Dynamics of grasshoppers (Orthoptera:Acrididae) at a rangeland-crop interface
by Robert L Gillespie

A thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Biological Sciences
Montana State University

Abstract:
Scientists and producers who plan to develop an integrated pest management (IPM) program for economically important grasshopper species in small grains will have to focus their attention on field borders in order to suppress populations before they exceed an economic injury level in the crop. Knowledge of grasshopper population and community dynamics at the grassland-crop interface will be required before any IPM program can be successfully implemented. Such an understanding requires the development of accurate and efficient sampling methods. The assessment of the spatial pattern of grasshoppers is the first step in development and evaluation of such sampling methods. The spatial distribution of grasshoppers in reseeded range was studied at two morning sample periods. Based on the results of this spatial pattern analysis, the data suggest that some adult grasshoppers are aggregated when ambient temperatures are below 13°C. Sampling rings encompassing 10% or more vegetative basal cover had significantly greater density estimates than rings containing less basal area. Grasshopper counts from three different sized sampling rings were similar when three observers sampled rings simultaneously at two morning sample periods. Thirty-one species of grasshoppers were collected in both habitats. Melanoplus sanguinipes, M. bivittatus, and M, packardii were the predominant species in the crop and these three species plus A. elliotti were the predominant species in the adjacent range. Comparison of grasshopper density estimates between range and crop at weekly sample intervals resulted in the following conclusions. At several study sites significant differences in weekly density estimates of Melanoplus sanguinipes, M. bivittatus, and M, packardii occurred suggesting that these species were dispersing between habitats. At 5 study sites such shifts were not evident or no consistent pattern emerged in the density estimate differences. These results suggest that there was no dispersal between habitats at these sites. Comparing density estimates between habitats through time can be used to study the dispersal of grasshoppers. Site specific environmental and population dynamic factors may be correlated to dispersal at a given site. Significant differences in the age structure of M. sanguinipes, M. bivittatus, and M. packardii were found between habitats. In 1988, such age structure differences suggested that older instars dispersed into a second habitat while the younger instars, with less dispersal capabilities, remained in the original habitat. In 1989, differences in the partitioning of age classes occurred between the two habitats, but no pattern emerged as in 1988. In 1990, significantly more older instars were collected in the crop than in the range at all sample periods, even though no dispersal was detected at two of three sites. Results of this portion of the study suggested that the nutritional quality of plants in the crop could have been greater than that in range. More research is needed to determine which factor or factors are correlated with the age structure differences in the two habitats.

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ABSTRACT

Scientists and producers who plan to develop an integrated pest management (IPM) program for economically important grasshopper species in small grains will have to focus their attention on field borders in order to suppress populations before they exceed an economic injury level in the crop. Knowledge of grasshopper population and community dynamics at the grassland-crop interface will be required before any IPM program can be successfully implemented. Such an understanding requires the development of accurate and efficient sampling methods. The assessment of the spatial pattern of grasshoppers is the first step in development and evaluation of such sampling methods. The spatial distribution of grasshoppers in reseeded range was studied at two morning sample periods. Based on the results of this spatial pattern analysis, the data suggest that some adult grasshoppers are aggregated when ambient temperatures are below 13°C. Sampling rings encompassing 10% or more vegetative basal cover had significantly greater density estimates than rings containing less basal area. Grasshopper counts from three different sized sampling rings were similar when three observers sampled rings simultaneously at two morning sample periods. Thirty-one species of grasshoppers were collected in both habitats. *Melanoplus sanguinipes, M. bivittatus,* and *M, packardii* were the predominant species in the crop and these three species plus *A. elliotti* were the predominant species in the adjacent range. Comparison of grasshopper density estimates between range and crop at weekly sample intervals resulted in the following conclusions. At several study sites significant differences in weekly density estimates of *Melanoplus sanguinipes, M. bivittatus,* and *M, packardii* occurred suggesting that these species were dispersing between habitats. At 5 study sites such shifts were not evident or no consistent pattern emerged in the density estimate differences. These results suggest that there was no dispersal between habitats at these sites. Comparing density estimates between habitats through time can be used to study the dispersal of grasshoppers. Site specific environmental and population dynamic factors may be correlated to dispersal at a given site. Significant differences in the age structure of *M. sanguinipes, M. bivittatus*, and *M. packardii* were found between habitats. In 1988, such age structure differences suggested that older instars dispersed into a second habitat while the younger instars, with less dispersal capabilities, remained in the original habitat. In 1989, differences in the partitioning of age classes occurred between the two habitats, but no pattern emerged as in 1988. In 1990, significantly more older instars were collected in the crop than in the range at all sample periods, even though no dispersal was detected at two of three sites. Results of this portion of the study suggested that the nutritional quality of plants in the crop could have been greater than that in range. More research is needed to determine which factor or factors are correlated with the age structure differences in the two habitats.

CHAPTER ONE

DYNAMICS OF GRASSHOPPERS (ORTHOPTERA:ACRIDIDAE) AT A RANGELAND/CROP INTERFACE

General Introduction

During the past 150 years, the introduction of agriculture has altered North American prairie ecosystems. Agriculture has produced two fairly discrete co-existing and adjacent plant communities which share common borders. The border between the two habitats form long and narrow transition zones, in which, the crop is almost always composed of a single plant species which exists in the environment for a short period before being harvested. The rangeland habitat may have been altered by cattle or sheep grazing or a reseeding program which replaced native grasses with one or a few introduced plant species.

Changes in the patterns of land use in North America, brought about by the introduction of agriculture and grazing by cattle and sheep, has most likely led to shifts in the grasshopper species complex in these rangelands. One important example is the apparent extinction of *Melanoplus spretus* (Walsh), the Rocky Mountain grasshopper, in the early 1900's. Lockwood and Debrey (1990) have hypothesized that the extinction of the Rocky Mountain Grasshopper occurred when preferred egglaying sites in river bottoms and sunny upland slopes bordering these streams were cultivated. In more recent work on multi-species rangeland grasshopper communities in Gallatin Co. Montana USA, the predominant grasshopper species and grasshopper species complex

was altered when a *Stipa commata* Trin. and Rupr. *Bouteloua gracilis* (H.B.K.) Lag. habitat type was reseeded to crested wheatgrass, *Agropyron cristatum* (L.) Gaertn. and alfalfa, *Medicago sativa* L. (Kemp et. al. 1990a).

Further, several authors suggest that the severity of outbreaks in the Great Plains has been enhanced by cultivation and grazing by cattle and sheep (Ball 1937, Buckell 1937 a, b, Parker 1937). Uvarov (1947, 1956 (1958), 1957, and 1962) has stated that world-wide grasshopper plagues are associated with agricultural development in semi-arid areas. He suggested that agricultural practices produce a large number of areas with a patchy mosaic of vegetative cover and that such areas are conducive to the population development, buildup, and eventual outbreaks of a few grasshopper species.

Such changes have occurred in Manitoba, Canada, when large areas of wet prairie, marshes, and mixed grass prairie were developed for grain farming (Bird et. al. 1966, Romanov and Bird 1966). The introduction of agriculture to this area led to road and ditch building, the draining of marshes, and the replacement of native vegetation by introduced grasses, cereal crops, and weeds. All of these activities led to the development of attractive and nutritious food plants and oviposition sites for species such as *Camnula pellucida* (Scudder), the clearwinged grasshopper, *Melanoplus bivittatus* (Say), the twostriped grasshopper, and *M. sanguinipes* (Fabricius) the migratory grasshopper (Bird and Romanov 1966, Bird et. al. 1966). It is interesting to note, that all three species are considered pest of crops and rangeland in Canada and the United States (Brooks 1958, Edwards 1964, Pfadt 1977, Harris 1985, Pfadt 1985, APHIS 1987, Gillespie 1987). In the United States, Parker (1937) felt that environmental conditions for certain species of grasshoppers have also been improved by human disturbances. Grain fields provide forage during nymphal and adult

development for a few grasshopper species long after native grasses have matured. Roadsides, railroad right-of-ways, fence rows, and ditch banks lined with weedy plant species that mature later than native grass also provide late season forage.

The scientists above have described how they believe the fragmentation of the prairie ecosystem, by human activities, has lead to the creation of a large number of ectones or transition zones which provide a favorable environment for the population development of a few species of grasshoppers. Uvarov (1956) felt such a favorable environment would be composed of two habitats, which he termed an oviposition and food-shelter habitat. It has been proposed that in early spring field borders composed of early maturing grasses such as crested wheatgrass, *Agropyron cristatum,* may provide a suitable food-shelter habitat for grasshopper species. It has been suggested, that later in the season, some grasshopper species can then move to the maturing crop to feed when rangeland forage is no longer suitable for their development. In late summer, these species can return to these "transition zones", which are composed of ditches, headlands, and rangeland bordering the crop, to lay eggs in areas of undisturbed soil (Pickford 1963, Edwards 1964).

If these ectones, composed of a crop and adjacent range, provide suitable habitats, as proposed by Parker (1937), and Uvarov (1956), then the study of the population and community dynamics of grasshopper species at a rangeland/crop interface should be relevant to scientists, government land managers, and producers. This information is required in order to develop an integrated pest management program for grasshoppers in the crops of Montana.

This study was developed to provide a basis for the development of pest management alternatives for grasshoppers at the interface between rangeland and crops. The first step was the selection of sampling methods to study the population and

community dynamics of grasshoppers. Appropriate sampling methods cannot be selected until the spatial pattern of the organisms to be studied is identified (Southwood 1978, Kershaw and Looney 1985, Ludwig and Reynolds 1988). The identification of the spatial pattern of grasshoppers at different morning sample periods was the objective of Chapter 2. The spatial pattern was assessed using several existing methods.

In Chapter 3, grasshopper species/habitat associations in rangeland and winter wheat were identified. Predominant grasshopper species in each habitat were identified and ranked by abundance. Grasshopper density estimates in each habitat were also compared to determine if differences between these estimates were the same over time or if there were temporal shifts in theses estimates. Lastly, in Chapter 4, a comparison of the age structure of *Melanoplus sanguinipes, M. packardii,* and *M. bivittatus* was made between winter wheat and adjacent rangeland to determine if the age structure in both habitats was similar or if they varied during certain sample periods.

CHAPTER TWO

DAILY SPATIAL DISPERSION OF GRASSHOPPER SPECIES (ORTHOPTERA:ACRIDIDAE) IN RANGELAND RESEEDED TO CRESTED WHEATGRASS (*AGROPYRON CRISTATUM*) (L.) GAERTN.

Introduction

Grasshoppers are a major component of the herbivore complex in rangeland communities. Within this complex, certain species can exhibit dramatic shifts in abundance both within and between years (Shotwell 1941, Smith 1954, Parker et. al. 1955, Edwards 1964, Kemp 1991). Shifts within a year can occur when nymphs of certain grasshopper species disperse short distances from hatching beds to feed on crops (Parker et. al. 1955, Pickford 1963, Edwards 1964, Riegert et. al. 1965, Gillespie pers. obs. 1986, 1987). Also, adult grasshoppers such as *Camnula pellucida* Scudder and *Melanoplus sanguinipes* (Fabricius) can migrate from one location to another. Such flights have been reported by several observers in eastern Montana and western North Dakota (Shotwell 1941, Parker et. al. 1955, Gillespie pers. obs. 1986, 1987).

Grasshopper densities can also vary between years when populations of some species increase from non-economic densities to outbreak densities (Strand 1934, Mills 1941, Pepper 1962, Gage and Mukerji 1977, Onsager and Hewitt 1982, Morrill 1983, Montana Department of Agriculture 1989). During peaks of abundance, which usually

coincide with reduced rainfall, grasshoppers often compete with livestock and wildlife for forage (Anderson 1961, 1970 Hewitt et. al 1976, Hewitt 1977, Capinera and Sechrist 1982b, Hewitt and Onsager 1983).

To reduce the impact that grasshoppers have on rangeland and crops, ranchers, farmers, and government land managers must understand the temporal and spatial aspects of grasshopper population dynamics within and between years. They must also be able to assess grasshopper population levels and predict outbreaks if they plan to effectively intervene with suppression techniques when grasshopper populations increase toward economic injury levels. Obtaining such an understanding requires the development of accurate and efficient sampling methods. The assessment of spatial pattern is the first step in the development and evaluation of such sampling methods.

In two previous studies, the spatial pattern of grasshoppers was assessed using different sized sampling rings. Grasshoppers flushed from these sampling rings were counted (Thompson 1987, Onsager 1991) and the counts placed in an observed frequency distribution. These distributions were compared to the expected frequency distribution of a Poisson distribution model (Onsager 1991) and a Poisson and negative binomial model by Thompson (1987). In both studies, the spatial pattern of grasshoppers was studied at one sample period which occurred between mid-morning and early afternoon when grasshoppers were active and readily flushed from sampling rings (Onsager 1977, 1991, Thompson 1987, 1988).

Onsager (1991) used 0.05, 0.10, and 0.25m^2 sampling rings to study the spatial pattern of grasshoppers in a *Stipa comata* Trin. and Rupr. *Bouteloua gracilis* (H.B.K.) Lag. (STCO/BOGR) habitat type (Meuggler and Stewart 1980) reseeded to *Agropyron cristatum* (L.) Gaertn. *Medicago sativa* L. (Agcr/Mesa). He concluded that the observed frequency distributions of all three sized rings approximated a Poisson

distribution. The results of this study suggest that future studies designed to estimate grasshopper densities in a Agcr/Mesa habitat, during mid-morning to early afternoon, should use a sampling design which assumes grasshoppers are randomly distributed.

Thompson (1987, 1988) studied the spatial pattern of grasshoppers in the short grass prairie of Colorado. He found that when the observed frequency distributions of five different sized rings were compared to the expected frequency distributions of a Poisson and negative binomial distribution model that these distributions fit both models in 98% of the samples. He also found that as the sampling rings increased in size from 0.10 to 1.00 m^2 the perception of non-randomness increased. In other native rangeland studies, which relied only on field observations, Anderson & Wright (1952), Anderson (1964), Prihar (1983) stated that grasshoppers were not randomly dispersed within a habitat. In a study of vegetation structure in arid rangelands of Texas, grasshopper species displayed definite preferences for microhabitats, and such preferences may have important effects on the spatial pattern of grasshoppers (Joern 1982).

Differences in the perception of the spatial pattern of grasshoppers in past studies may be due to sampling and observations that were made at different times, during the day or year, when the spatial pattern of grasshoppers was different. It has been hypothesized that the spatial dispersion of grasshoppers may change on a daily or weekly basis as grasshoppers move within and between habitats in response to thermal conditions (Parker 1930, Shotwell 1941, Anderson et. al 1979, Kemp 1986) changes in availability of food plants (Otte and Joern 1977, Joern 1979b), and variation in vegetative structure (Anderson 1964, Clark 1948, Uvarov 1977).

Grasshoppers appear to respond to different thermal conditions in the environment by various behavioral strategies (Uvarov 1977, Anderson et. al. 1979). For example, in response to low ambient temperatures Parker (1982) found that *Dactylotum bicolor*

(Thomas) concentrated in the plant canopy where they could maintain the highest body temperatures. Sheltering from cold has also been described for other temperate species where they often spend cold nights near the ground aggregated in dense vegetation (Uvarov 1977). *Schistocerca gregaria* adults, exposed to cold winter conditions in Morocco, clumped deep inside low vegetation and in rock crevices when air temperature was about 8°C (Waloff pers. comm. in Uvarov 1977).

Daily shifts in the spatial pattern of grasshoppers may also affect the accuracy of density estimates taken at different times and/or temperatures during the day. For example, in a study of the Moroccan locust, *Dociostaurus maroceanus* Thunberg., the percent of the population occupying areas with 100% vegetative cover changed from 30% in early morning before 930h to 40% after 930h as individuals in the population moved from sparse to dense vegetation (Southwood 1978). Sampling at different times during the day would have resulted in two different density estimates in this study (Southwood 1978). While generating grasshopper counts to study the spatial pattern of grasshoppers in short grass prairie, Thompson (1988) found that density estimates made at temperatures below 15°C were 400% lower than those made when temperatures exceeded 25°C.

Two types of observations made by myself and coworkers at study sites in 1988 and 1989 in reseeded rangeland seemed to support the conclusions of the studies above and led to the design of the following study. In 1988, while sampling grasshoppers in winter wheat and the adjacent rangeland just after dawn, grasshopper densities appeared to be lower early in the morning when compared to those at mid-morning or early afternoon. We thought there might be two possible explanations for such observations. First, it was possible that grasshoppers resumed daily activity when ambient temperatures reached a certain threshold. Thus, the appearance of lower

grasshopper density in the rangeland and crop was due to grasshopper inactivity early in the morning when compared to mid-morning or early afternoon. While comparing different absolute density estimates techniques early in the morning, in 1989, I noticed that adult grasshoppers appeared to be aggregated in clumps of crested wheatgrass and alfalfa. These observations led to the second explanation, the spatial distribution of adult grasshoppers may change while sampling from early morning to mid-morning as they resume daily activity in response to increasing ambient temperatures. Sampling under the assumption that grasshoppers are randomly distributed early in the morning, when in fact they are clumped, could result in different density estimates at a study site at different times of the day.

I established a study to monitor several aspects of the spatial pattern of grasshoppers at two morning sample periods in reseeded rangeland. First, I maintained different sample periods during the morning to assess the spatial pattern of adult grasshoppers at different ambient temperatures and determine if the pattern remained constant through time. In addition, I sampled at different ambient temperatures to determine if density estimates were affected by changes in these temperatures across two sample periods. I also assessed the basal area of vegetation encompassed by each sampling ring to determine if grasshopper density estimates remain the same as basal plant area increases in the sampling rings. Finally, density estimates produced by three observers counting three different sized sampling rings simultaneously, were compared to determine if these estimates were similar at two sample periods.

Review of Sampling Methods

The three types of dispersion are random, aggregated, and regular. Each affects the sample design, sampling strategy, the size and type of subsampling units, the

methods of data analysis, and interpretation of results (Karandinos 1976, Southwood 1976, Elliot 1977, Greg-Smith 1983, Kershaw and Looney 1985, Ludwig and Reynolds 1988). Once the underlying spatial pattern of a plant or animal has been identified, we can propose and test hypotheses that suggest which environmental factors are correlated with the structure of ecological communities (Greig-Smith 1983, Ludwig and Reynolds 1988). For example, after identifying the spatial pattern of ant nests as clumped, Dorchester (1981 in Kershaw and Looney 1988) found that the clumped pattern was influenced by slope exposure, moisture, and rabbit grazing.

Several techniques have been developed to detect the spatial pattern of organisms. Ludwig and Reynolds divide these techniques into methods which rely on natural and arbitrary sample units for spatial pattern analysis. Natural sample units are defined as units where organisms occur in discrete segments of a habitat. Some examples include aphids on a leaf, insects in fruit, or detritivores in dung pats (Ludwig and Reynolds 1988). Arbitrary sample units, such as quadrats, have to be used when sampling organisms in continuous habitats, such as trees in a forest, zooplankton in the ocean, or grasses in a prairie. Sample statistics, such as the mean number of trees, generated using arbitrary sample units may convey less meaningful information than those produced using natural sample units because selection of different sized sample units in a continuous habitat may result in different conclusions (Ludwig and Reynolds 1988).

Ludwig and Reynolds (1988) discuss some of the methods developed to study the spatial pattern of organisms using natural and arbitrary sample units. One technique that relies on natural sample units is the comparison of an observed frequency distribution of sample unit counts to a distribution model. To use this method, a researcher summarizes the number of individuals counted per sample unit into a frequency distribution. Such frequency distributions are composed of frequency

classes. One class consists of all sample units with 0 individuals, a second is all sample units with 1 individual; sample unit counts continue to be assigned to classes until all individual counts are placed into a frequency class. The observed frequency distribution produced by the sampling study is then compared to a statistical frequency distribution model, such as the Poisson for random spatial patterns where the mean number of individuals per sample unit is equal to the variance of the sample. Other commonly used models are the negative binomial for clumped spatial pattern, where the mean is less than the variance and the positive binomial for regular or uniform spatial pattern, where the mean is greater than the variance. This method is often used to study the spatial pattern of organisms in continuous habitats even though results may be affected by the researcher's choice of sample unit size (Ludwig and Reynolds 1988).

Ludwig and Reynolds (1988) also describe spatial pattern analysis methods using arbitrary sample units in continuous habitats. Quadrat-variance methods are one example of such techniques. Researchers, using quadrat-variance methods, plot the mean-variance ratio over a range of different sized sampling units to determine if there is an abrupt departure from a ratio of one at a given sample unit size. Such abrupt departures occur when the sample unit size approximates the clump size of the organism (Ludwig and Reynolds 1988). Also, if the observed distribution is random, the expected number of individuals per quadrat remains relatively constant as the sample unit size is systematically increased by adding quadrats to a block of sample units. If the observed distribution is clumped, the number of individuals per sample unit will be influenced by increasing the sample unit size. When the sample unit size approximates the clump size, the mean will be less than the variance. When the sample unit size is smaller or larger than the clump size the mean will be approximately equal to the variance (Ludwig and Reynolds 1988).

A second group of methods used to describe the spatial pattern of organisms in continuous habitats are distance or plotless sampling techniques (Ludwig and Reynolds 1988). One such method is the nearest-neighbor technique. In this technique, a transect or several transects can be laid out in the habitat to help the observer locate and avoid resampling individuals, however, the use of a transect is not required when using these methods. An observer begins at one end of the transect and searches for an individual organism. When the first individual is located, its location is noted and then a search begins for its nearest conspecific neighbor. When the nearest neighbor is located, the distance between the first individual and its nearest neighbor is measured and recorded. This method is repeated until the entire length of the transect or transects has been sampled. The mean observed nearest neighbor distance is compared to an expected distance to determine whether the distribution of individuals is random, clumped, or regular (Campbell and Clarke 1971, Matthews and Matthews 1982).

Plotless sampling methods have been successfully used to study the spatial pattern of plants and fairly sessile animals. Unfortunately, they are difficult to use when studying the spatial pattern of highly mobile organisms, like many insects. Given the problems faced with spatial pattern analysis and the fact that the observed frequency distribution of some organisms can fit more than one distribution model, Ludwig and Reynolds (1988) recommend using more than one method when studying the spatial pattern of organisms.

One of the reasons for studying the spatial pattern of an organism is to design a sampling method which provides an accurate estimate of an organisms density. One such density estimate can be obtained by totaling the number of organisms per sample unit and dividing by the number of sample units. This sample statistic is the mean which can be used to estimate the absolute density of the organism at a study site; the

standard error of the sample mean can also be calculated and indicates the amount of error in the sample mean when used to estimate the population mean. Such direct density estimates are important because they measure the number of organisms per sample unit area. Control decisions are often based on such absolute density estimates. Inaccurate estimates may lead to a poor conclusion concerning the grasshopper population under study, and ultimately, lead to the application of controls when none are warranted. Selecting the proper sampling design, sampling unit size and accounting for temporal variation in counts within a day will improve the precision of population estimates. However, none of this can be done without identifying the spatial pattern of the organisms before sampling begins.

This problem affects commonly used grasshopper sampling techniques, such as ring samples, night cages, drop cages, and slam samplers. The latter three sampling devices use some form of cage to enclose an area of vegetation. Night cages are placed out in a study area late at night or pre-dawn. Dirt is banked around the cages to prevent escape by grasshoppers. After dawn, grasshoppers enclosed in the cage are counted to arrive at a density estimate. Areas enclosed by a night cage vary depending on the study (Onsager 1977, Evans et. al. 1983).

Drop cages and slam samplers are used at night or early in the morning while grasshoppers are relatively inactive. When the drop cage is used in the early morning, the sampler moves rapidly to an area and slams the cage to the soil surface. The lid of the drop cage is slowly lifted while vacuuming up the trapped grasshoppers. A muslin sleeve is placed in the end of the vacuum hose to capture grasshoppers before they pass through the fan of the vacuum. This procedure is then repeated at a series of predetermined sites (Onsager 1977, Onsager and Hewitt 1982, Onsager 1991, see Chapter 3 for discussion).

A slam sampler is similar to a drop cage with the following modifications. The cage of the slam sampler is connected to a long rod approximately five meters in length. Attached perpendicular to the end of the rod is a 0.5 meter handle. To capture grasshoppers, the cage is placed in the front of the sampler. The sampler stands on the handle and uses a rope attached to the cage to pull it up over and past the samplers head. Gravity pulls the cage to the soil surface. The cage lands behind the sampler capturing the grasshoppers enclosed by the cage (Woods pers. com.).

Rising ambient temperatures during sampling can also affect density estimates, by influencing the capture efficiency of early morning sampling methods such as drop cages and/or slam samplers (Onsager 1991). For this reason, the three sampling methods described above are more effective when grasshoppers are inactive at night or very early morning when grasshopper body temperatures are lower (Onsager 1991). Unfortunately, such temperatures rarely prevail throughout a sampling period. Increased activity of grasshoppers in response to increasing ambient temperatures results in a decreased capture rate, and thus less accurate density estimates (Onsager 1991).

Methods and Materials

Study Site

The study site was located 15 km south of Three Forks (T1S, R2E, S18, longitude 111°30' latitude 45°45') Gallatin County, Montana, USA. The three dominant plant species at the study were crested wheatgrass *Agropyron cristatum*, alfalfa *Medicago sativa*, and blue grama *Bouteloua gracilis* (H.B.K.) Lag.

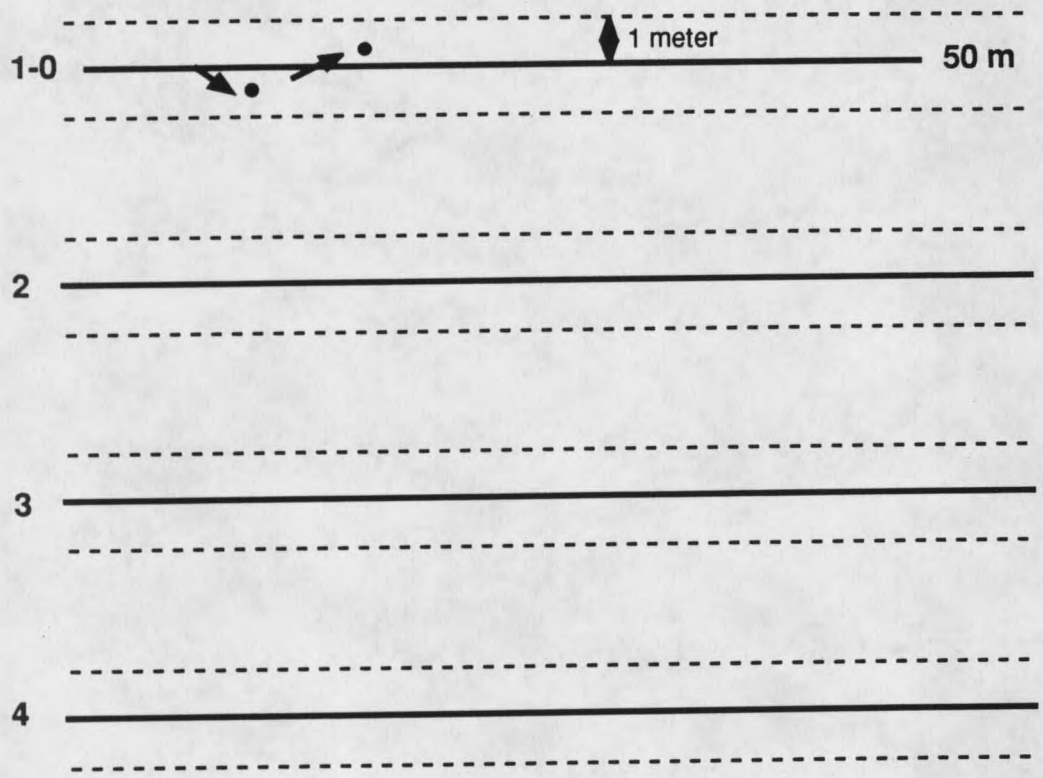
Preliminary Spatial Pattern Study

To study the spatial distribution of *Melanoplus packardii* Scudder using a nearest-neighbor technique (Clarke and Campbell 1971, Southwood 1978, Matthews and Matthews 1982), four 50 meter transects were laid out in an east-west direction (Figure 1). Two observers began at one end of a transect and attempted to locate all *M. packardii* within 1.0 m of each side of the transect. When a *M. packardii* was located, the distance to its nearest conspecific neighbor was measured to the closest 1.0 cm even if the neighbor was outside the area sampled. This technique was repeated along the entire length of all four transects. The null hypothesis tested with this study, was that, the spatial pattern of *M. packardii* was random along all four transects.

The mean observed distance between nearest-neighbors (r_O) and the average expected distance between individuals (r_E) was calculated. The degree to which the sample population of *M. packardii* departed from randomness (R) was measured by the ratio $R = r_O/r_E$ (Campbell and Clarke 1971, Matthews and Matthews 1982). If the sample population was randomly distributed, R would be close to 1. If the sample population was clumped, R would be smaller than 1 and if regular R would be greater

than 1. A standard z score was computed to determine if any departure from randomness was of statistical significance. *R* was considered statistically significant if z was 1.96 or greater (Matthews and Matthews 1982). Mean nearest neighbor distances for each transect were calculated and tested for conformity to a random distribution (Matthew and Matthew 1982).

Figure 1. Sampling design for nearest-neighbor test to measure the spatial pattern of *M. packardii*.



Spatial Pattern Study

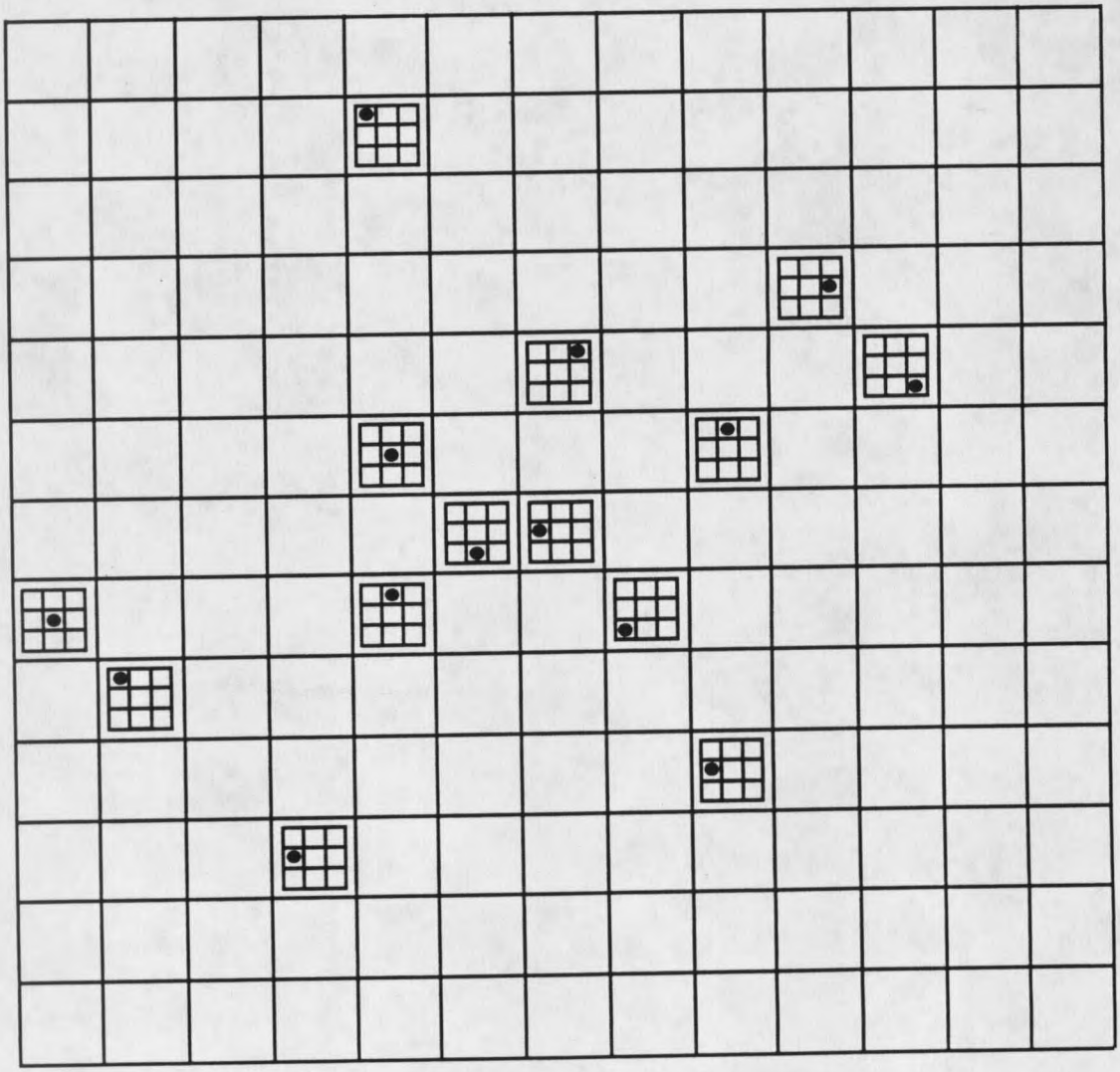
Sample Plot Designs. At the 1990 study site, two sample plots (East Block and West Block) were established. A plot consisted of 169 10 x 10 meter quadrats (Figure 2). One sampling ring made of 3 gauge aluminum wire was placed within a randomly selected quadrat. There were 80, 0.05m^2 rings, 40 0.10m^2 rings, and 16, 0.25m^2 rings (total of 136 rings) for each set of 169 quadrats. The total area encompassed in the three ring size classes was equal (4m^2) and allowed comparison of grasshopper densities per square meter between ring size classes. In order to avoid disturbing grasshoppers in adjacent rings during sampling, each ring was placed at least 6m from any neighboring ring. This restriction limited the random placement of a ring to nine grid sites within a quadrat. The nine potential ring sites within a quadrat encompassed a 4 x 4 meter area (Figure 2).

Sampling. A block of 136 rings was sampled either in the early morning or mid-morning. The first block of rings was selected at random and sampled in early morning followed by the second block of rings in mid-morning. The order of sampling was then reversed on the following day. This allowed comparison of grasshopper densities between time of day and blocks. Grasshoppers encompassed by the rings were flushed and recorded as the observer slowly approached the ring. A 2.5 meter stick was used to assist in the flushing of grasshoppers (Onsager and Henry 1977).

Temperatures during the study varied from 6-14°C at the initiation of sampling and from 14-18°C at the termination of early morning sampling. Early morning sampling began approximately 20 min after sunrise between O620h and 0720h over the duration of the study and was terminated between 0800h and 0830h. Mid-morning sampling

began between 0900h and 0930h when temperatures ranged from 16-28°C. Sampling was terminated between 1000h and 1040h when temperatures ranged between 20-32°C. Ambient air temperatures were recorded by placing a glass mercury thermometer 10 cm above the soil surface. The thermometer case was placed so its broad surface was parallel to the sun rays to avoid excessive heating of the thermometer.

Figure 2. Ring randomization scheme for density estimate study 136 rings were randomly assigned to 169 10x10 meter quadrants: 180, 0.05m^2; 40, 0.10m^2 ; 16, 0.25m^2 rings. A 4x4 meter grid containing 9 blocks was placed in each quadrant. A ring was randomly placed in one of the nine blocks.



Spatial Pattern Analysis Using Distribution Models

The 136 subsample rings in which one ring was randomly placed in a quadrat were recorded separately so that the data could be assigned to the appropriate ring size. Grasshopper counts were summarized in frequency tables. Counts in the tables for each ring size were used to test the hypotheses that the spatial distribution of grasshoppers during early and mid-morning sampling periods approximated a Poisson and negative binomial distributions. The data were tested under two null hypotheses because (Ludwig and Reynolds 1988) found that sample populations could fit more than one distribution model. Data from this portion of the study were analyzed using the statistical programs Poisson.Bas and NegBinom.Bas developed by Ludwig and Reynolds (1988). The Poisson.Bas program calculated expected Poisson probabilities for x number of grasshoppers per subsample unit.

Multiplying N (the number of observations) by the expected Poisson probabilities produced the expected number of grasshoppers per subsample unit. A Chi-squared test was used to test the goodness of fit between expected and observed frequencies. The program NegBinom.Bas follows a similar procedure, but computes expected frequencies for sample populations in which their distribution is clumped or aggregated and tests for goodness of fit.

Spatial Pattern Analysis Using Morisita's Index of Dispersion.

Morisita's index of dispersion (I_d) was plotted against increasing subsample sizes to determine if I_d remained constant over changing subsample sizes or increased abruptly when the size of the subsample unit approximated the clump size (Ludwig and Reynolds 1988). If an abrupt change occurred in the graph this was evidence that dis-