

**DOES PRODUCTIVITY MATTER? AN INVESTIGATION OF HABITAT USE BY
INSECT AND SMALL MAMMAL HERBIVORES IN A GRASSLAND SYSTEM**

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The following faculty members have examined the final copy of this thesis for form and content, and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science with a major in Biology.

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DEDICATION

This thesis is dedicated to my dad, Sunil, my mom, Subhadra and my brother, Suchit who helped me get to where I am today by being both my support and role models.

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All good things in life have to end and the end is bitter-sweet. Bitter, since I have to part from those people with whom I have associated over a period of time; and sweet, since it gives me a tremendous sense of fulfillment on the completion of the task undertaken. Now as I am on the threshold of taking the world on my own, I can't help but make a journey down the memory-lane and I fondly recall some of the experiences encountered by me in the past three years, while working on my thesis.

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ABSTRACT

Although some ecological theory predicts that herbivore density should increase with plant quality or biomass, few studies have directly measured the response of multiple groups of grassland herbivores to changes in plant production. In this study, I experimentally manipulated plant biomass by fertilizer addition and measured density and diversity of small mammals and insects (primarily Rodentia and Orthoptera). A total of 245 small mammals representing 9 species were captured during the study. For the three most common species, 82% of mammals comprised of *Peromyscus leucopus* and *Peromyscus maniculatus* while *Sigmodon hispidus* dominated captures of mammals > 100g. The density of the rodent community was higher in fertilized than in unfertilized plots. However, I detected no effect of increased plant biomass on small mammal diversity. The body mass of *S. hispidus* and *P. leucopus* was higher in the fertilized than in unfertilized plots but no effect was observed for the *P. leucopus*. For insect herbivores, grasshopper biomass, density as well as diversity were higher in fertilized than unfertilized plots. Collectively these results from multiple herbivore groups are consistent suggesting that plant productivity influences the composition of small mammal and grasshopper assemblages in grassland systems.

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LIST OF ABBREVIATIONS

ANOVA	Analysis of Variance
<i>F</i>	Fisher's distribution
$\text{g N m}^{-2}\text{yr}^{-1}$	Grams per Nitrogen per square meter per year
NaClO	Sodium Hypochlorite
NPK	Nitrogen Phosphorous Potassium
<i>P</i>	Probability
<i>t</i>	Student's t-test

CHAPTER 1

INTRODUCTION

A fundamental question in ecology is what determines species population density and diversity. Although many abiotic (topography, moisture, pH, nutrient availability) and biotic factors (competition, predation, mutualism) likely affect the distribution and abundance of species, primary productivity is emerging as a key determinant of both plant and animal abundance and diversity (Huntly, 1991; Mittlebach *et al.*, 2001; Houseman and Gross, 2011). For herbivores, plant biomass potentially limits population growth rates so that density and diversity of these herbivores may vary with plant production. Although numerous published studies have explored this relationship, no consensus has emerged and considerable debate endures concerning the influence of productivity on herbivore density and diversity in terrestrial ecosystems (Cyr and Pace, 1993; Van de Koppel, 1996; Siemann *et al.*, 1998; Haddad *et al.*, 2000; Kuijper and Bakker, 2005).

Several hypotheses have been proposed to explain the relationship between herbivore density and ecosystem fertility. The plant vigor hypothesis (PVH) suggests that herbivore density increases with productivity as plant defensive chemicals decrease with increased soil fertility leading to increased herbivore density (Price, 1991). Alternatively, the plant stress hypothesis (PSH) hypothesizes that herbivore density decreases with productivity, as increased growth rates are associated with production of high amounts of unpalatable defensive compounds that generate less nutritious food for organisms (White, 1969). Consequently, herbivore density should decrease with productivity. A third hypothesis, known as the intermediate productivity hypothesis (IPH), proposes that density of herbivores increases along productivity gradients to an optimum at intermediate productivity. Any

further increase of primary productivity results in a decrease in herbivore density (Tilman, 1982; Abramsky and Rosenzweig, 1984). At low productivity, plants biomass is too low to support herbivores. Increases in plant quantity and quality favors herbivore density and hence will peak at intermediate level. However, at high productivity herbivore density decreases due to an increase in tall relatively unpalatable plant species which is least attracted by herbivores (Van de Koppel *et al.*, 1996; Olf *et al.*, 1997; Huisman *et al.*, 1999). This hypothesis results in a unimodal relationship between productivity and herbivore density.

In addition to herbivore density, herbivore diversity may be either positively or unimodally related to productivity and at least three hypotheses have been proposed to explain these relationships. The first is the 'consumer rarity' hypothesis also called the 'energy limitation' hypothesis, which states that the number of individuals that a habitat can sustain is limited by energy (Connell and Orias, 1964; MacArthur, 1965; Wright, 1983; Abrams 1995; Currie, 1991). If the number of individuals increases with energy (productivity), then greater energy (productivity) should increase density and probability that a site will include more species. Consequently, herbivore diversity should increase with productivity (Preston, 1962). Second, the 'resource rarity' hypothesis, also called the 'more specialization' hypothesis, predicts that herbivore species that survive on limited resources are unable to persist at low productivity. As productivity increases, the number of herbivore species that have resource supplies above their minimal requirements (Schoener 1976, Abrams 1988b) increases enabling a greater number of species to exist (MacArthur, 1969; Abrams, 1988; Abrams, 1995; DeAngelis, 1995). Thus, herbivore diversity increases with productivity. Finally, the 'environmental heterogeneity' hypothesis, also called the 'quality threshold' hypothesis assumes that herbivore diversity is related to resource heterogeneity (Abrams, 1988; Van der Wal *et al.*, 2000). In this case, low productive sites have homogenous resources due to low plant

diversity. As plant productivity increases, plant diversity will increase, making resources more heterogeneous for consumer species and leading to increased herbivore diversity. However, plant diversity may decline at very high productivity due to increasing dominance by a few plant species leading to decreased resource heterogeneity. Consequently, a unimodal relationship between plant productivity and herbivore diversity may occur.

Empirical studies that quantify the relationship between herbivore density and productivity have utilized several approaches but to date a consensus on the productivity-herbivore density relationship has yet to emerge. Most of the evidence comes from observational or correlational studies which report that herbivore density can be positively (Beukema, 1991; Sarda *et al.*, 1996; Frank, 1998; Pitta *et al.*, 1998; Kuijper and Bakker, 2005), negatively (Sager and Richman, 1991; Cyr and Pace, 1993; Pringle *et al.*, 2007) or unimodally (Van de Koppel, 1996) related to productivity. One possible reason for the disparate results is that observational studies may not adequately account for uncontrolled factors that covary with productivity. Although experiments should control for such factors, experiments have not always found a positive relationship between productivity and herbivore density (McQueen *et al.*, 1986; Milchunas *et al.*, 1988; Proulx and Mazumder, 1998) and have not been able to satisfactorily explain the productivity-herbivore density relationship.

Similar to herbivore density, it is unclear whether productivity has a positive or negative effect on herbivore diversity (Rohde, 1992). Observational studies suggest that herbivore diversity can have a unimodal (Riebesell, 1974; Southwood *et al.*, 1979; Leibold, 1999) as well as monotonically increasing (Connell and Orias 1964; Nagel, 1979; Crisp *et al.*, 1998) or decreasing (Murdoch *et al.*, 1972; Riebesell, 1974) relationship with productivity. Although lack of experimental control might explain the variable results, there is currently insufficient

experimental evidence to support a consistent relationship particularly in terrestrial systems (Carpenter and Kitchell, 1988). Field experiments have found herbivore diversity to increase (Siemann *et al.*, 1998; Hall *et al.*, 2000; Bracken and Nielsen, 2004) or decrease (DiTommaso and Aarsen, 1989; Schindler, 1990; Haddad *et al.*, 2000) with productivity. A particular problem associated with several of the available field experiments is that the studies include manipulation of plant diversity which may itself affect plant productivity and consumer diversity (Naeem *et al.*, 1995; Tilman *et al.*, 1996). In addition, studies have generally looked at the relationship between plant and insect communities by utilizing a single plant species (Southwood, 1961; Claridge and Wilson 1981; Owen, 1988; Ritchie, 2000; Joern and Mole, 2005; Husheer *et al.*, 2006). Thus, it is unclear whether the different outcomes observed are due to variation among herbivores, plant communities, different types of natural systems, or details of the experimental approach used in particular studies. A more powerful approach would be to examine different herbivore groups and diverse plant community within a single natural system, using a consistent methodology, and to compare the influence of productivity on herbivore diversity.

Despite the global importance of grasslands, the experimental studies of the relationships between productivity and herbivores are mainly derived from aquatic or rocky shore habitats (Sih *et al.*, 1985; Denno, 2003; Gruner *et al.*, 2008). This omission is surprising given that grasslands historically comprised a substantial portion of terrestrial ecosystems (Gurevitch, Scheiner and Fox, 2006). Those that do represent grasslands are often old fields, which may not adequately reflect the critical factors found in grass-dominated systems (Hurd *et al.*, 1971; Hurd and Wolf, 1974; Sedlacek *et al.*, 1988; Andow, 1991). Grasslands are generally habitats for wide array of herbivores, especially arthropods and both large and small mammals (Crawley, 1989; Huntley, 1991) and the response of herbivores to plant production

may vary with different herbivore groups. However, studies have usually portrayed the effect of plants on one herbivore group rather than its effect on multiple herbivore groups simultaneously. Furthermore, most experimental studies that manipulate soil fertility in grasslands have been carried out either as microcosms or in common garden experiments (Fraser and Grime, 1999; Buckland and Grime, 2000). Most of these studies looked at the effect of fertility on growth and development and abundance of individual plant species rather than the entire plant community and how it further affects the herbivores.

In this study, I experimentally manipulated plant biomass by fertilizer addition in a grassland ecosystem and measured density and diversity of small mammals and insects (primarily Rodentia and Orthoptera) to test the importance of plant productivity and its relation to herbivore abundance. Vertebrate herbivores such as rats, mice and voles as well as invertebrates such as insects undoubtedly play an important role in grassland ecosystems, and this experiment was intended to test whether biomass, density and diversity of two groups of herbivore communities varied with manipulated soil fertility (increased plant production).

CHAPTER 2

METHODOLOGIES

Study Site

This experiment was conducted at the Ninnescah Reserve, which is part of the Wichita State Biological Field Station, near Viola KS (37.49N latitude, 97.64W longitude) and consists of 330 acres of native prairie, restored prairie, wetlands, and riparian woodland along the Ninnescah River. The site was under row-crop agriculture for several decades until 1988 when the majority of the site was reseeded to native grassland.

Experimental Design

To test the effect of grassland productivity on small mammal and insect habitat use, six pairs of plots were established, half of which were assigned to a fertilization treatment (Fig 1.). Three paired plots were established in the spring of 2005 (Shrestha, 2009). In 2009, an additional set of three paired plots were added to the experiment to increase replication. Although, the size of the area fertilized for the original three plots varied between 900 and 1600 m² during 2005-2009, all plots were standardized to 30x30 m in spring 2009. Urea-based nitrogen fertilizer was applied in late spring at a target rate of 12 g N m⁻² yr⁻¹ from 2005-8 and a slow release 20-10-3 NPK (Professional turf fertilizer, Howard Johnson's Enterprises, Milwaukee Wisconsin) thereafter. As part of the management regime, prescribed burning was applied every year in the spring between 1988 to 1994 on the west side of the prairie and between 1990 to 1998 on the east side. All areas remained unburned until 2010 when a partial burn was completed. However, only two out of the six pairs of plots were burned due to difficult burning conditions.

Small Mammal Sampling

I censused small mammals between April-October 2010. In each plot, four Sherman traps (762 x 889 x 305 mm) and two pitfall traps were located using a stratified random procedure to minimize clustering of traps within any plot (Fig 2.). Pitfall traps consisted of 60 L plastic buckets (402 mm diameter at the top, 332 mm diameter at the bottom, and 540 mm depth) that were buried so that the top of the bucket was level with the soil surface. Both Sherman and pitfall traps were baited with commercially available scratch grain (a mixture of cracked corn, wheat and grain sorghum). Traps contained cotton bedding as means of natural insulation and nesting material for the trapped mammals. During each sample month, traps were baited and checked for three consecutive days (Brady and Slade, 2001). Captured animals were identified, massed, and uniquely marked with a numbered Monel eartag (National Band and Tag Company, Newport, Kentucky). Captured animals were then released at the point of capture. After the three day trapping sequence, traps were removed from the field and disinfected by soaking in a 10% NaClO solution for 5 minutes and thoroughly rinsed with water (Yunger and Randa, 1999).

Insect Sampling

Insect data were collected in July, August, and September 2010 using a sweep netting technique (Haddad et al., 2000; Siemann, 1998). Insects were sampled along 3 parallel transects in each plot within 4 to 5 hours of sunrise. Each transect was 30 meters long at 8 meter intervals. The collected insects were placed inside a jar and kept in ice to reduce activity and minimize predation on insect herbivores from spiders. Insects were stored below 0°C until they could be sorted and massed by three categories: grasshoppers, other herbivores and carnivores. Additionally, grasshoppers were identified to species and counted as they are

considered a conspicuous, primary consumer among herbivorous insects in grassland systems (Meyer et al., 2002; Rodell, 1977).

Plant Sampling

To quantify differences in plant productivity among plots, above-ground biomass was sampled 1 m from each trapping point in a randomly selected compass direction. If the sample point fell on a walkway, an alternative compass direction was obtained. At each plant sampling point, plant percent cover was estimated in a 1 x 1 m quadrat by comparing aerial plant cover of each species to a reference card with known area. Plant biomass was sampled along two, 8 cm strips within the 1 x 1 m quadrat with a handheld clipper (Black & Decker, SSC1000 Type 1). Because plant material was sampled late in the growing season, live and standing dead plant material were pooled. Litter was sampled by clipping plant material lying on the ground in the two, 8x100 cm strips.

Statistical Analysis

Herbivore density, diversity and average animal mass over the sampling period were tested using mixed model, repeated measures ANOVA with fertilization as a main effect and plot as a repeated measure. For mammal density, I calculated monthly estimates of population density for the two dominant species (*Sigmodon hispidus* and *Peromyscus leucopus*) using the Jolly Seber Model (Krebs, 1989). Fertilizer effects on plant biomass were analyzed with a t-test (Siegel & Castellan 1988). All statistical analyses were performed using SAS 9.2. Data were transformed when necessary to meet statistical assumptions.

CHAPTER 3

RESULTS

Effect of Fertilization on Plant Communities

Fertilization led to a weak but apparent increase in standing plant biomass ($t = 2.11$; $P = 0.08$; Fig. 3), but no effect on the litter biomass ($t = 0.79$; $P = 0.46$; Fig. 3). There was an anomalous response in one block in which the fertilized plot had lower biomass than the control. This may have occurred because of legacy effects or differences in soil conditions. After removing this block from the analysis, standing plant biomass was higher in the fertilized rather than unfertilized plots ($t = 4.54$; $P = 0.01$), but litter did not differ among treatments ($t = 0.10$; $P = 0.9$). In addition, there was no difference in plant richness among treatments ($t_5 = 0.65$; $P = 0.54$).

Effect of Fertilization on Small Mammal Communities

A total of 245 small mammals were captured over the entire study. This total included *Peromyscus leucopus* (106), *Sigmodon hispidus* (98), *Peromyscus maniculatus* (14) that were captured repeatedly (Table 1). For population densities of *P. leucopus* I found no significant interaction between fertilization and time ($F_{6, 65} = 1.84$; $P = 0.1$, Fig. 4) and, although there was no effect of time ($F_{6, 65} = 1.83$; $P = 0.10$), densities were higher in fertilized plots ($F_{1, 65} = 6.17$; $P = 0.01$). For *S. hispidus* density, there was a significant interaction between fertilization and time ($F_{6, 65} = 3.37$; $P = 0.005$, Fig. 5) which suggested that density was higher in the fertilized plots in the month of October ($t_{65} = 2.67$; $P = 0.009$). In addition there was a main effect of time ($F_{6, 65} = 7.77$; $P < 0.0001$) as density was lower in April and October when compared with the mid-summer months especially with June ($t_{65} > 2.13$; $P < 0.03$).

In addition to density, I found fertilization effects on the average mass of small mammals. There was a significant interaction between fertilization and time on the average mass of *S. hispidus* ($F_{6, 39} = 2.55$; $P = 0.03$, Fig. 6) with larger animals found in unfertilized plots early in the growing season (May; $t_{39} = 2.23$; $P = 0.03$). However, by the end of the growing season, larger animals were found in fertilized plots (August: $t_{39} = 1.86$; $P = 0.06$ and September: $t_{39} = 1.71$; $P = 0.09$). There was also a main effect of time on the average mass of *S. hispidus* ($F_{6, 39} = 2.55$; $P < 0.0001$) with peak mass occurring in May ($t_{39} = 3.43$; $P = 0.0014$) and June ($t_{39} = 2.19$; $P = 0.03$). Tests for average mass of *P. leucopus* were not conclusive as no maximum likelihood statistical solution could be obtained.

For mammal species richness, there was no interaction between fertilization and time ($F_{6, 54} = 1.05$, $P = 0.40$) and no effect of fertilization. There was a detectable difference in richness among months ($F_{6, 54} = 3.05$, $P = 0.01$) but these results need to be viewed with caution because of the few species captured (three).

Effect of Fertilization on Insect Communities

I captured a total of 96 grasshopper individuals representing nine different species (Table 2). There was significant interaction between fertilization and time ($F_{2, 25} = 9.52$; $P = 0.0008$). Grasshopper density was higher in fertilized plots ($F_{1, 25} = 12.15$; $P = 0.0018$, Fig. 7) but only in July ($F_{2, 25} = 7.37$; $P < 0.003$).

For average grasshopper mass, there was a significant interaction between fertilization and time ($F_{2, 22} = 3.37$; $P = 0.05$). Grasshopper mass was higher in the fertilized than unfertilized plots in August ($F_{2, 22} = 6.57$; $P = 0.005$, Fig. 8). For non-grasshopper species mass, I tested for differences in total mass as the individual species were not identified and hence the

densities for each species were not known. Total mass of non-grasshopper species showed a marginal interaction between fertilization and time ($F_{2, 24} = 2.73$; $P = 0.08$; Fig. 9) which suggested that total mass in the fertilized plots was higher in July ($t_{24} = 2.02$; $P = 0.05$), but this pattern reversed in August where total mass was higher in unfertilized than fertilized plots ($t_{24} = 3.77$; $P = 0.0009$). Because of high variability no statistical inferences could be drawn for spider abundance.

There was no significant interaction between fertilization and time ($F_{2, 19} = 0.36$, $P = 0.70$) on grasshopper diversity. Grasshopper richness was higher in fertilized than unfertilized plots ($F_{1, 9} = 5.12$, $P = 0.03$, Fig. 10) and also varied with time with peak richness occurring in August ($F_{2, 19} = 20.86$, $P < 0.0001$).

CHAPTER 4

DISCUSSION

In spite of the potential importance of productivity to herbivore abundance, there have been relatively few studies in grasslands, especially involving multiple groups of herbivores. This study showed that the density and average mass of small mammal and insect communities generally increased with enhanced fertility. Likewise, enhanced productivity increased diversity of grasshoppers. These facts that productivity had a consistent positive effect on both small mammal and insect communities lend support to the plant vigor hypothesis in this grassland system.

Effect of Fertility on Small Mammal Communities

Density of individual mammal species (*S. hispidus* and *P. leucopus*) was consistently higher in fertilized compared to unfertilized plots. The increase in density may be attributed to increased plant production, which may provide enhanced food resources. In addition changes in plant tissue quality could have also contributed to some of the increase in populations of these small mammals. These observations are in general agreement with the plant vigor hypothesis and support results reported for old fields and forests (Miller, 1968; Hansson, 1978; Reichman and Smith, 1985; Huntly and Inouye, 1987; Inouye *et al.*, 1987; Hobbs *et al.*, 1988; Jones, 1990; Lambert *et al.*, 2006). However, my results cannot rule out the possibility that at least part of the increased mammal density may be linked with increased vertical structure or cover of the vegetation (Hansson, 1978; Brady and Slade, 2001). Although separating the effects of food resources from structural cover is a challenging task that has rarely been attempted, the connection between biomass and mammal density remains

a useful relationship that can be used to predict small mammal density even if the exact mechanism driving such differences remain unknown.

In addition to density, average mass of the small mammal community also increased with productivity. This result is consistent with results reported by Cole and Batzli (1978) in an old field and Yunger (2002) in woodland. A study by Grant et al. (1977) in a short grass prairie supported the view that variation in body mass and small mammal community structure is tightly coupled with vegetation quality and structure. In addition, several studies have reported grass height and density to be an important component of *Sigmodon* habitat (Goertz, 1964; Kaufman and Fleharty, 1974). Also, *S. hispidus*, a grazing herbivore, is reported to primarily feed on grasses (Fleharty and Olson, 1969) which could possibly explain the gain in body mass for these individuals in the fertilized plots. On the other hand, *Peromyscus*, which can be carnivorous, may be attracted to the arthropods rather than plant biomass (Grant *et al.*, 1977). The increase in average mass in the unfertilized plots during the early growing season still remains as an inconclusive question. Despite the link either directly or indirectly to plant production, increases in mammal size may also be a consequence of an increase in forage quality or availability of refuges and/or by reducing predation risk, but discriminating among these possibilities will require additional experimentation.

Richness of small mammals did not show a strong response to increased fertility most likely due to the capture of just three species during the study. It may be likely that the habitat did not provide right conditions for other small mammals (e.g. *Perognathus flavescens*, *Reithrodontomys megalotis* and *Dipodomys ordii*). Or perhaps my sampling strategy was only capable of capturing a few types of species.

Effect of Fertility on Insect Communities

Grasshoppers showed a significant increase in density in the fertilized plots primarily due to an increase of the two most common species, grass feeding melanopline tribe, *Phoetalis nebracensis* and *Melanoplus femurrubrum*. This observation supports the plant vigor hypothesis and is attributable to the increased plant mass or tissue nutrient content (Mattson 1980; Scriber 1984) – a result consistent with studies on grasshoppers and other insects (Hurd et al. 1971; Hurd and Wolf 1974; Kirchner 1977; Werner et al., 1983; Sih et al., 1985; Sedlacek et al. 1988; Huang & Sih, 1990; Feltmate & Williams, 1991; Schmitz, 1994; Walde, 1995; Siemann 1998). Although changes in plant community composition and vegetation structure are thought to be important criteria for habitat selection by grasshoppers (Anderson, 1964), my experimental results suggest that productivity alone can account for changes in density. Similar to the patterns for small mammals, plant biomass appears to exhibit important effects on density, but further experiments will be necessary to determine whether plant quantity or quality contributes to such increases.

Similar to grasshopper density, average mass of grasshoppers and total non-grasshopper mass also increased with plant productivity. This result supports several other short term studies in prairie system (Belovsky 1986; Belovsky and Slade, 1993; Moorehead, 1993). Joern (1985) reported that presence of high resource quality and absence of predators (e.g. spiders) would cause grasshoppers to experience the highest rate of development and achieve larger final adult size. My results are consistent with this view given the relatively low abundance of predatory insects (e.g. spider) in this system.

In addition to size and abundance, grasshopper diversity also increased with productivity supporting the energy limitation hypothesis and the results of other studies conducted in

prairie and rangeland (Sala, 1988; Fielding and Brusven, 1993; Evans, 1998; Joern, 2005). However, the resource rarity hypothesis cannot be ruled out as there was an overall difference in productivity among the treatment plots during mid-summer months. My results do not support the environmental heterogeneity hypothesis as I found no difference in plant richness among treatments and hence increased grasshopper diversity occurred through changes in productivity alone as there was no apparent difference in plant heterogeneity.

Seasonal Variation in Small Mammal Communities

A considerable seasonal fluctuation in the density of small mammals was observed in this grassland system. Although *S. hispidus* breeds all year round, the density was lower in October and May with a peak in July. A possible explanation for this pattern is that early in the growing season there is a greater availability of young, nutritious grass shoots that may allow increased growth rates or reproductive potential, but that either quality of food resources or the levels of predation increase late in the growing season. *Peromyscus leucopus* did not show the same pattern with densities being more consistent across the months. This result supports the study done by Terman (1968) who showed that the population dynamics of *Peromyscus* and is characterized by less variation in population density than that reported for other small terrestrial mammals. This regulation may be attributed to *Peromyscus* being able to utilize a greater range of food items that have more consistent availability throughout the growing season than *S. hispidus*.

Seasonal Variation in Insect Communities

Grasshopper density varied among the three months sampled but not to the same extent as the non-grasshopper species. Variation in this study is consistent with other studies, in which peak abundance occurs during mid-summer (Dempster, 1963). Hatching usually takes place

from May to August (Lockwood and Lockwood, 2008) suggesting that warm dry weather (Gage and Mukerji, 1977) and the abundance of high quantity and quality plant material facilitates accelerated individual growth and development (Johnson and Mundel, 1987; Yang and Joern, 1994a, b; Joern and Behmer, 1997) decreasing exposure time to any potential predators. Conversely, fertilized plots may attract more individuals rather than leading to increased growth rates.

In contrast to grasshoppers, other insects in this grassland system fluctuated considerably over time presumably due to a greater representation of insect species that include a broad array of seasonal phenologies. Interestingly, the effect of fertilization appeared to neither increase nor decrease total non-grasshopper insect mass suggesting that either particular species or functional groups may have differential responses to enhanced productivity.

In addition to system fertility, predators can play an important role in the ecosystem as by limiting population densities and potentially creating trophic cascades either directly or indirectly (Lima and Dill, 1990). In the current study, I assume that predators have a roughly equal effect between the treatments. There may have been differences among blocks but predators should have equal access to both the fertilized and unfertilized plots. If anything, predators may have reduced the effect of fertilization on small mammal or insect density by foraging in plots with greater herbivore densities. Conversely, the enhanced biomass may make it more difficult for predators to locate prey, but this possibility seems less likely given the modest increases in plant biomass observed in my experiment. Nevertheless, additional experiments that manipulate access to fertilized plots by predators will be necessary to conclusively demonstrate the relative roles of fertility and predation on herbivore abundance.

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APPENDIX

Table 1. Count of small mammal species by treatment and sampling months.

Species	April 2010		May 2010		June 2010		July 2010		August 2010		September 2010		October 2010	
	UF	F	UF	F	UF	F	UF	F	UF	F	UF	F	UF	F
<i>P. leucopus</i>	6	12	0	5	11	20	12	14	10	11	6	6	5	9
<i>P. maniculatus</i>	0	1	2	1	0	2	1	4	0	1	1	0	0	0
<i>S. hispidus</i>	3	5	7	5	7	10	7	11	13	24	17	13	8	19

Table 2. Count of grasshopper species by treatment and sampling months.

Species	July 2010		August 2010		September 2010	
	UF	F	UF	F	UF	F
<i>H. speciosa</i>	0	0	0	1	0	0
<i>M. bivittatus</i>	1	3	2	4	0	0
<i>M. diffentialis</i>	0	2	1	2	0	0
<i>M. femurrubrum</i>	0	0	3	5	0	2
<i>Mermiria spp.</i>	0	1	3	1	0	0
<i>P. nebrascensis</i>	1	3	6	6	11	11
<i>S. admirabilis</i>	0	0	1	0	0	0
<i>S. campestris</i>	0	0	0	1	0	0
<i>S. obscura</i>	0	0	0	1	0	0
<i>nymph</i>	2	15	3	2	1	0
<i>unidentifiable</i>	0	4	0	0	0	0

Figures

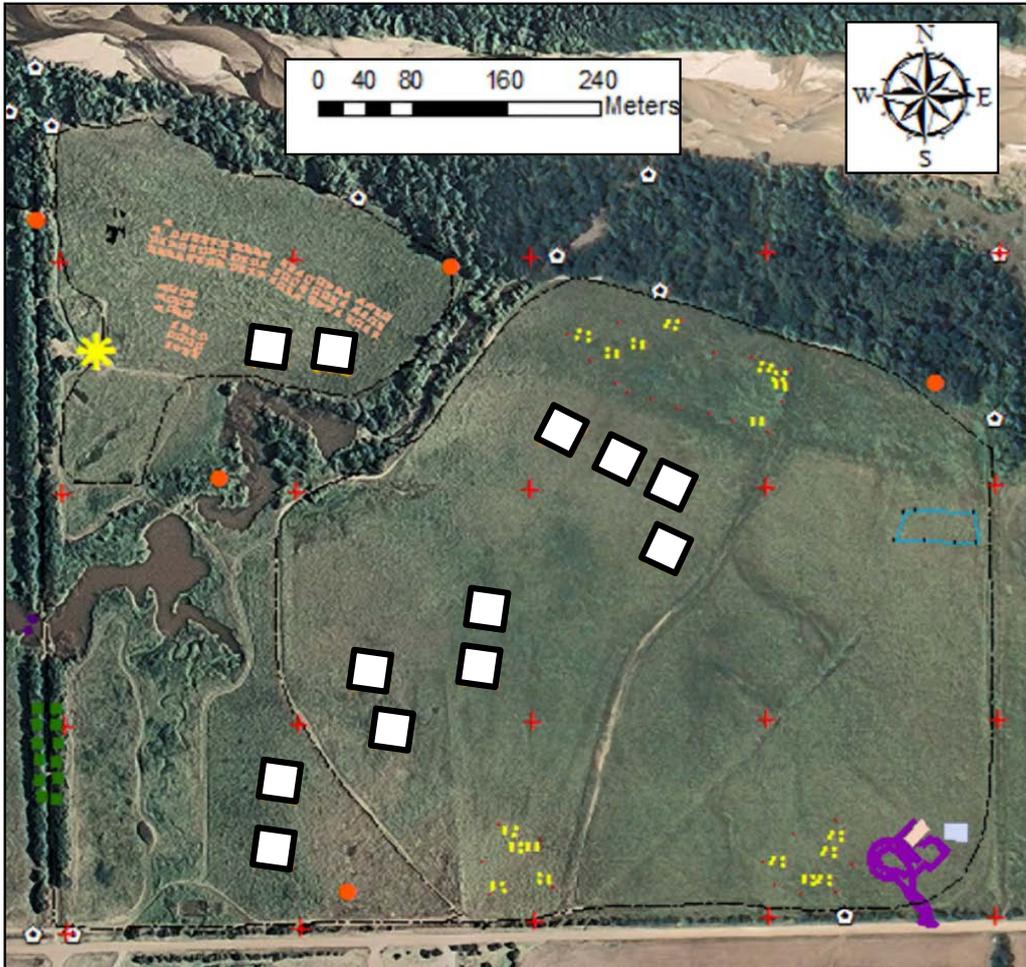


Fig 1. Map of Ninnescah with the plot locations indicated by white squares.

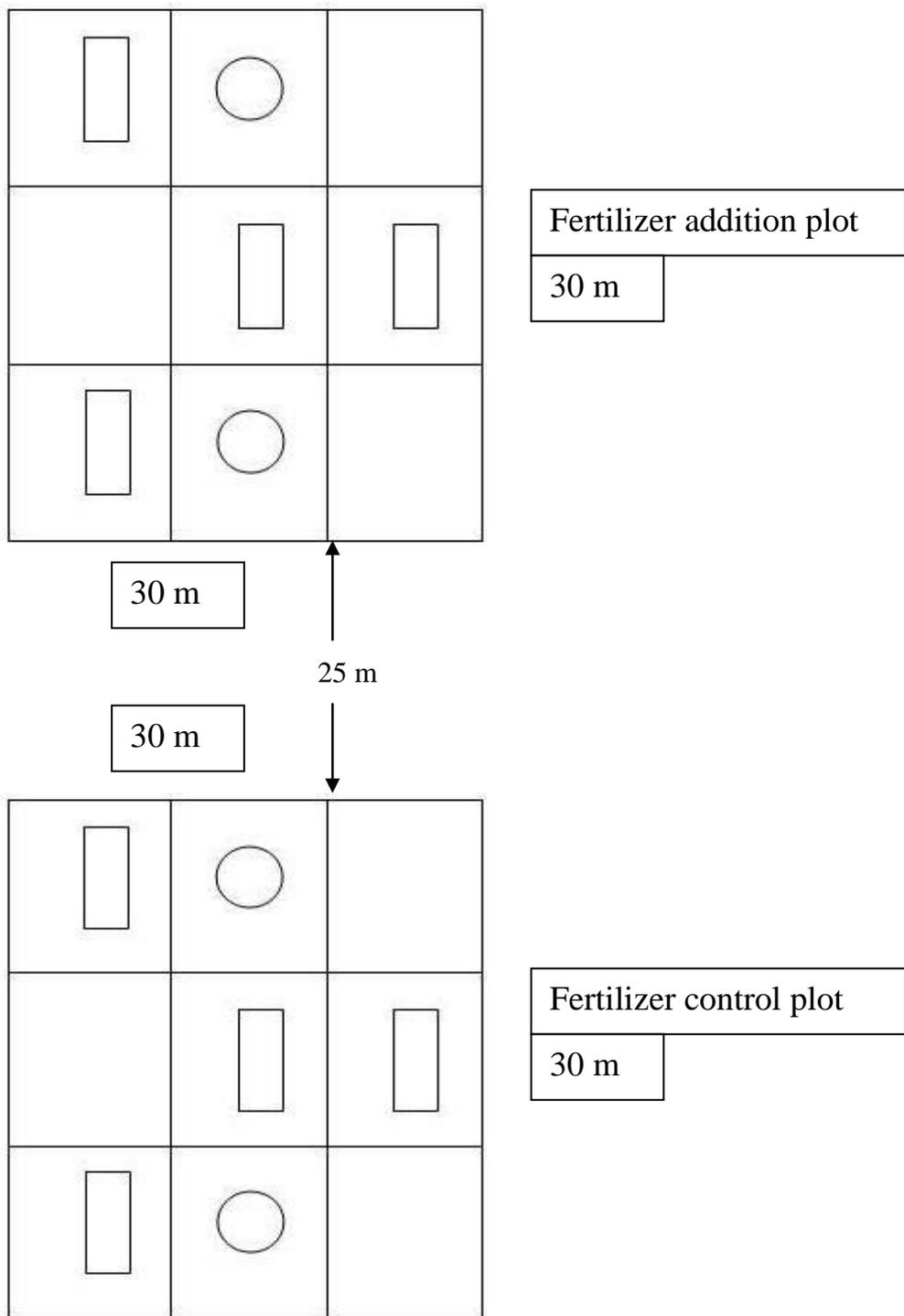


Fig 2. Representation of one block composed of a 30 m x 30 m fertilizer addition plot paired with a 30 m x 30 m fertilizer control plot. Rectangles within the 30 m x 30 m plots are locations of Sherman traps and circles are locations of Pitfall traps.

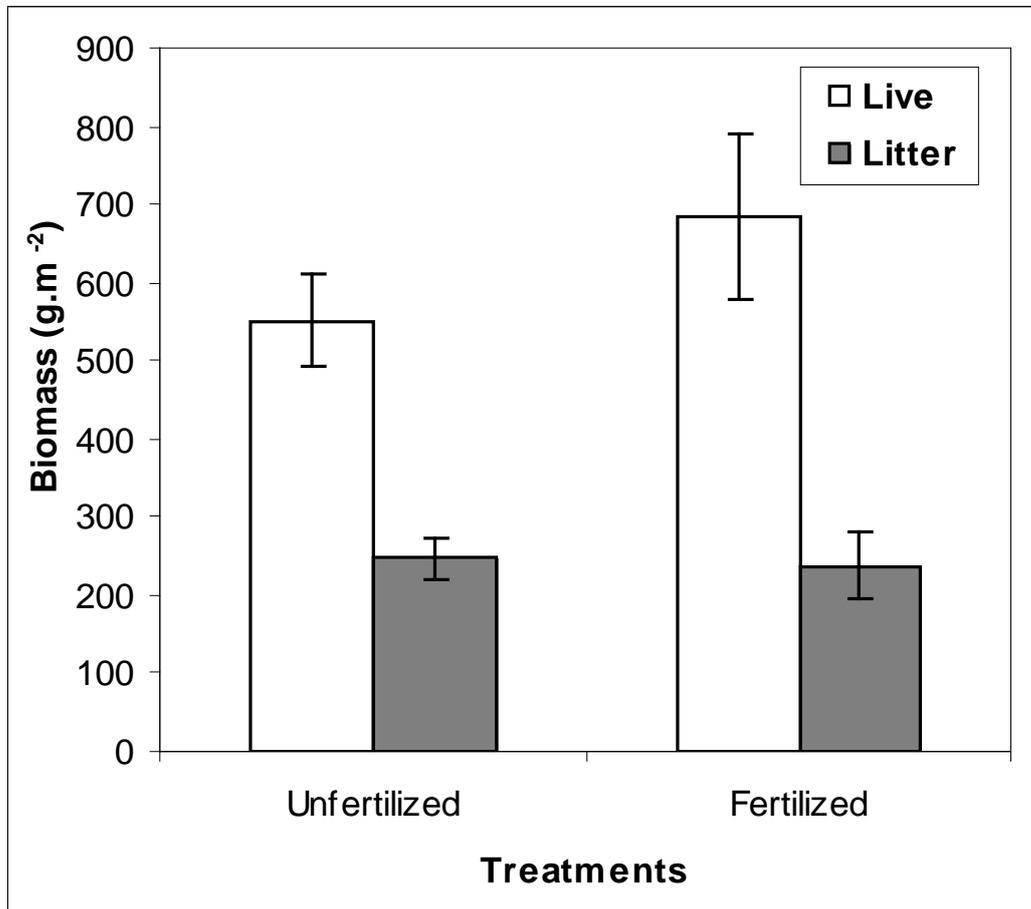


Fig 3. Standing crop biomass and litter vs. fertility. Means \pm standard errors are shown.

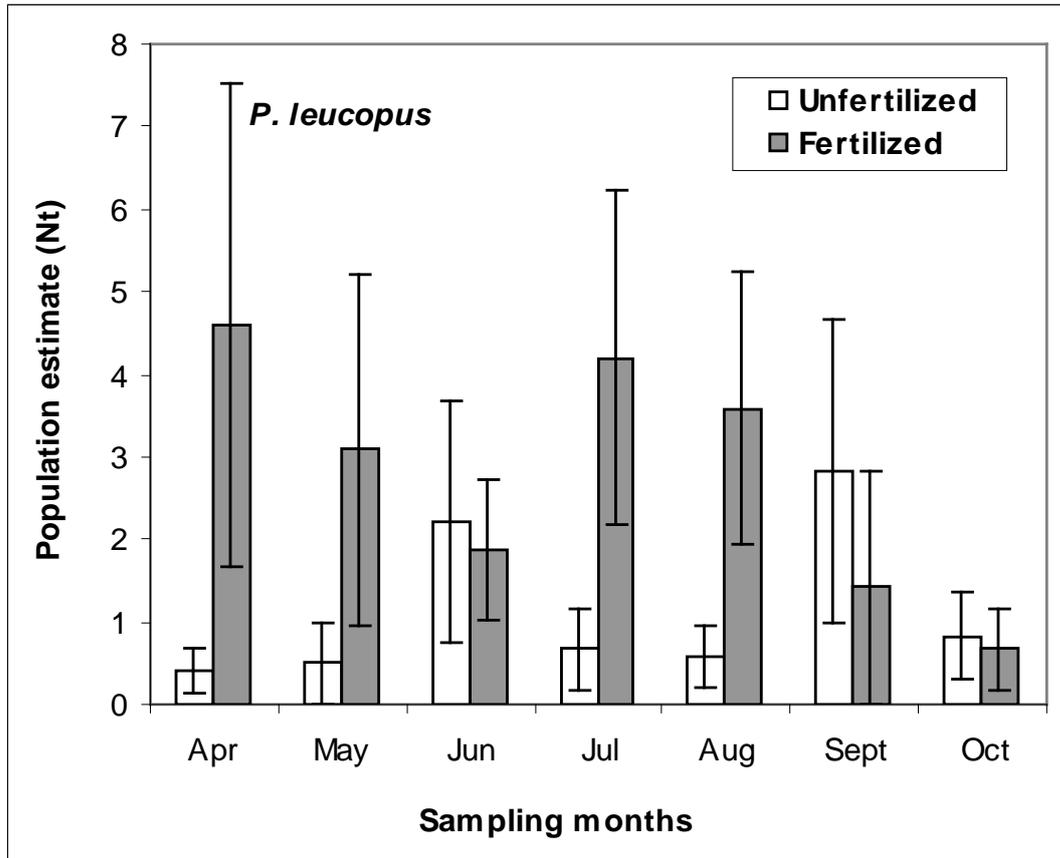


Fig 4. Population estimate of *P. leucopus* in relation to fertilizer addition. Means \pm standard errors are shown.

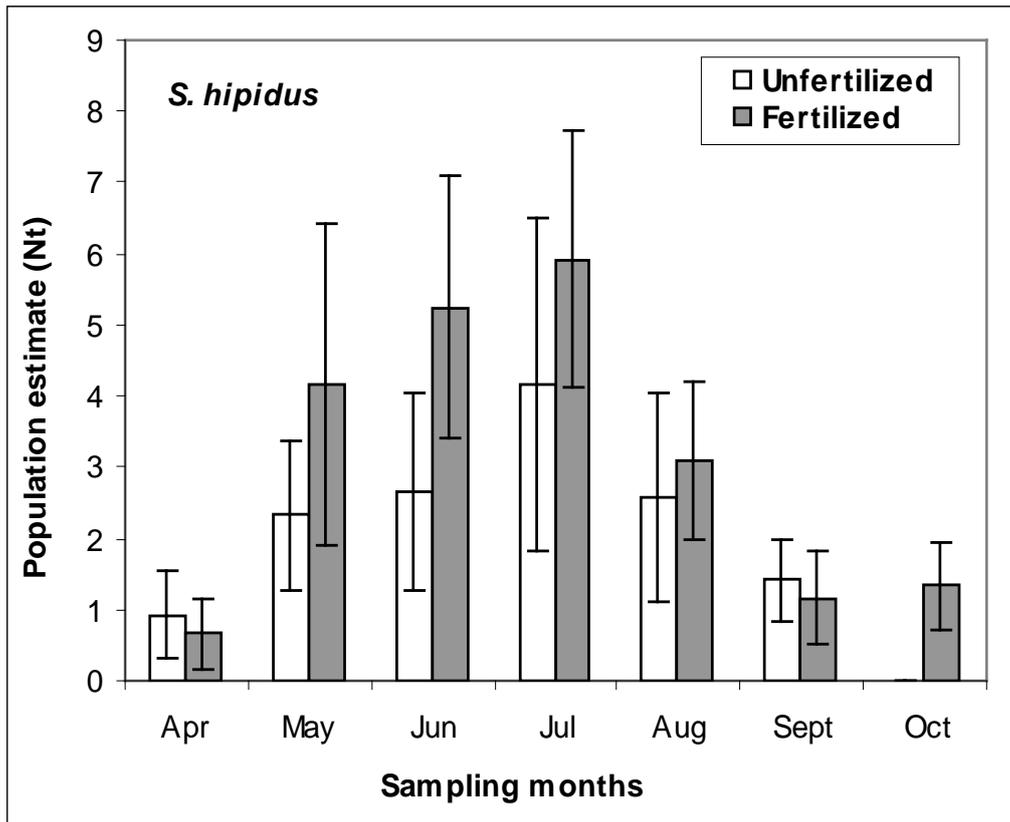


Fig 5. Population estimate of *S. hispidus* in relation to fertilizer addition. Means \pm standard errors are shown.

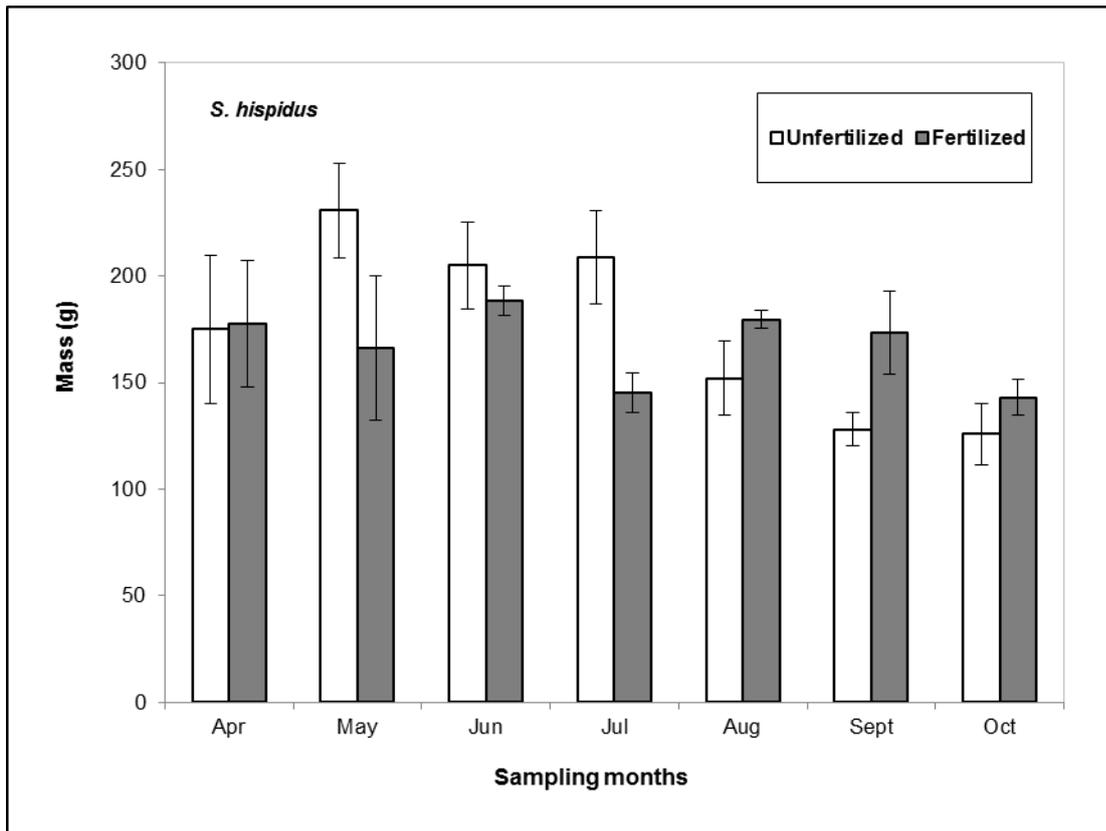


Fig 6. Average mass of *S. hispidus* in relation to fertilizer addition. Means \pm standard errors are shown.

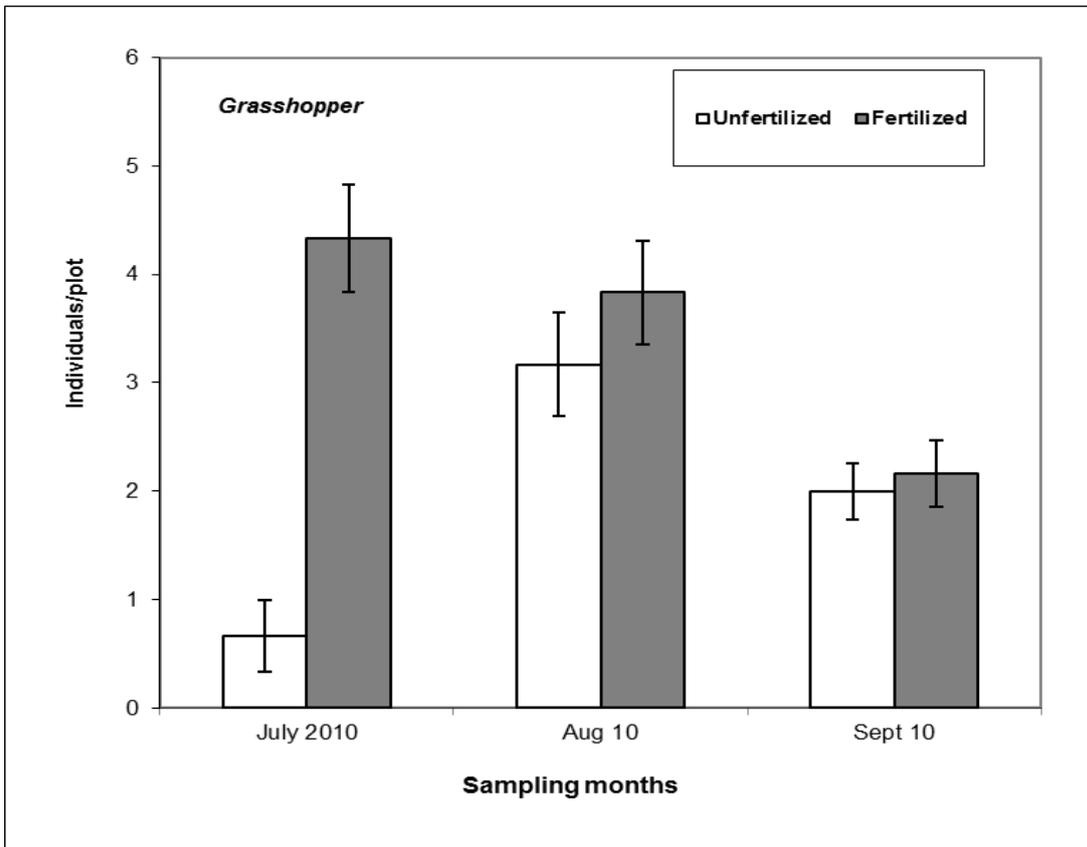


Fig 7. Density of grasshoppers in relation to fertilizer addition for a given sampling period. Means \pm standard errors are shown.

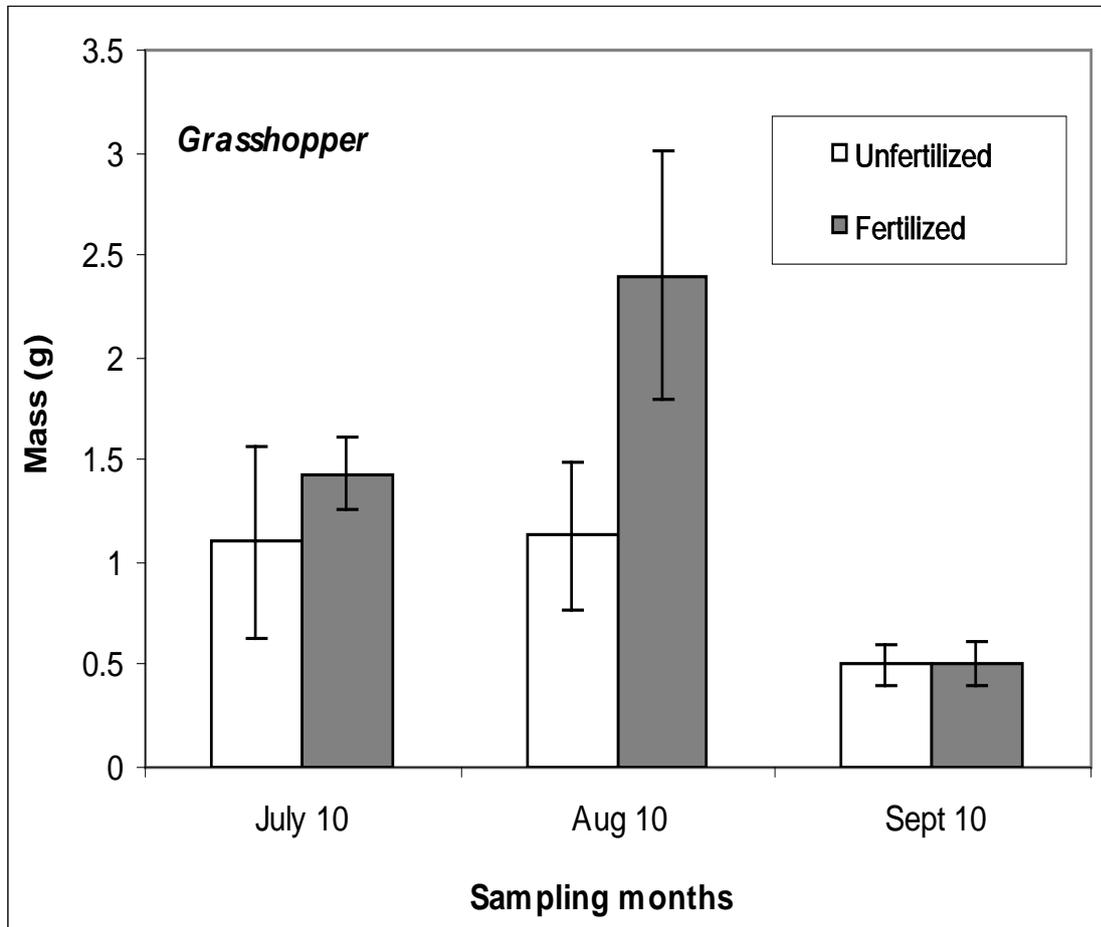


Fig 8. Average mass of grasshoppers in relation to fertilizer addition for a given sampling period. Means \pm standard errors are shown.

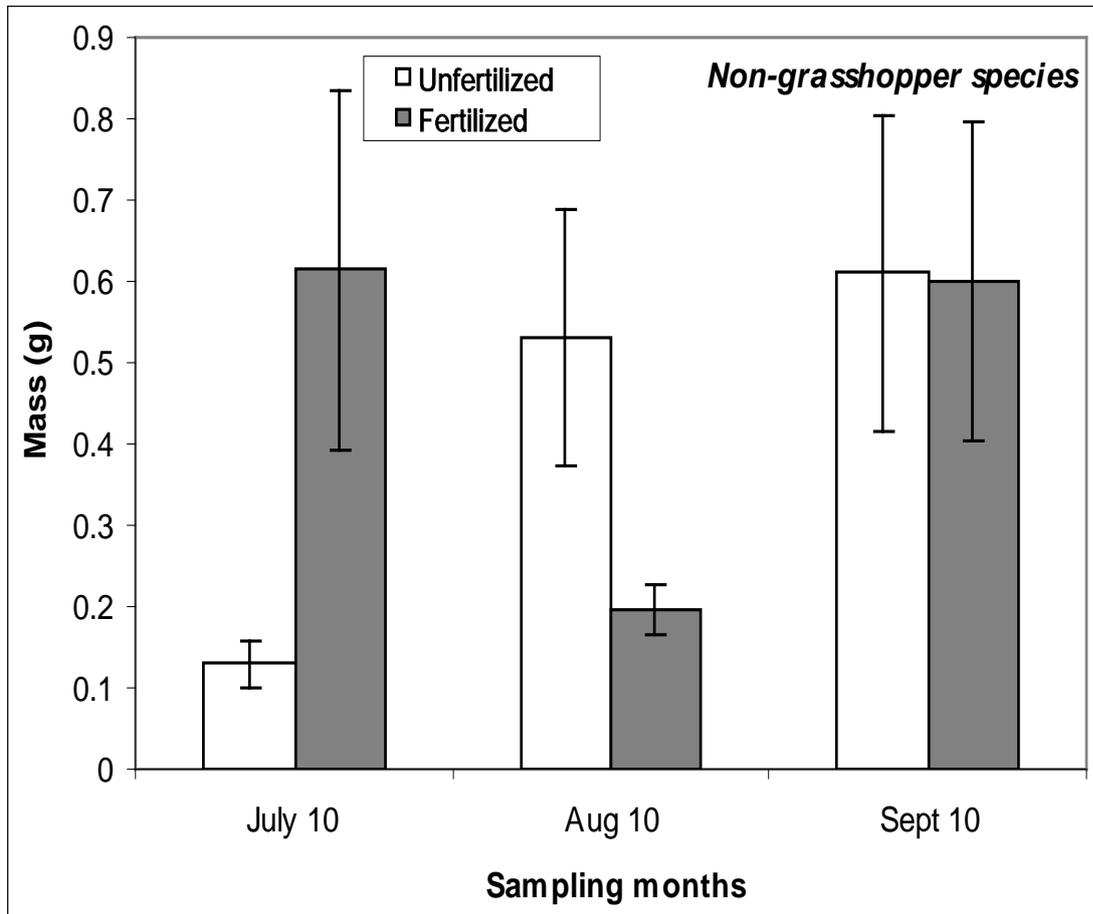


Fig 9. Total mass of non-grasshopper species in relation to fertilizer addition for a given sampling period. Means \pm standard errors are shown.

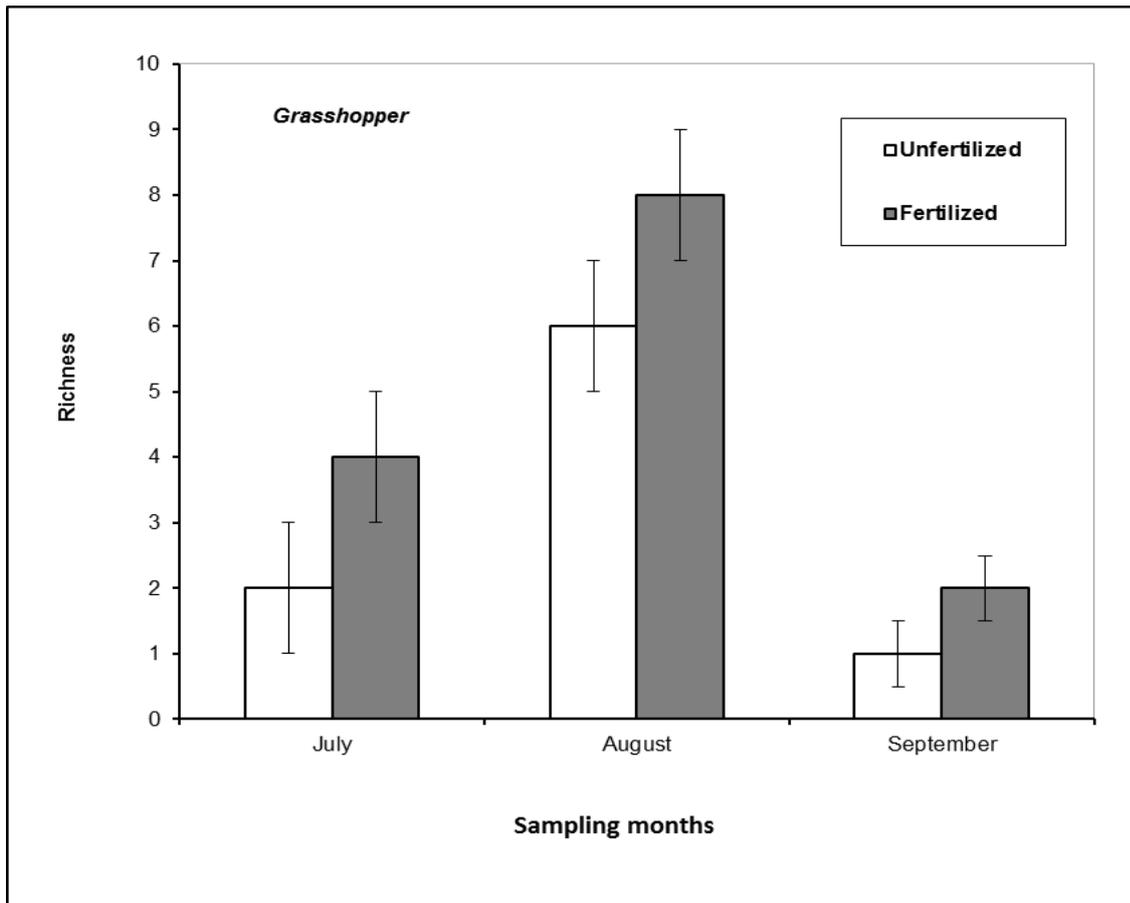


Fig 10. Grasshopper richness in relation to fertilizer addition. Means \pm standard errors are shown.