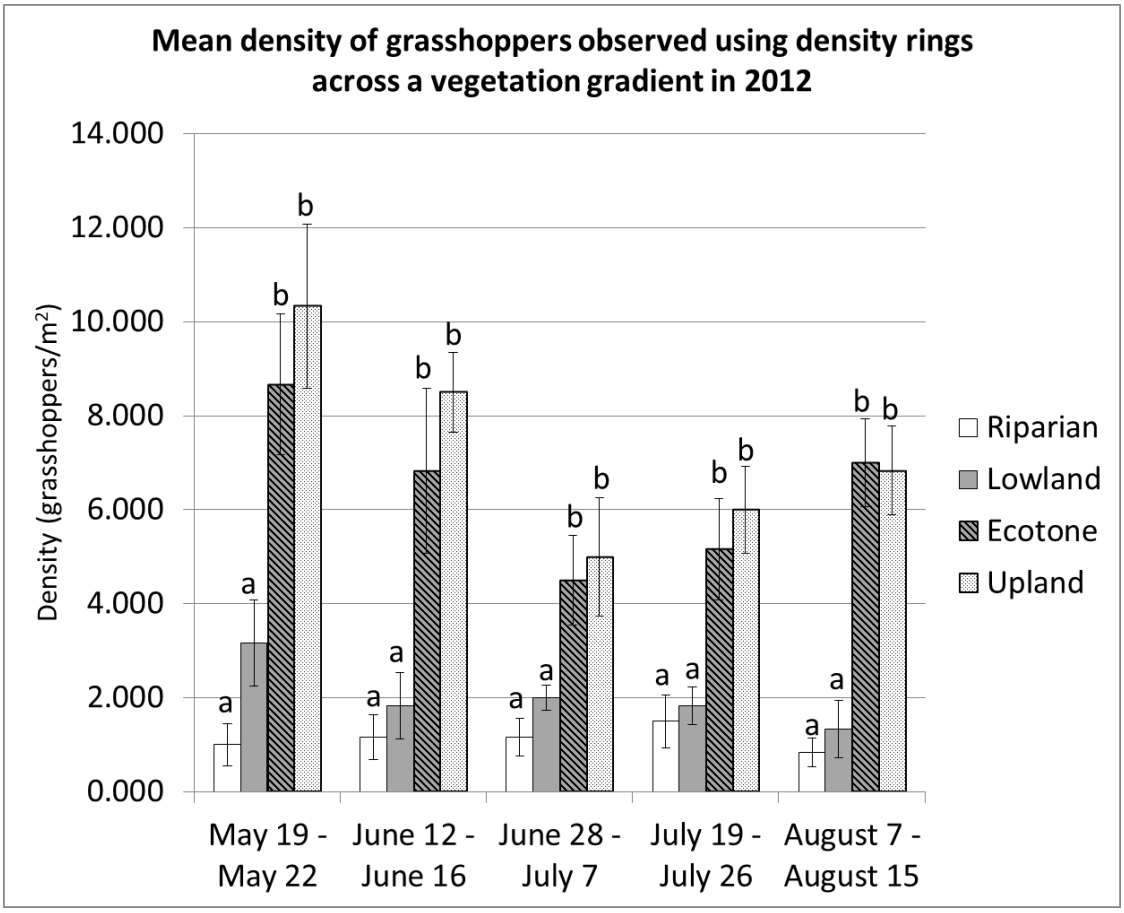

Figure 7: The densities of grasshoppers per m^2 as determined by density ring observations during five sampling events in 2012. Two means with the same letter within a sampling event are not significantly different ($p < 0.05$).

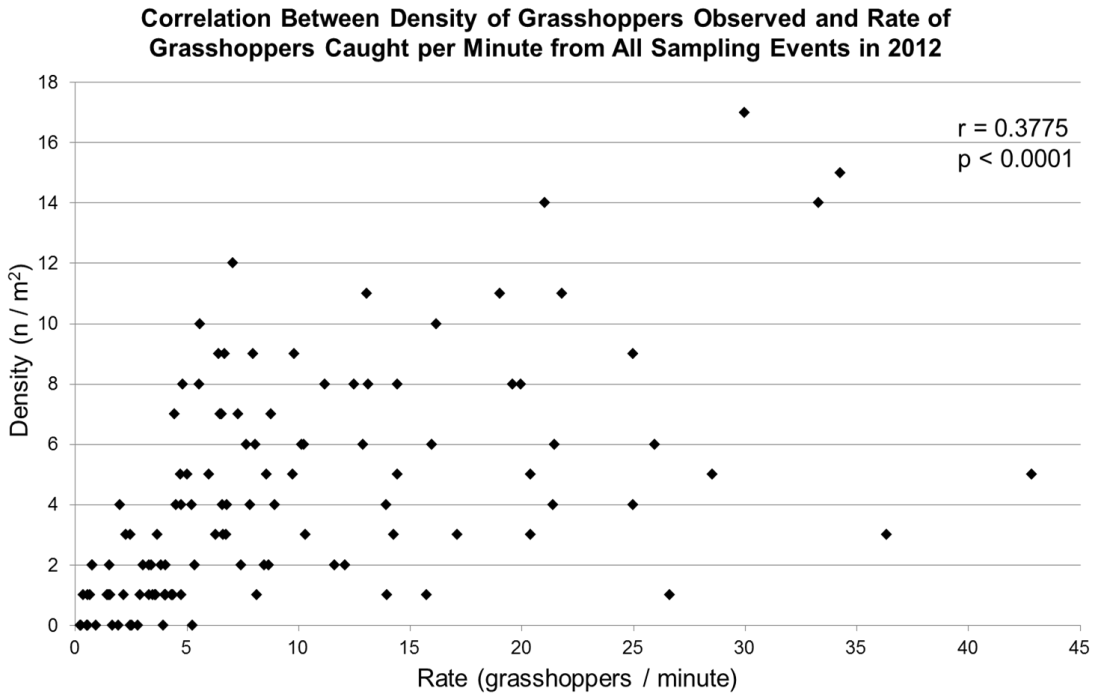

Figure 8: Correlation between the density of grasshoppers observed by density rings and the rate of grasshoppers caught per minute by BAMN sampling in 2012. There is a positive correlation between the density and rate ($r = 0.3775$, $p < 0.0001$). Three points with rates over 60 were removed from the figure, but remained in the analysis.

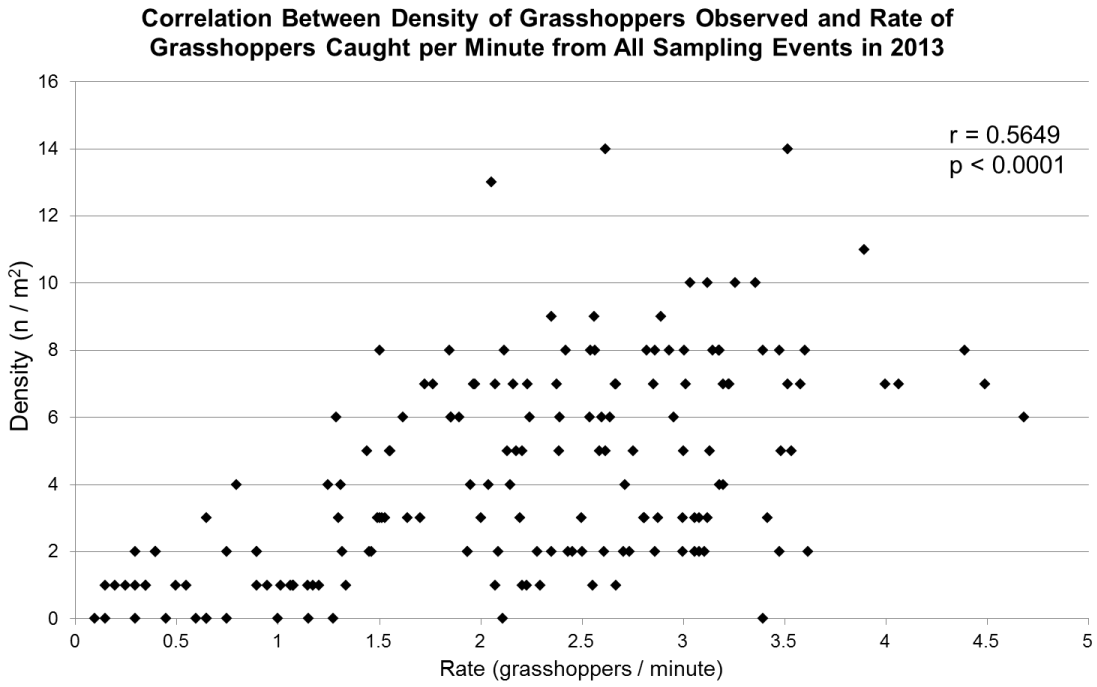

Figure 9: Correlation between the density of grasshoppers observed by density rings and the rate of grasshoppers caught per minute by BAMN sampling in 2013. There is a positive correlation between the density and rate ($r = 0.5649$, $p < 0.0001$).

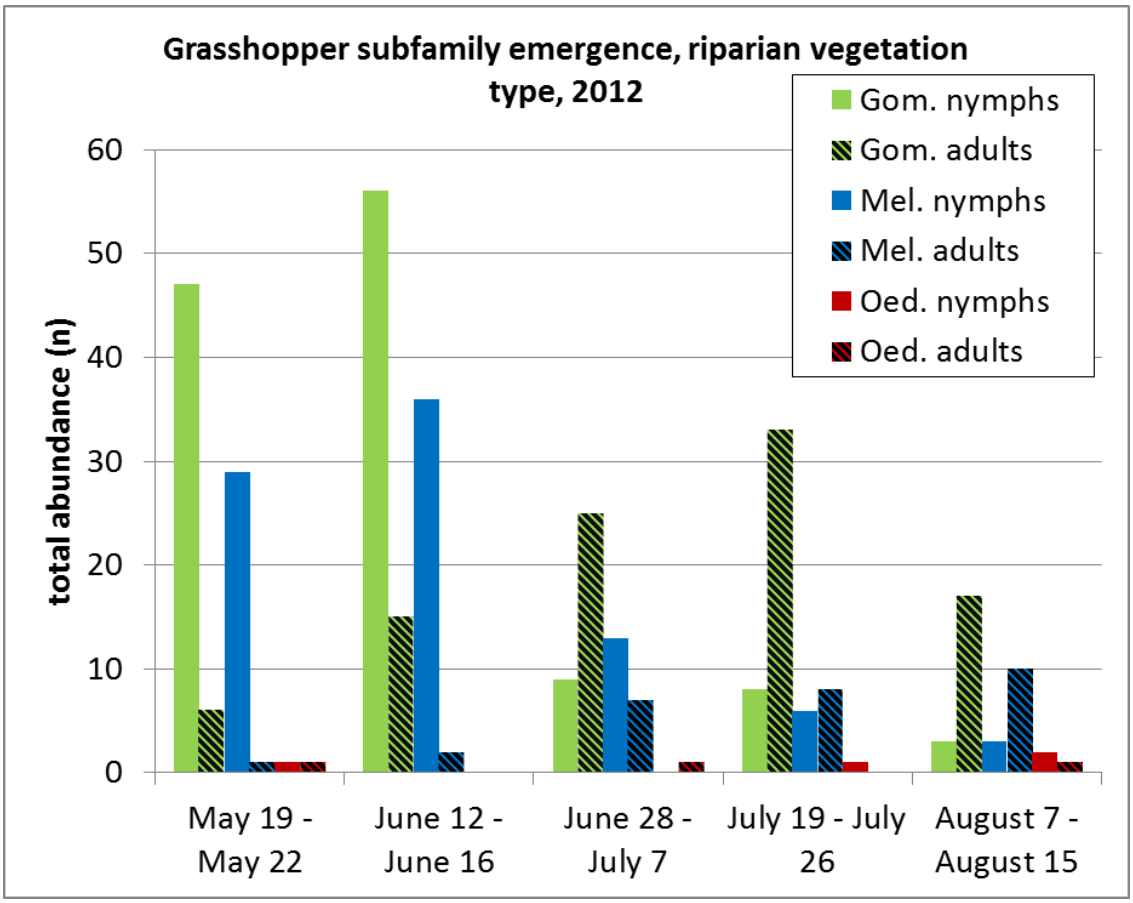

Figure 10: Grasshopper subfamily nymphal and adult emergence during the 2012 sampling season in the riparian vegetation type.

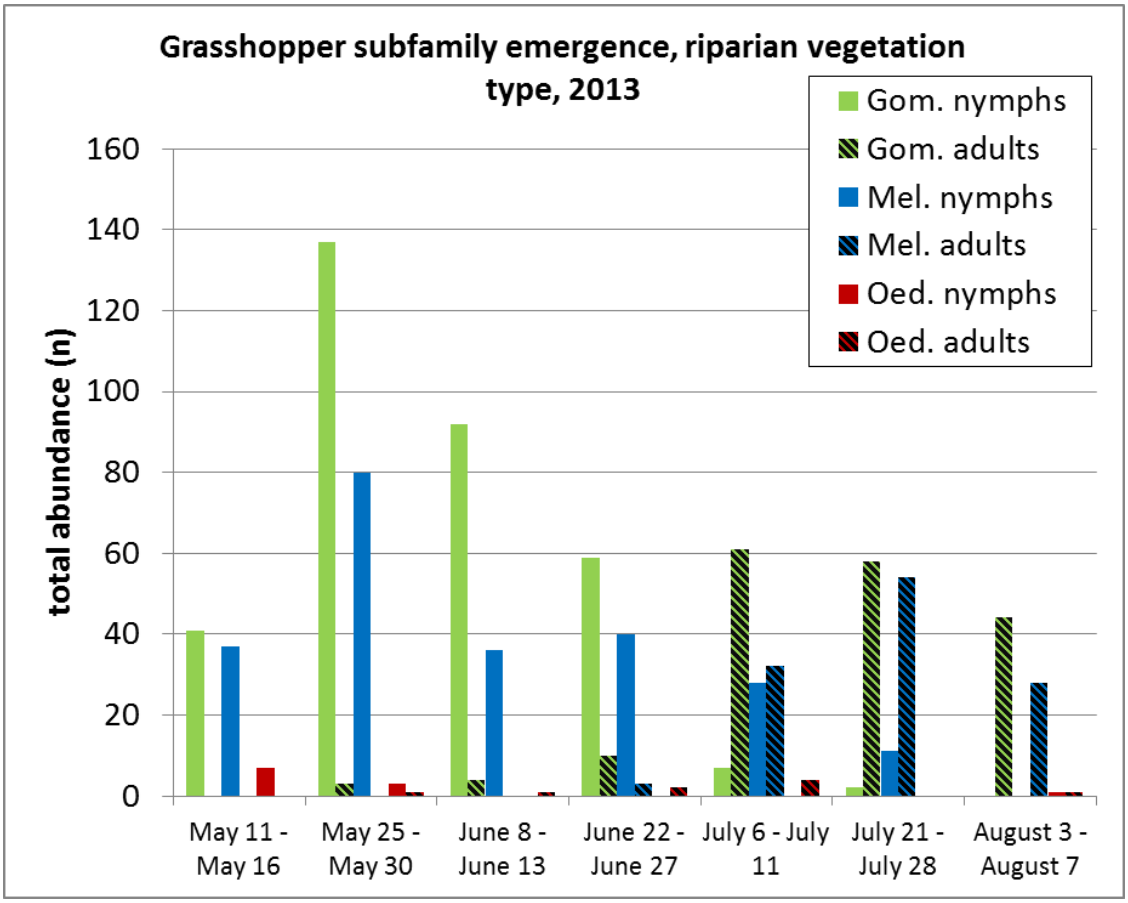

Figure 11: Grasshopper subfamily nymphal and adult emergence during the 2013 sampling season in the riparian vegetation type.

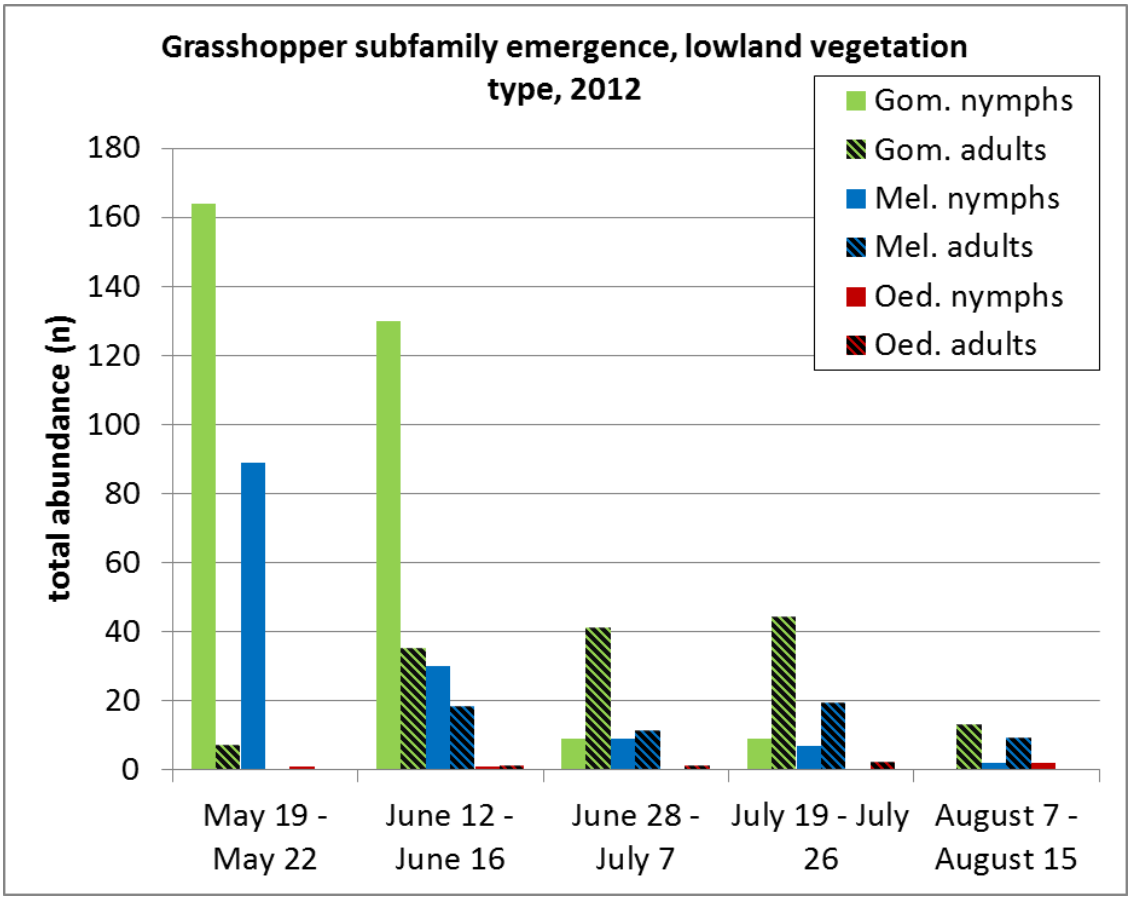

Figure 12: Grasshopper subfamily nymphal and adult emergence during the 2012 sampling season in the lowland vegetation type.

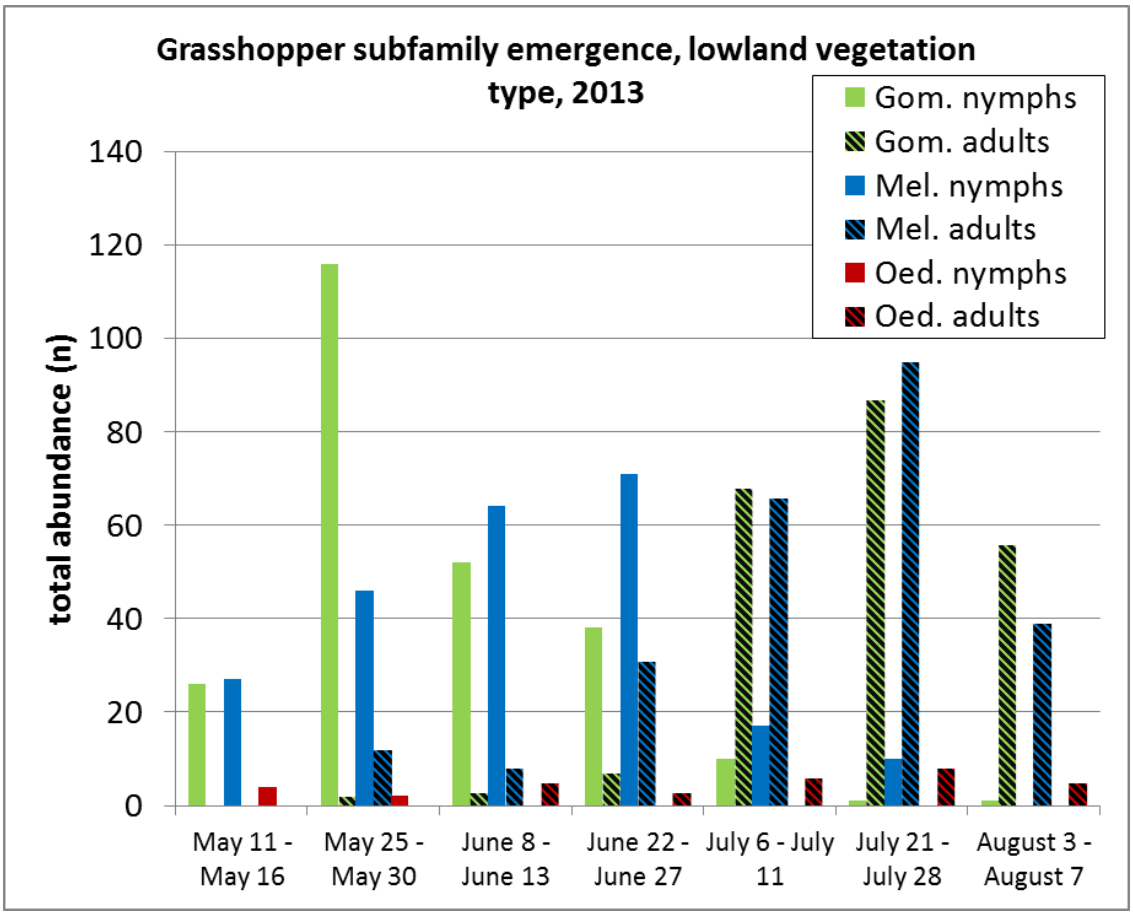

Figure 13: Grasshopper subfamily nymphal and adult emergence during the 2013 sampling season in the lowland vegetation type.

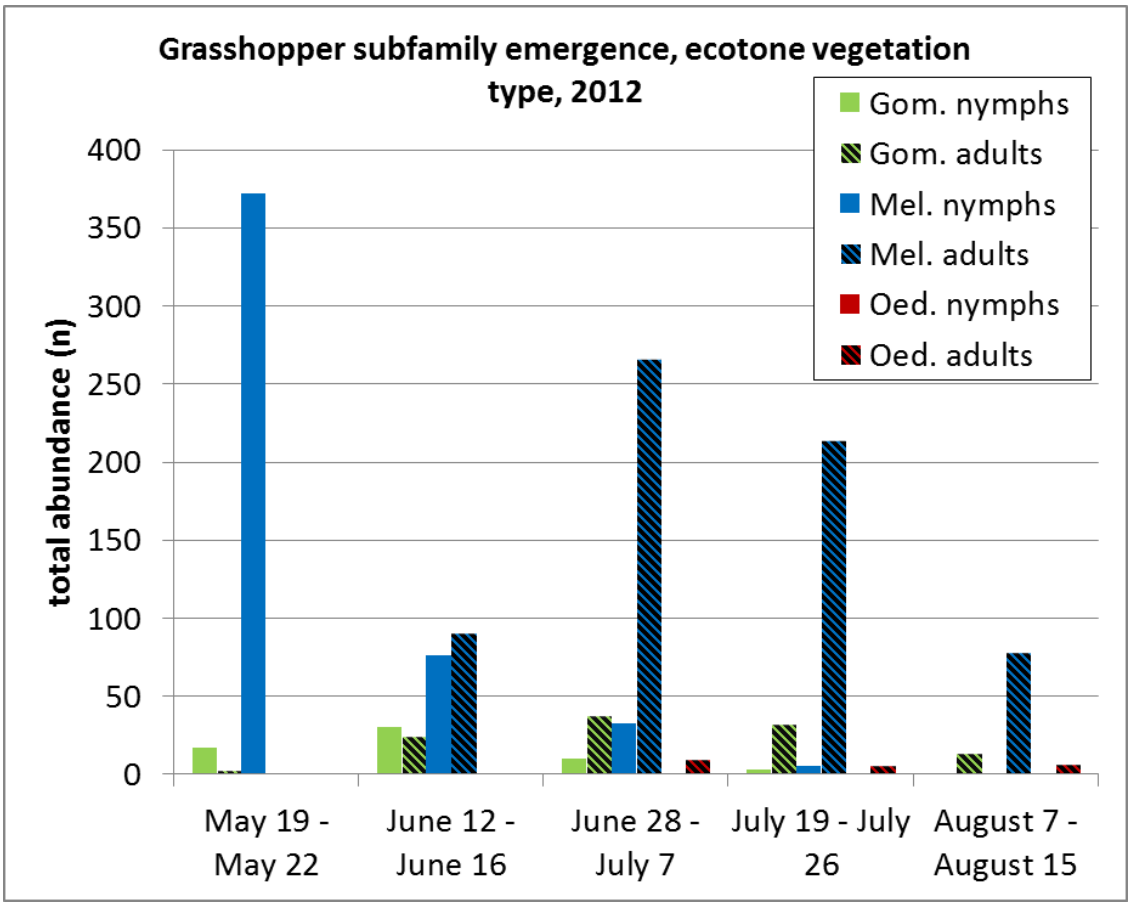

Figure 14: Grasshopper subfamily nymphal and adult emergence during the 2012 sampling season in the ecotone vegetation type.

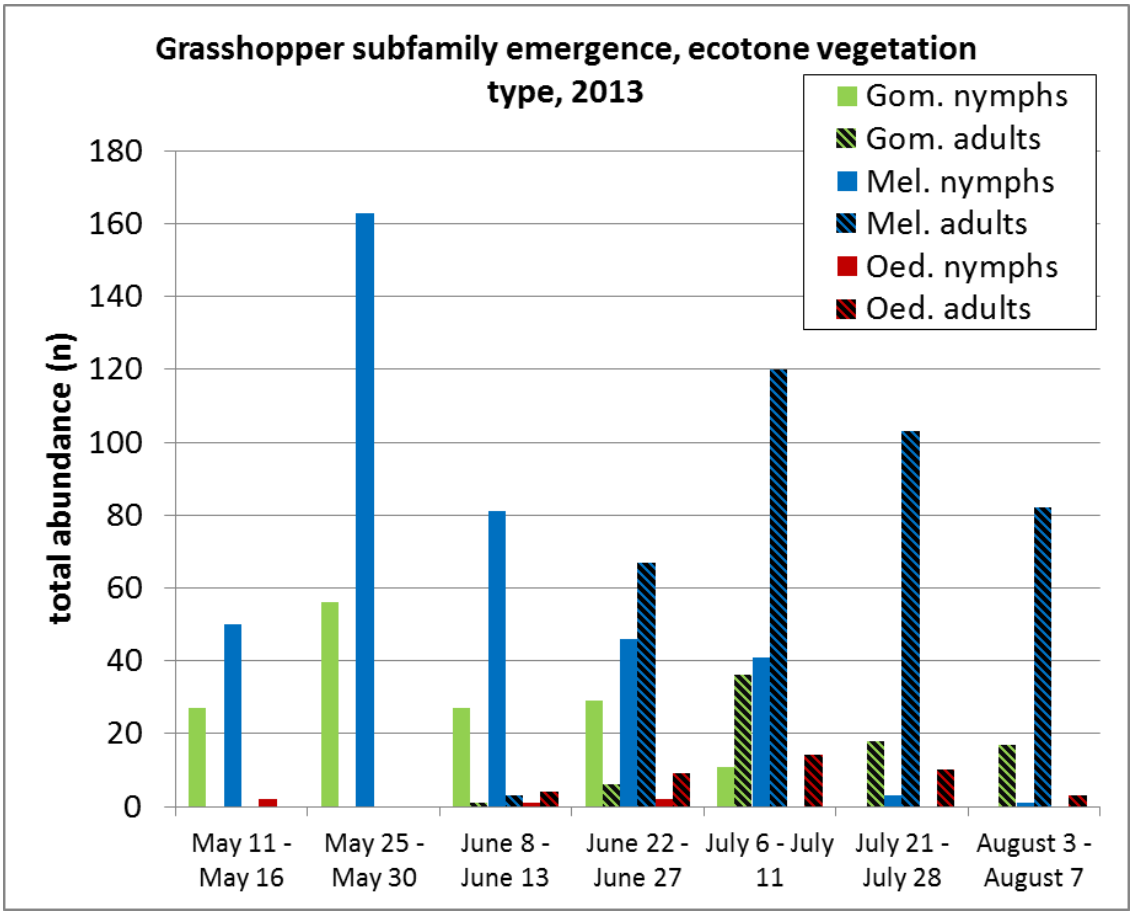

Figure 15: Grasshopper subfamily nymphal and adult emergence during the 2013 sampling season in the ecotone vegetation type.

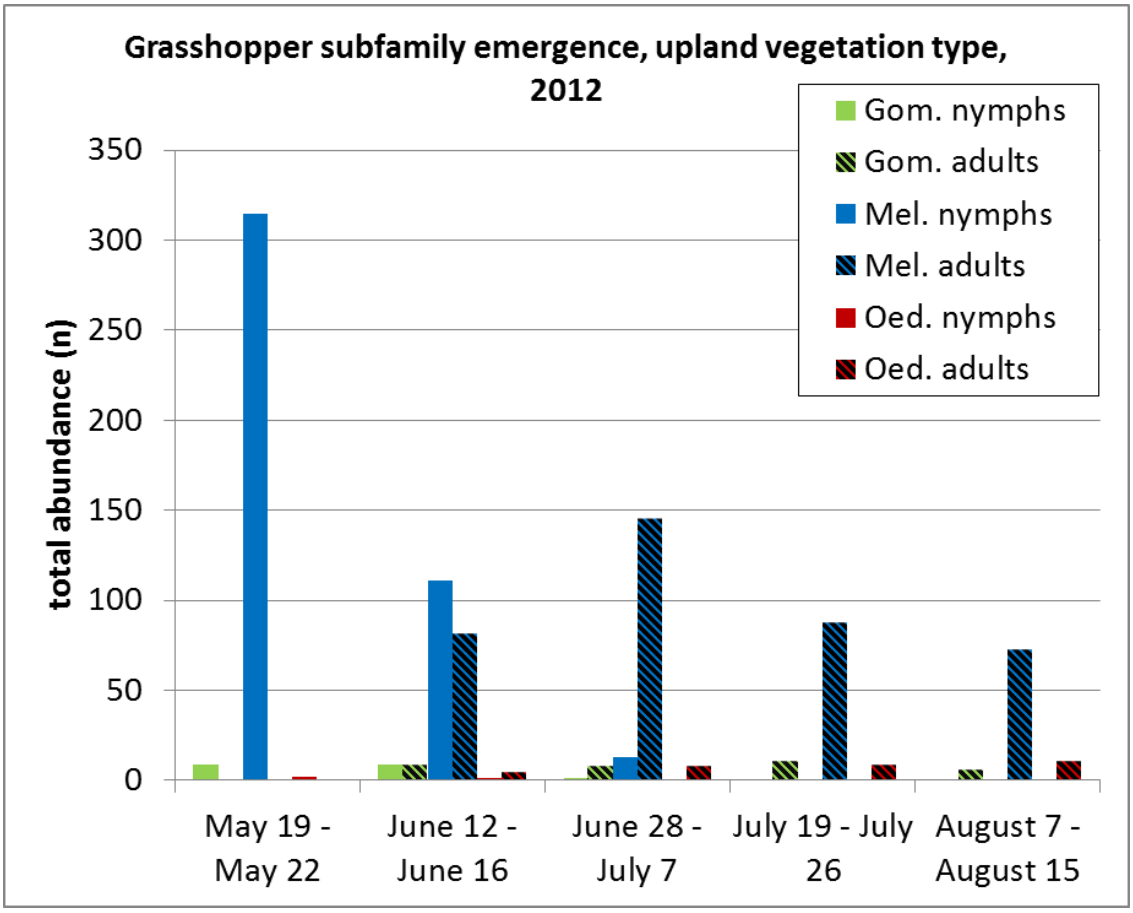

Figure 16: Grasshopper subfamily nymphal and adult emergence during the 2012 sampling season in the upland vegetation type.

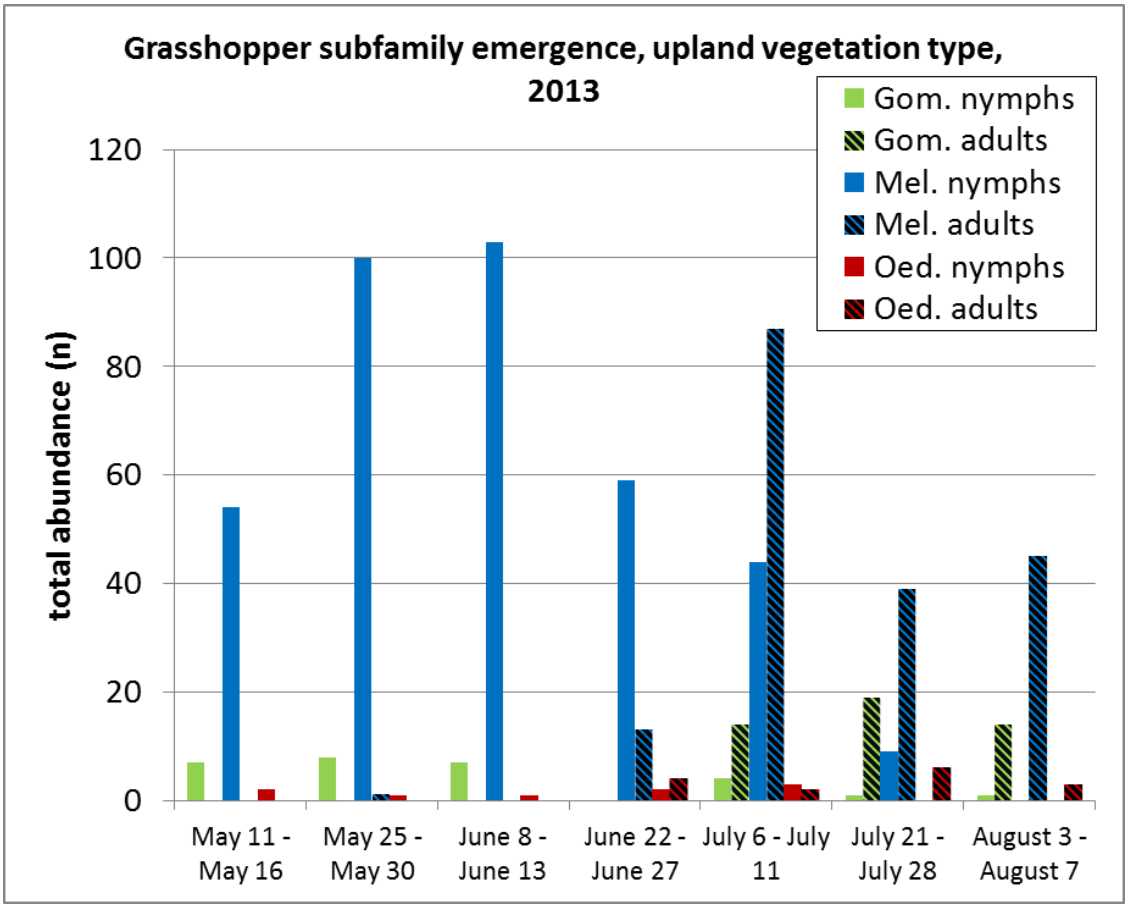

Figure 17: Grasshopper subfamily nymphal and adult emergence during the 2013 sampling season in the upland vegetation type.

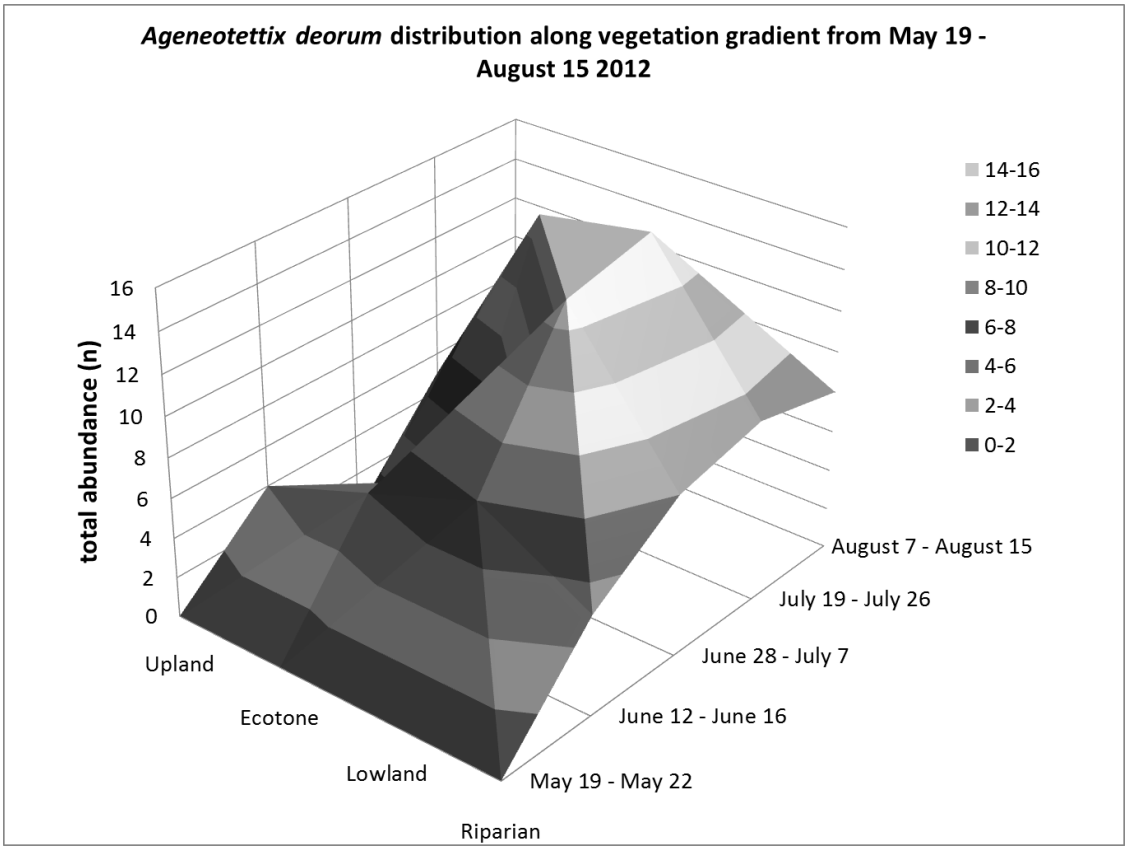

Figure 18: Total abundance and distribution along the vegetation gradient of *Ageneotettix deorum* during the 2012 sampling season.

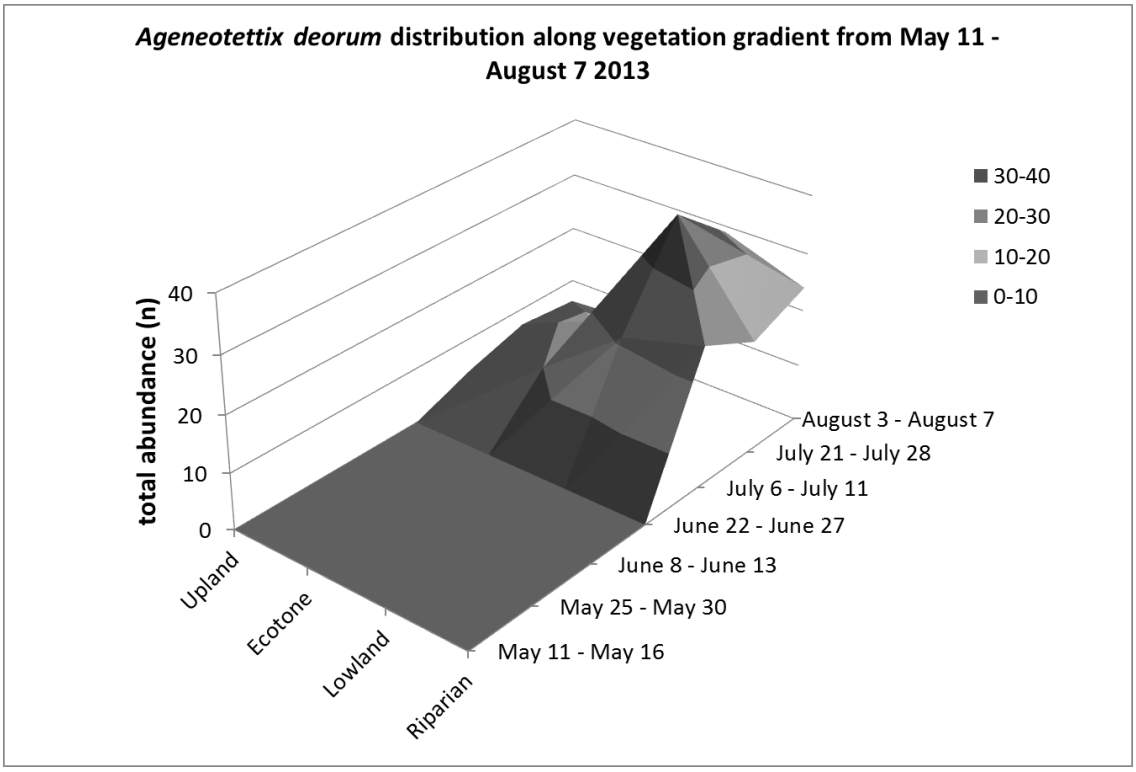

Figure 19: Total abundance and distribution along the vegetation gradient of *Ageneotettix deorum* during the 2013 sampling season.

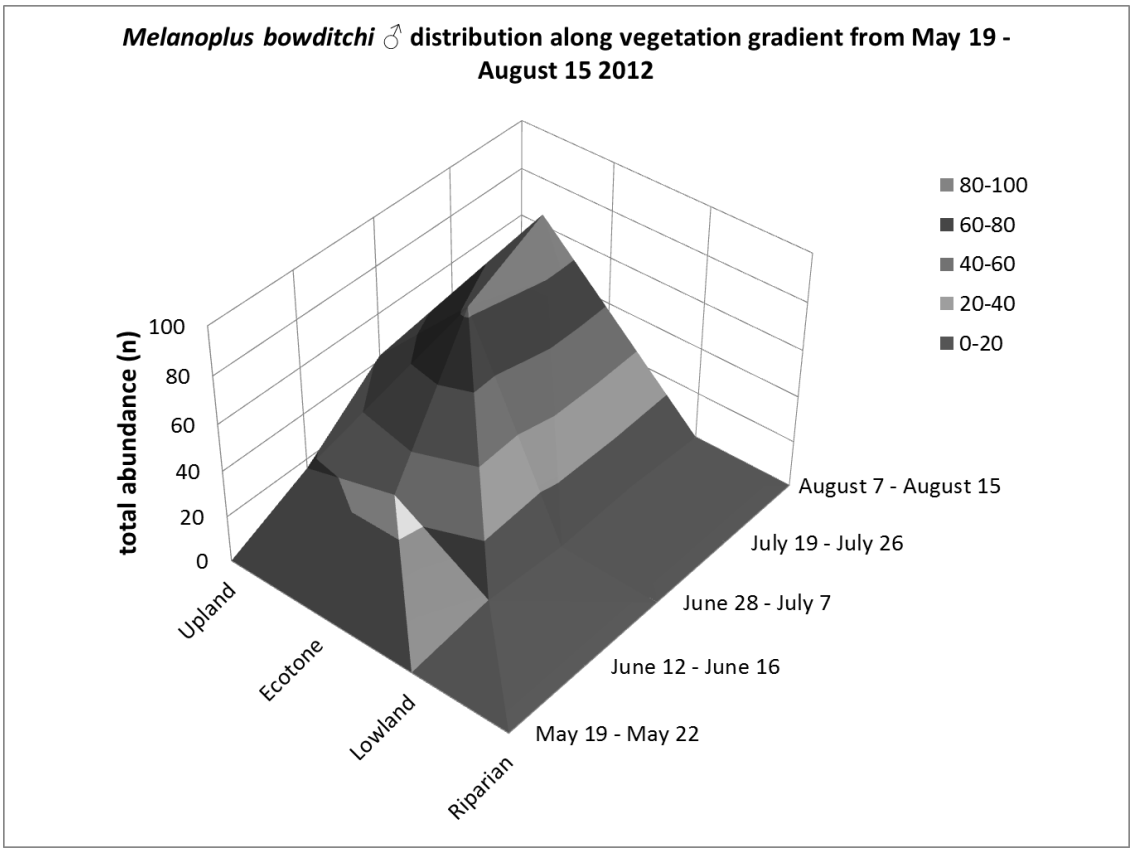

Figure 20: Total abundance and distribution along the vegetation gradient of *Melanoplus bowditchi* ♂during the 2012 sampling season.

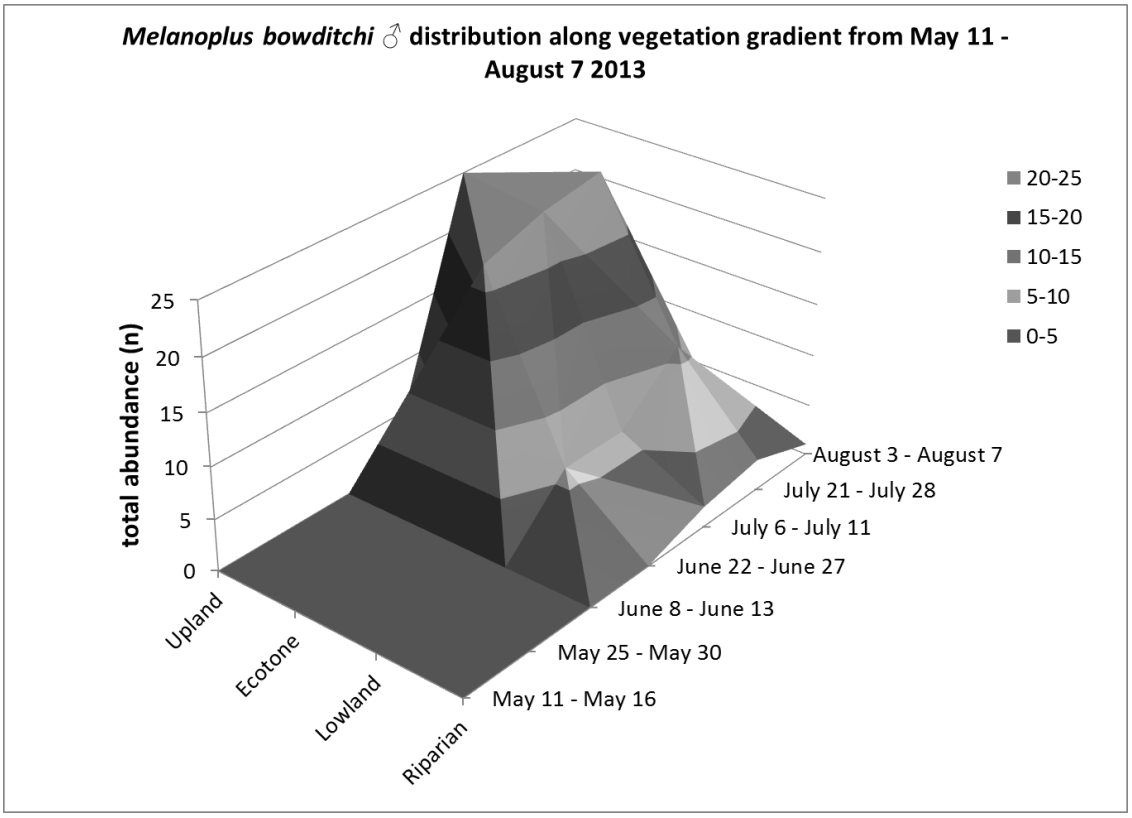

Figure 21: Total abundance and distribution along the vegetation gradient of *Melanoplus bowditchi* during the 2013 sampling season.

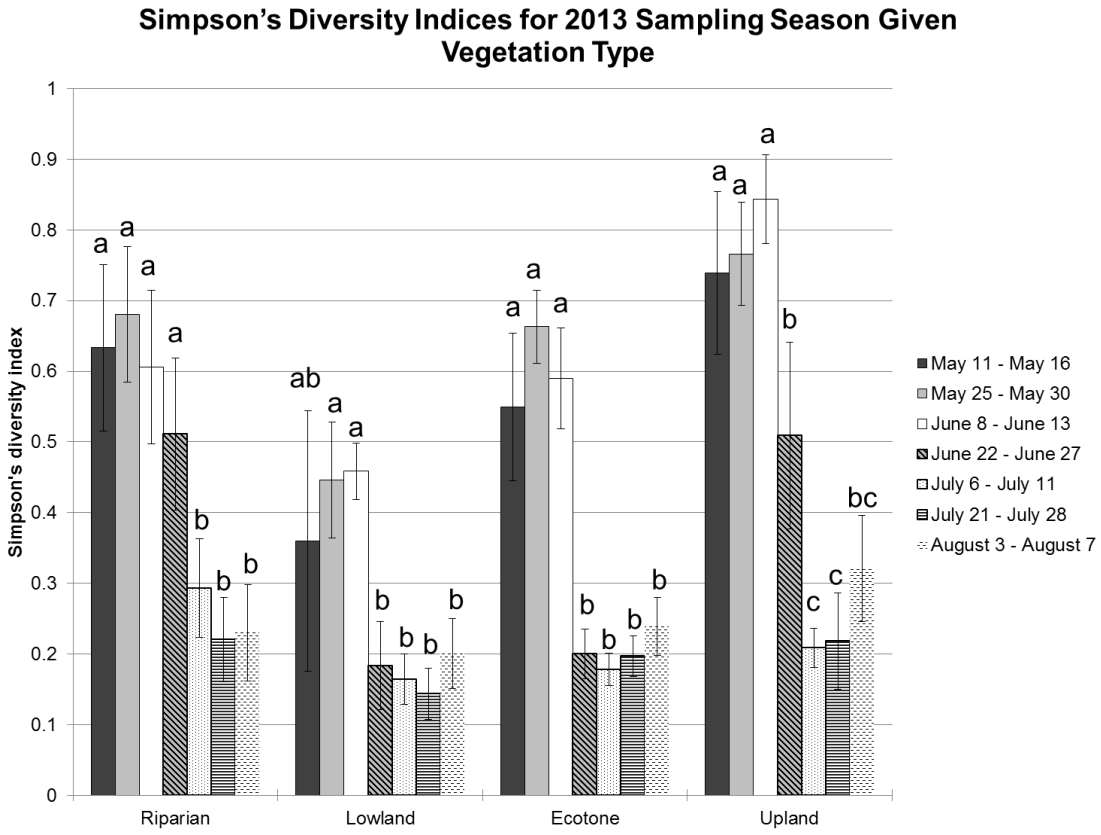

Figure 22: Simpson's diversity indices for each sampling event in 2013 given vegetation type. Simpson's diversity indices are unit-less values between 0 and 1. As the value approaches 1, the diversity decreases. Two means within the same vegetation type with the same letter are not significantly different using a protected pairwise t-test ($p < 0.05$).

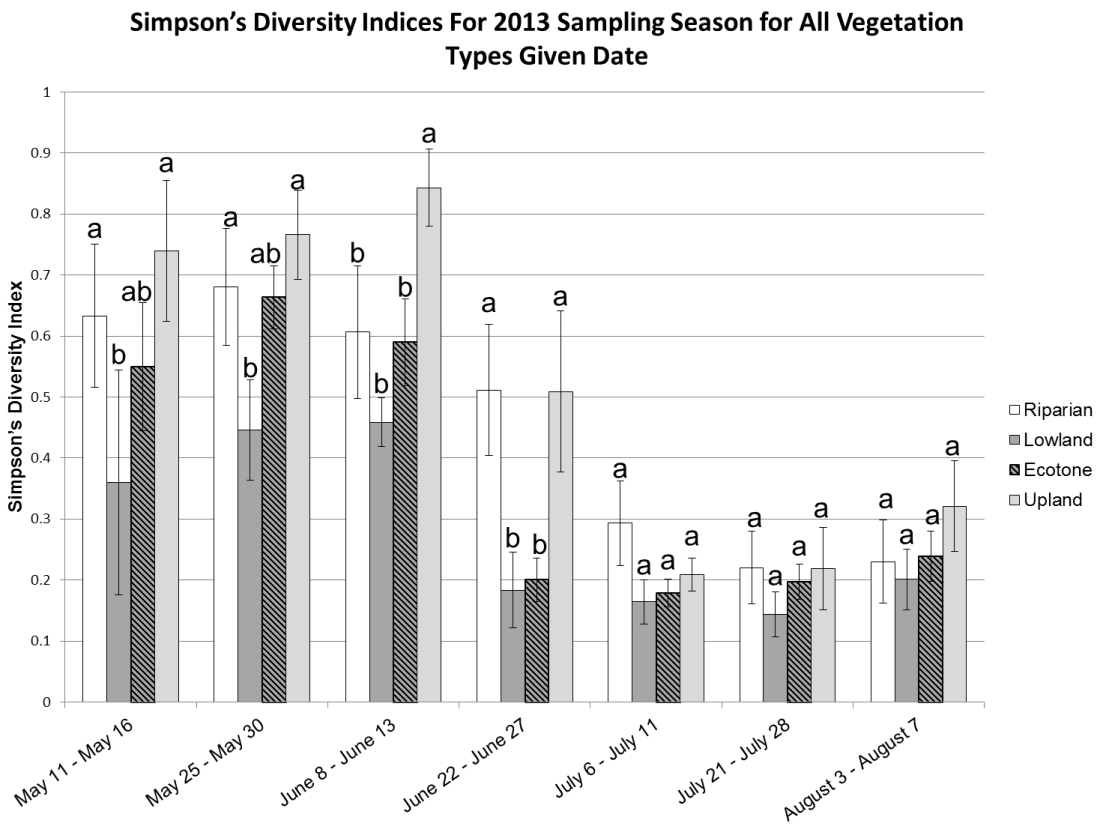

Figure 23: Simpson's diversity indices for each sampling event in 2013 given date. Simpson's diversity indices are unit-less values between 0 and 1. As the value approaches 1, the diversity decreases. Two means within the same vegetation type with the same letter are not significantly different using a protected pairwise t-test ($p < 0.05$).

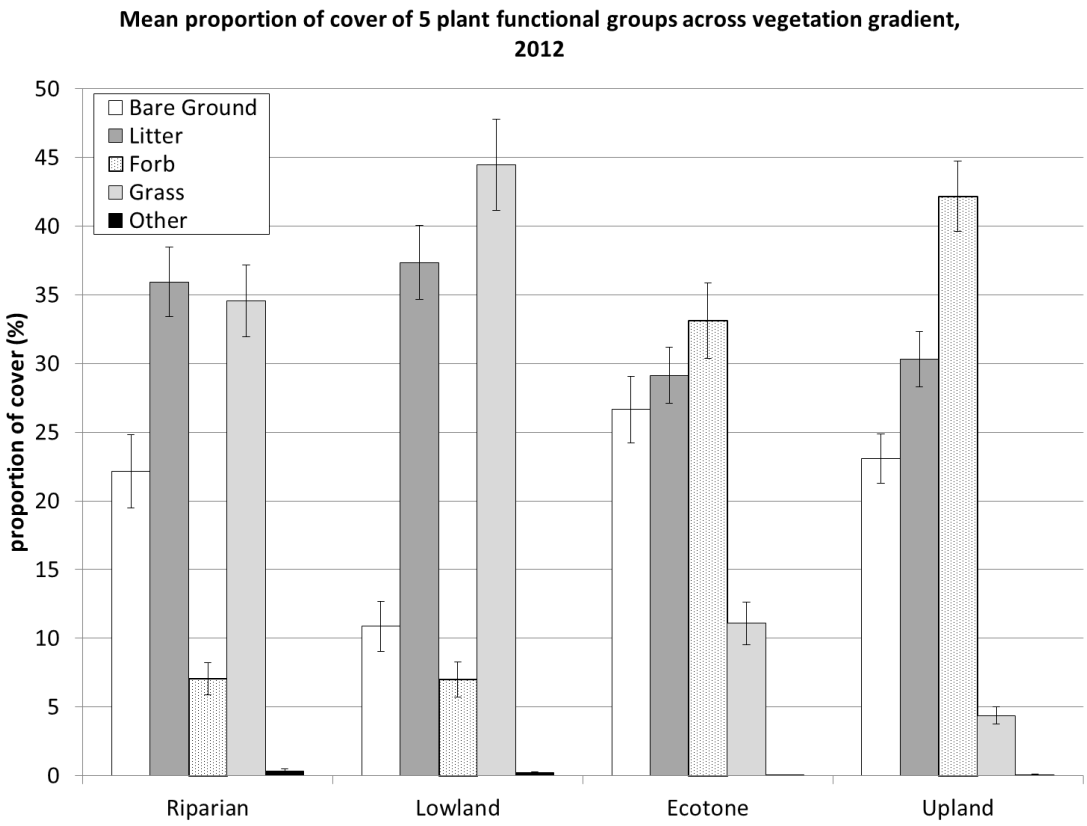

Figure 24: Mean proportion of cover of 5 functional groups in each vegetation type sampled during 2012.

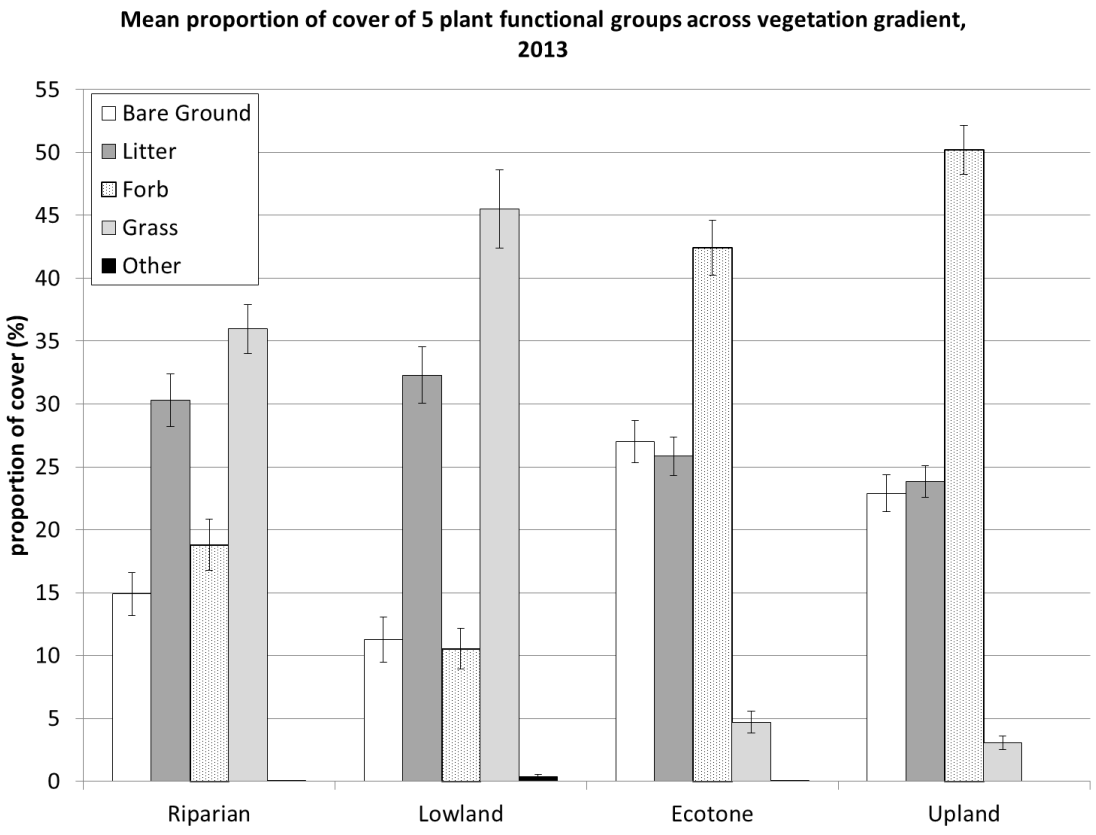

Figure 25: Mean proportion of cover of 5 functional groups in each vegetation type sampled during 2013.

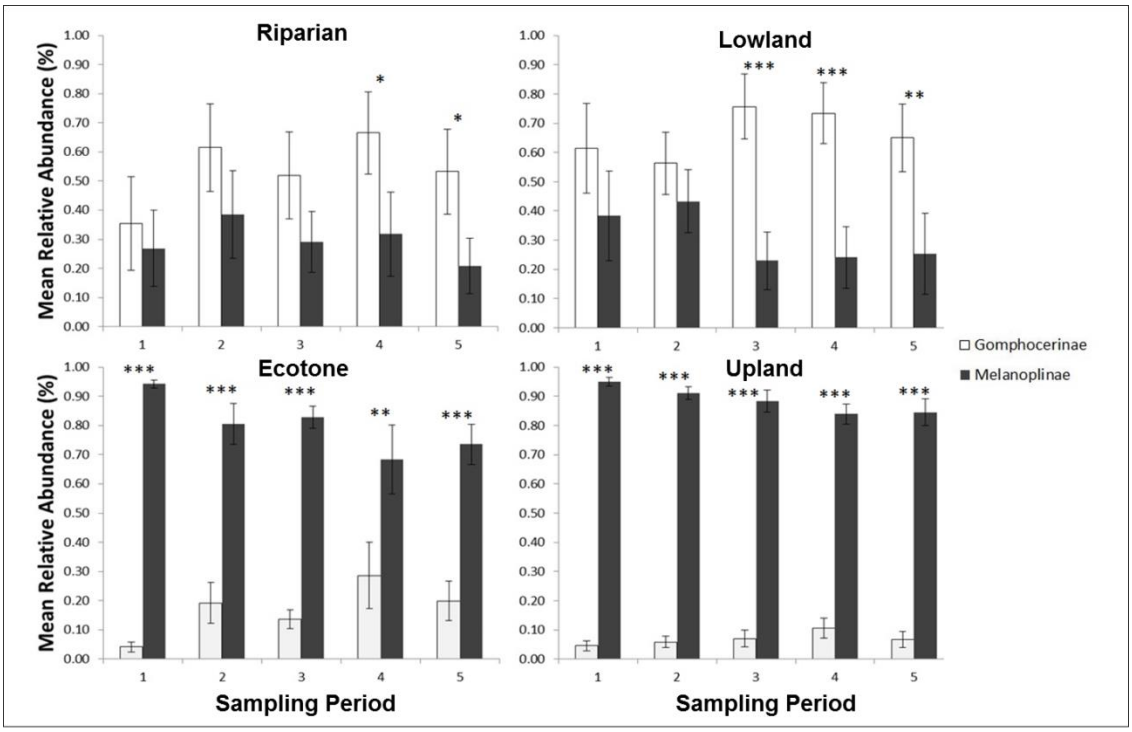

Figure 26: Comparisons between mean relative abundance estimates of Gomphocerinae and Melanoplinae grasshoppers in 4 vegetation types at 5 periods during the summer of 2012 ("1": May 19 – May 22; "2": June 12 – June 16; "3": June 28 – July 7; "4": July 19 – July 26; "5": August 7 – August 15). Significant differences between Gomphocerinae and Melanoplinae relative abundance estimates in each habitat type during each sampling event are indicated by *, **, or *** ($p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively). Total number of grasshoppers in each mean relative abundance comparison are as follows: riparian: $n_1=83$, $n_2=109$, $n_3=104$, $n_4=82$, $n_5=65$; lowland: $n_1=260$, $n_2=213$, $n_3=232$, $n_4=191$, $n_5=186$; ecotone: $n_1=391$, $n_2=220$, $n_3=172$, $n_4=172$, $n_5=193$; upland: $n_1=324$, $n_2=209$, $n_3=188$, $n_4=139$, $n_5=145$.

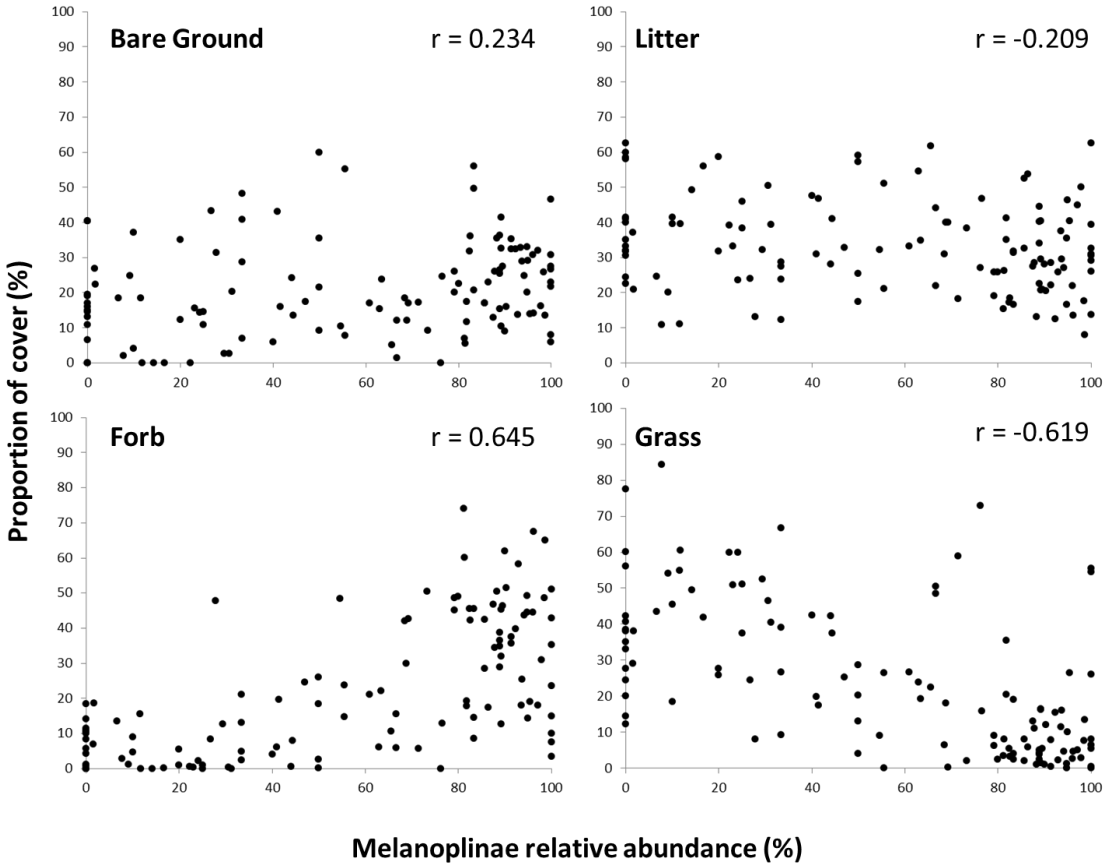

Figure 27: The proportion of cover of four plant functional groups correlated with Melanoplinae relative abundance. The relative abundance of Melanoplinae grasshoppers had significant correlations with four of the five plant functional group cover proportions. Bare ground ($r = 0.234$, $p = 0.01$) and forb cover ($r = 0.645$, $p < 0.0001$) were both positively correlated with Melanoplinae relative abundance. Litter ($r = -0.209$, $p = 0.0223$) and grass cover ($r = -0.619$, $p < 0.0001$) were both negatively correlated with Melanoplinae relative abundance. The "other" plant functional group showed no significant correlation with relative abundance of either subfamily.

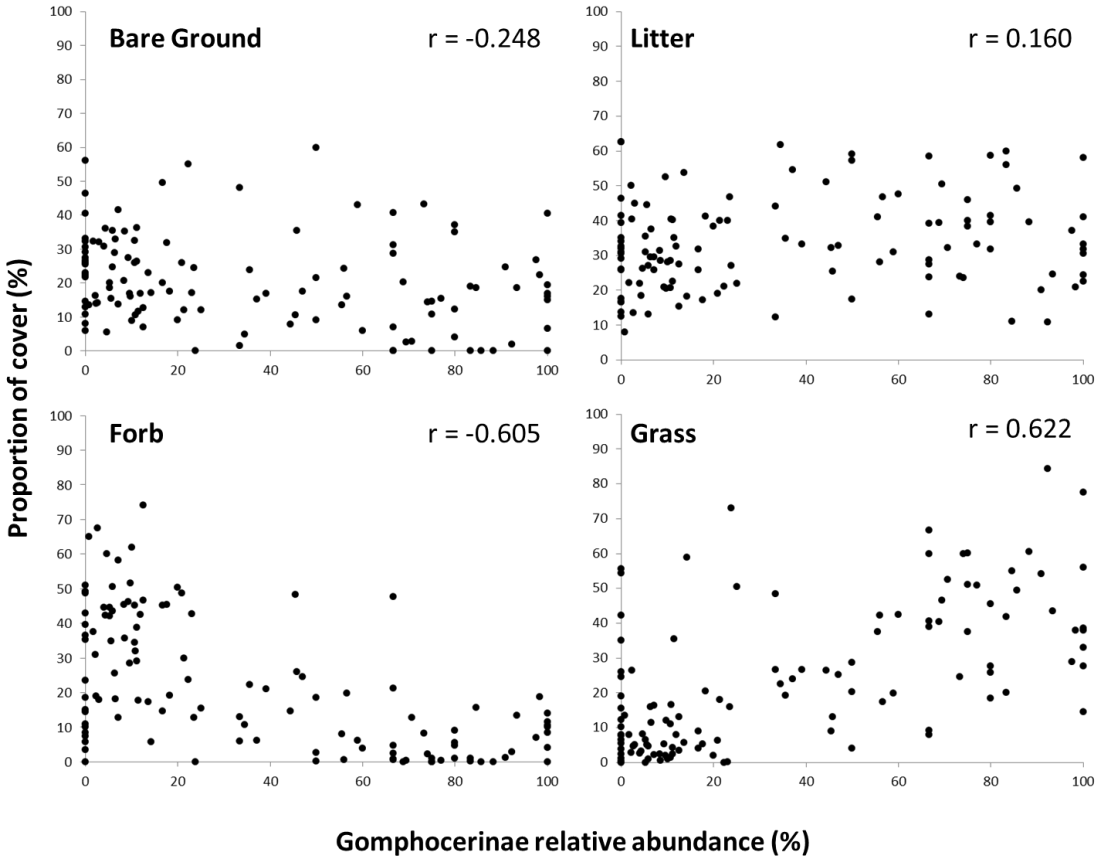

Figure 28: The proportion of cover of four plant functional groups correlated with Gomphocerinae relative abundance. The relative abundance of Gomphocerinae grasshoppers was significantly correlated with only three of the five plant functional groups. Bare ground ($r = -0.248$, $p = 0.0062$) and forb cover ($r = -0.605$, $p < 0.0001$) were both negatively correlated with Gomphocerinae relative abundance. Grass cover ($r = 0.622$, $p < 0.0001$) was positively correlated with Gomphocerinae relative abundance. The "other" plant functional group showed no significant correlation with relative abundance of either subfamily.

Appendix D – Unpublished Data

	Vegetation Type			
	Riparian	Lowland	Ecotone	Upland
Total nests	3	7	8	43
Hatched nests	0	3	4	24

Table 9: Total and successfully-hatched Northern Bobwhite nests on the Beaver River Wildlife Management Area, Beaver County, OK recorded in 2012 and 2013 (Tanner et al., *unpublished data*).

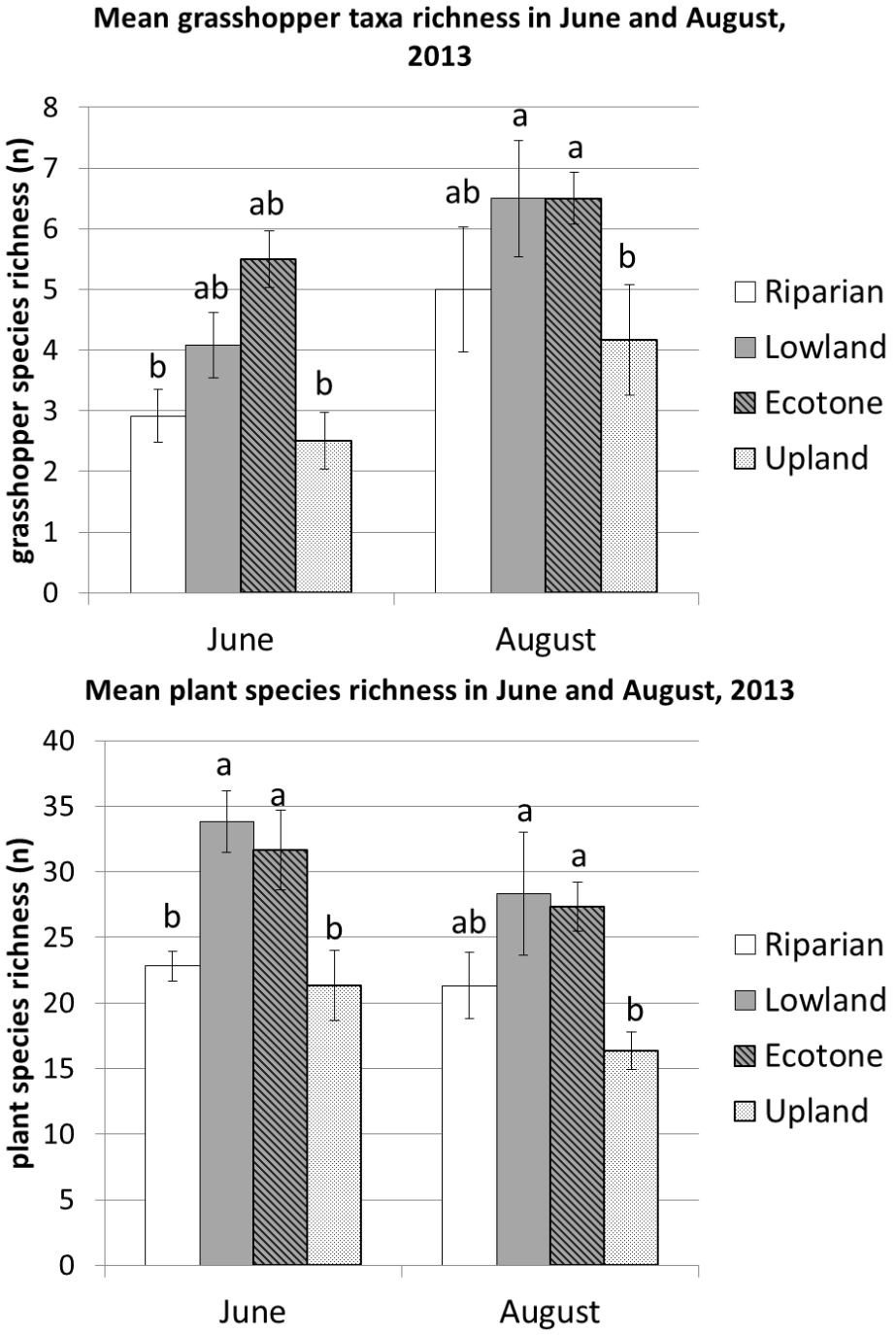

Figure 29: Mean grasshopper taxa richness and plant species richness sampled from June and August, 2013 in each of the vegetation types. Differences in grasshopper taxa richness and plant species richness were analyzed using analysis of variance with repeated measures. An autoregressive period 1 covariance structure was used to model the intratransect variation across time (SAS version 9.3, SAS Institute, Cary, NC). Different letters indicate significant differences ($p < 0.05$) between richness values of different vegetation types within a sampling month (June or August) (Fishbein et al., *unpublished data*).

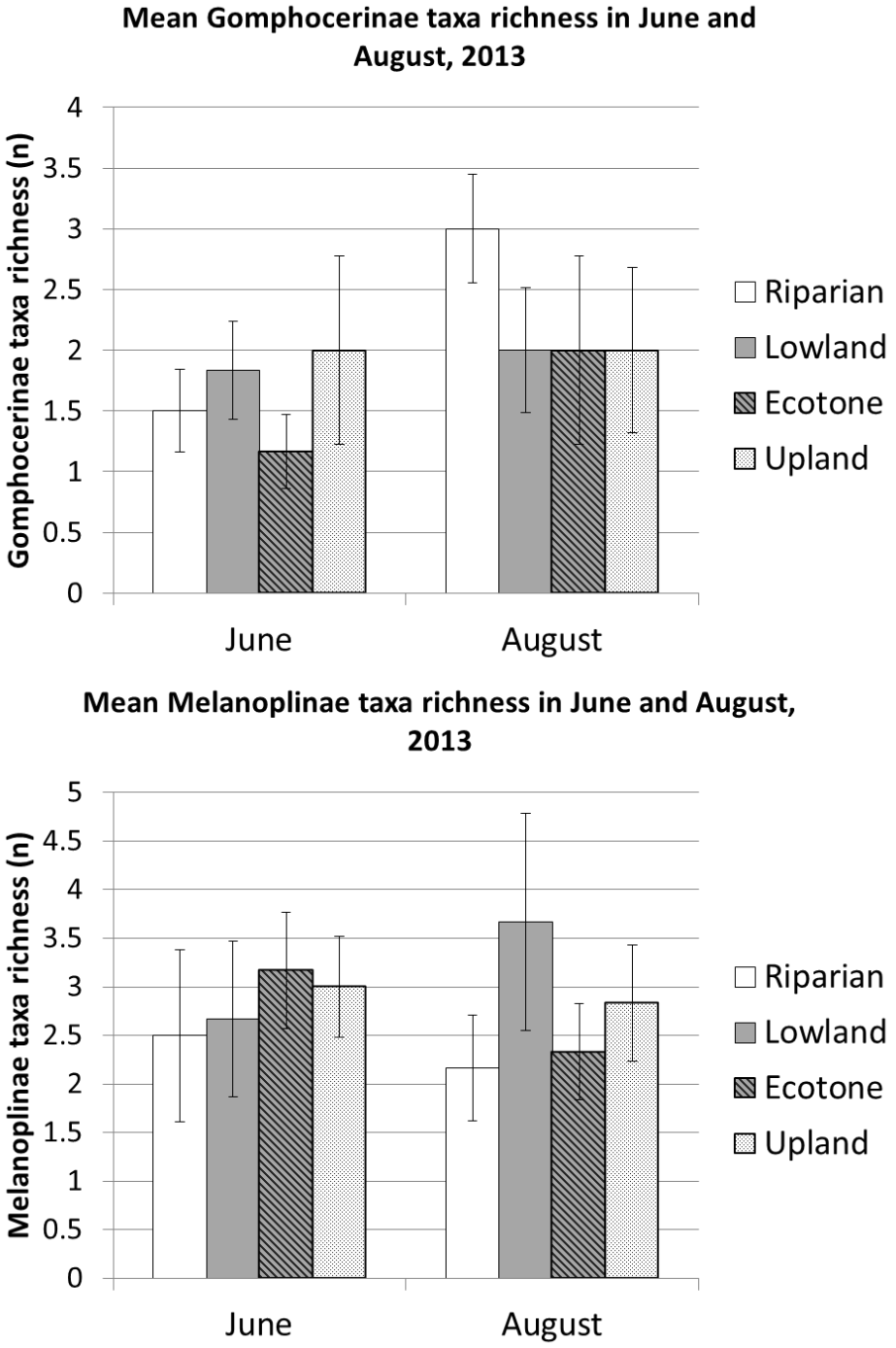

Figure 30: Mean Gomphocerinae and Melanoplinae richness sampled from June and August, 2013 in each of the vegetation types. Grasshopper taxa richness was analyzed using analysis of variance with repeated measures. An autoregressive period 1 covariance structure was used to model the intratransect variation across time (SAS version 9.3, SAS Institute, Cary, NC). No significant differences were detected (Fishbein et al., *unpublished data*).

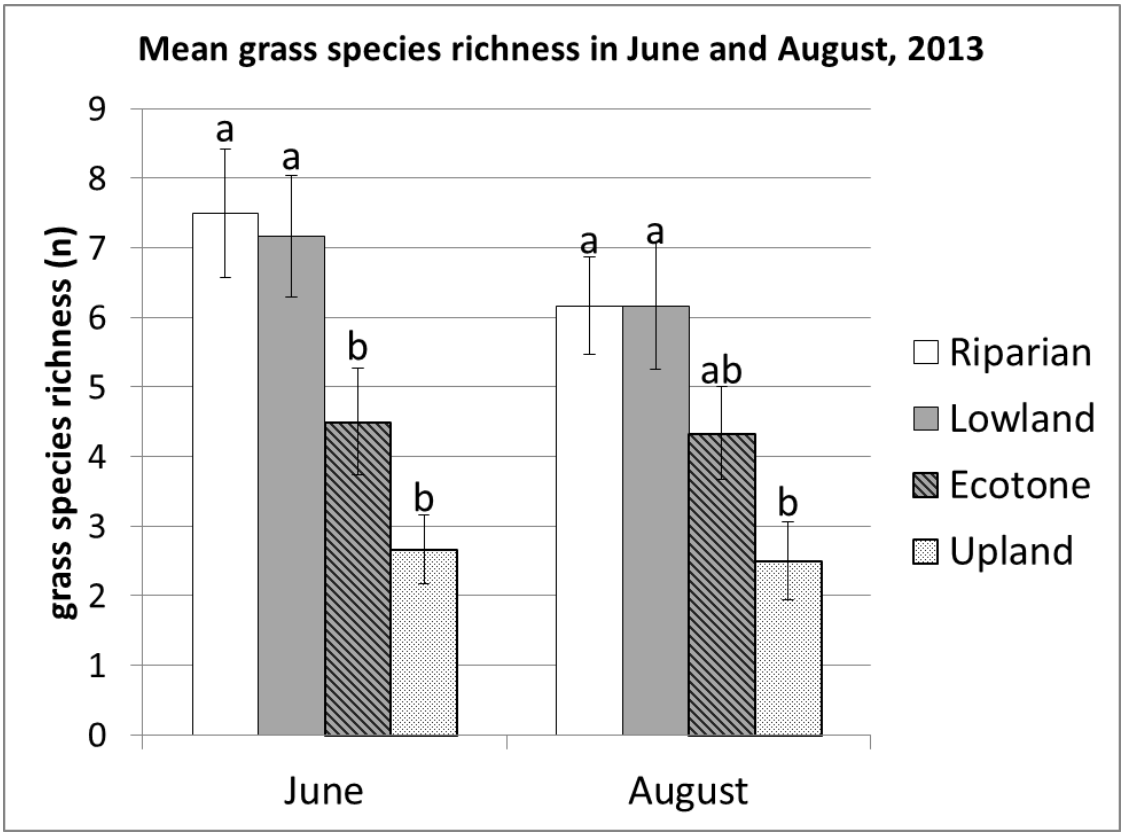

Figure 31: Mean grass species richness recorded in June and August of 2013. Differences in grass species richness were analyzed using analysis of variance with repeated measures. An autoregressive period 1 covariance structure was used to model the intratransect variation across time (SAS version 9.3, SAS Institute, Cary, NC). Different letters indicate significant differences ($p < 0.05$) between richness values of different vegetation types within a sampling month (June or August) (Fishbein et al., *unpublished data*).

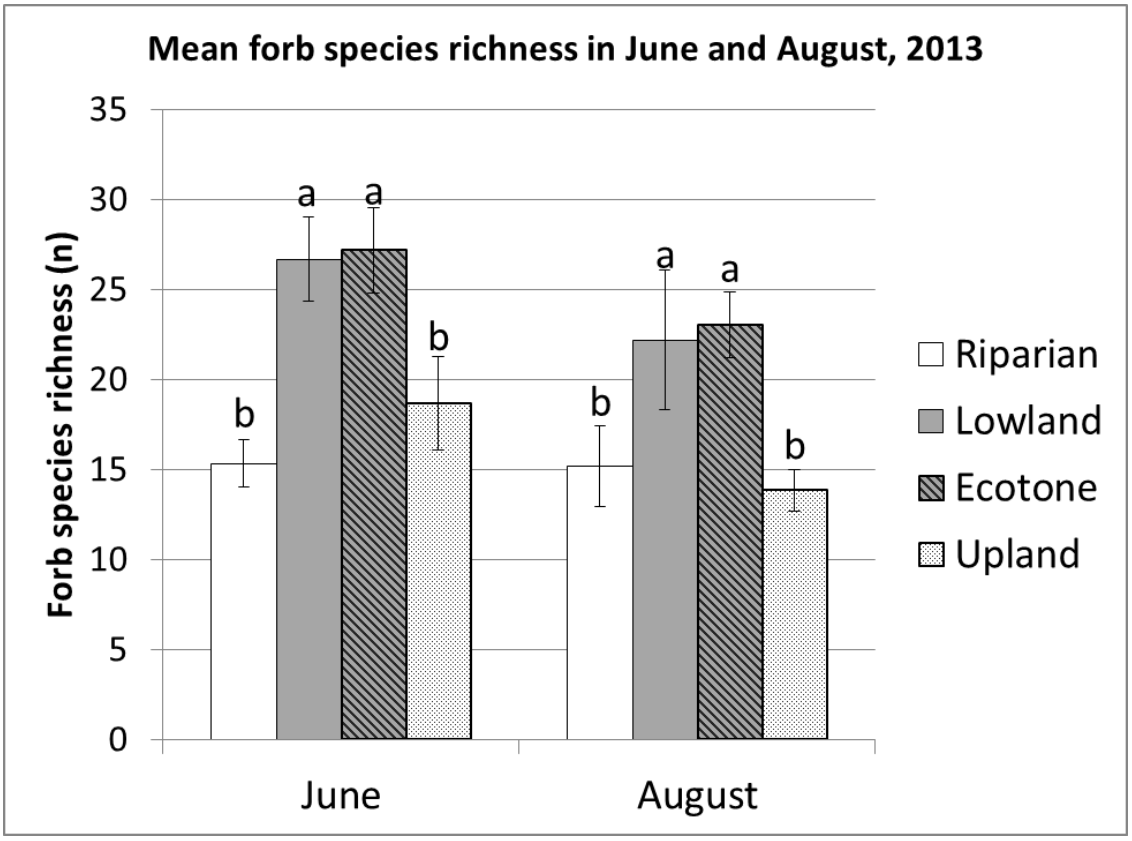

Figure 32: Mean forb species richness recorded in June and August of 2013. Differences in forb species richness were analyzed using analysis of variance with repeated measures. An autoregressive period 1 covariance structure was used to model the intratransect variation across time (SAS version 9.3, SAS Institute, Cary, NC). Different letters indicate significant differences ($p < 0.05$) between richness values of different vegetation types within a sampling month (June or August) (Fishbein et al., *unpublished data*).

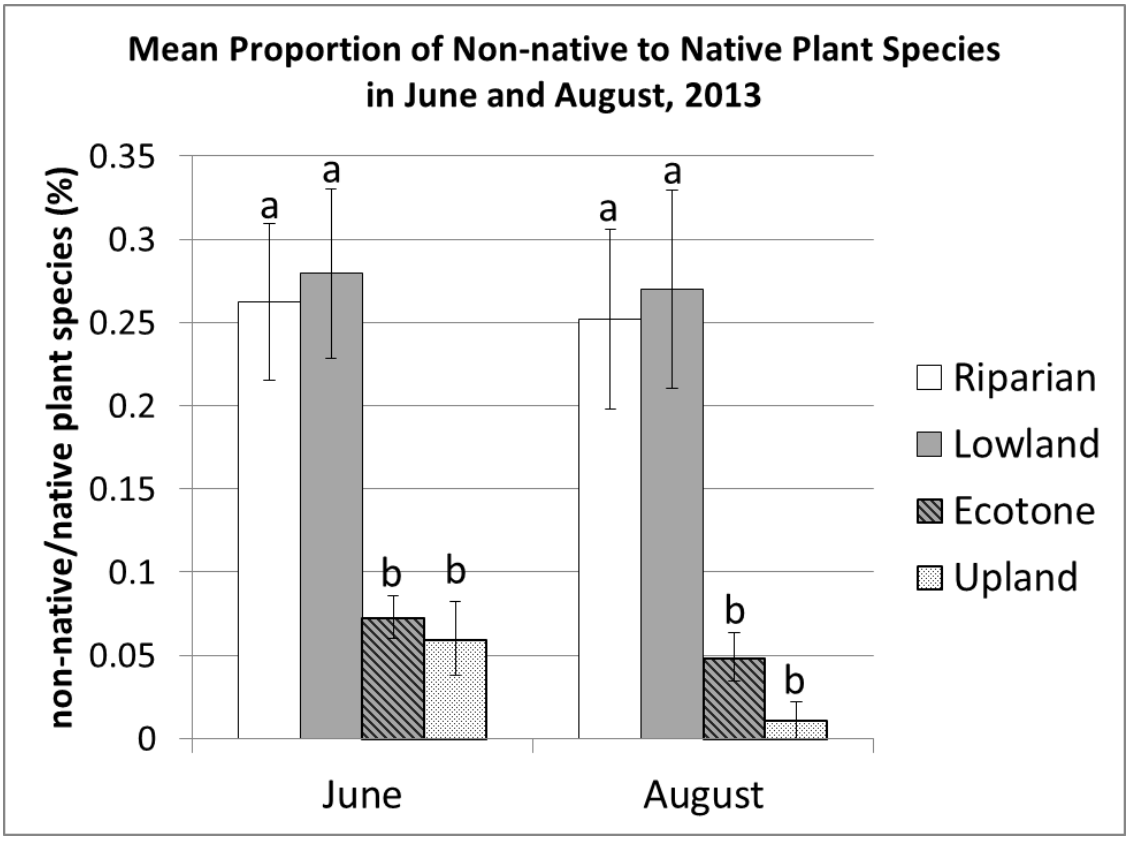

Figure 33: Mean proportion of non-native to native plant species in June and August of 2013. Differences in non-native to native plant species ratios were analyzed using analysis of variance with repeated measures. An autoregressive period 1 covariance structure was used to model the intratransect variation across time (SAS version 9.3, SAS Institute, Cary, NC). Different letters indicate significant differences ($p < 0.05$) between richness values of different vegetation types within a sampling month (June or August) (Fishbein et al., *unpublished data*).

VITA

Kenneth Edmond Masloski

Candidate for the Degree of

Master of Science

Thesis: COMPARATIVE SAMPLING METHODS AND COMMUNITY COMPOSITION OF GRASSHOPPERS (ORTHOPTERA: ACRIDIDAE) IN NORTHERN BOBWHITE HABITAT

Major Field: Entomology and Plant Pathology

Biographical:

Education:

Completed the requirements for the Master of Science in Entomology and Plant Pathology at Oklahoma State University, Stillwater, Oklahoma in May, 2014.

Completed the requirements for the Bachelor of Arts in Biology at the University of Maine at Farmington, Farmington, Maine in 2010.

Completed the requirements for the Bachelor of Arts in English at the University of Maine at Farmington, Farmington, Maine in 2006.

Experience:

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President, Fall 2013 – Spring 2014
GPSGA Representative, Fall 2012 – Spring 2013

Teaching Assistant, Fall 2013 & Spring 2014. Oklahoma State University.
Courses: ENTO 4464 "Insect Biology and Classification" (Fall 2013)
ENTO 2003 "Insects and Society" (Spring 2014)

Professional Memberships:

Entomological Society of America, Southwestern Branch, 2012 – present
Orthopterist's Society, 2013 – present
Society of Southwestern Entomologists, 2014