



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

© Copyright by Robert L Gillespie (1992)

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.

**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
Bozeman, Montana

April 1992

D378
34127

APPROVAL

of a thesis submitted by

Robert L. Gillespie

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

19 May 92
Date

Matthew Lavin
Co-Chairman, Graduate Committee

19 May 1992
Date

W.P. [Signature]
Co-Chairman, Graduate Committee

Approved for the Major Department

21 May 1992
Date

Robert S. Moore
Head, Major Department

Approved for the College of Graduate Studies

May 29, 1992
Date

Henry J. Parsons
Graduate Dean

STATEMENT OF PERMISSION TO USE

In presenting this thesis in partial fulfillment of the requirements for a doctoral degree at Montana State University, I agree that the Library shall make it available to borrowers under rules of the Library. I further agree that copying of this thesis is allowable only for scholarly purposes, consistent with "fair use" as prescribed in the U.S. Copyright Law. Requests for extensive copying or reproduction of this thesis should be referred to University Microfilms International, 300 North Zeeb Road, Ann Arbor, Michigan 48106, to whom I have granted "the exclusive right to reproduce and distribute copies of the dissertation in and from microfilm and the right to reproduce and distribute by abstract in any format."

Signature

Robert L. Gillespie

Date

6/12/92

ACKNOWLEDGMENTS

I am very grateful to Dr. William P. Kemp for his friendship and support while supervising this dissertation. His knowledge and experience have been most valuable. I also thank my other committee members, Dr. Kevin O'Neill for lab space and instilling in me an interest in behavioral and evolutionary biology, Dr. Matthew Lavin for introducing me to the joys of plants, Dr. Patricia Munholland for all her guidance in statistics, Dr. Gregory Johnson for his help in applied entomology, and Dr. Theodore Weaver III for providing his assistance in plant ecology. Thanks go also to Dr. Michael Wells for serving as graduate representative. I thank Stephen Biamonte for his help collecting and sorting grasshoppers in 1988, and Erin O. Hooten for her help in sorting and identifying grasshoppers in 1988 and 1989. I would also like to thank Jeffrey Holmes for his help in procuring collecting supplies and equipment, in sampling grasshoppers, and help with sampling designs and problems.

I especially want to thank my family, Caitlin, Luke, and Jean for their love and patience while I completed this degree. Without their help and support I could not have finished the requirements for this degree. Lastly, I want to thank Jean, my wife, for her support and all her help with the computer, graphics and the layout of the dissertation.

TABLE OF CONTENTS

	Page
APPROVAL.....	ii
STATEMENT OF PERMISSION TO USE.....	iii
ACKNOWLEDGEMENTS.....	iv
TABLE OF CONTENTS.....	v
LIST OF TABLES.....	vii
LIST OF FIGURES.....	viii
ABSTRACT.....	ix
1. DYNAMICS OF GRASSHOPPERS (ORTHOPTERA: ACRIDIDAE) AT A RANGELAND/CROP INTERFACE.....	1
General Introduction.....	1
2. DAILY SPATIAL DISPERSION OF GRASSHOPPER SPECIES (ORTHOPTERA:ACRIDIDAE) IN RANGELAND RESEEDED TO CRESTED WHEATGRASS (<i>AGROPYRON CRISTATUM</i>) (L.) GAERTN.....	5
Introduction.....	5
Review of Sampling Methods.....	9
Methods and Materials.....	
Study Site.....	15
Preliminary Spatial Pattern Study.....	15
Spatial Pattern Study.....	17
Sample Plot Designs.....	17
Sampling.....	17
Spatial Pattern Analysis Using Distribution Models.....	19
Spatial Pattern Analysis Using Morisita's Index of Dispersion.....	19
Spatial Pattern Data Analysis Density Estimates.....	20
Vegetation Basal Area and Grasshopper Density Comparisons.....	21
Potential Sampling Bias Evaluated Using Three Different Sized Rings.....	22
Results.....	
Preliminary Spatial Pattern Analysis.....	22
Spatial Pattern Analysis Using Distribution Models.....	24
Spatial Pattern Analysis Using Morisita's Index of Dispersion.....	24
Grasshopper Density Estimate Comparisons.....	27
Grasshopper Density Estimates Compared to Percent Basal Area Estimates of Vegetation.....	28
Variation in Density Estimates by Three Observers.....	31
Discussion.....	
Spatial Pattern of Grasshoppers.....	32
Grasshopper Density and Ring Basal Cover.....	38
Variation in Density Estimates by Three Samplers.....	38

TABLE OF CONTENTS Continued.

	Page
3. HABITAT ASSOCIATIONS AND TEMPORAL SHIFTS IN DENSITIES OF GRASSHOPPER SPECIES (ORTHOPTERA: ACRIDIDAE) BETWEEN WINTER WHEAT (TRITICUM AESTIVUM L.) AND ADJACENT RANGELAND	40
Introduction.....	40
Methods and Materials	
Study Site.....	44
Sampling Design, Equipment, and Regime	44
Sampling Regime.....	48
Data Analysis.....	50
Results	
Grasshopper Species Occupying Winter Wheat and Adjacent Field Borders	52
Predominant Grasshopper Species in Rangeland Over the Entire Study	
Period.....	58
Comparison of the Number of Species Collected Between Habitats	58
Species Comparison at Reseeded Sites	61
Comparison of Predominant Species Between Habitats	61
Yearly Comparison of Species Dominance.....	61
Comparison of Species By Sampling Methods	63
Comparison of Temporal Density Estimates Using a Sweep Net versus a	
Drop Cage.....	63
Density Estimate Comparison Between Habitats	63
Discussion	
Grasshopper Species Occupying Winter Wheat and Adjacent Range	74
Density Estimate Comparisons Between Two Habitats.....	76
4. COMPARISON OF DEVELOPMENTAL DIFFERENCES AMONG THREE MELANOPLUS SPP. (ORTHOPTERA: ACRIDIDAE) IN WINTER WHEAT AND ADJACENT RANGELAND	82
Introduction.....	82
Methods and Materials	
Study Site.....	85
Sampling Design.....	85
Data Analysis.....	86
Results.....	88
Discussion	94
5. GENERAL SUMMARY.....	99
LITERATURE CITED.....	102

LIST OF TABLES

Table	Page
1. Grasshopper sample populations fit to a Poisson and Negative Binomial Distribution Models.....	25
2. Cumulative Morisita's Index of Dispersion compared to increasing sample sizes.....	26
3. Grasshopper density comparisons between early and mid-morning sampling periods utilizing 0.05m ² rings.....	27
4. Comparison of grasshopper densities between early morning and mid-morning sampling periods using 0.05, 0.10, and 0.25m ² rings.....	29
5. Grasshopper density estimates, early morning(EMS) vs mid-morning(MMS) sampling periods.....	30
6. Grasshopper densities utilizing three different sized sampling rings for 1990...	30
7. Plant basal cover compared to grasshopper density.....	31
8. Absolute density estimates of three observers sampling rings simultaneously. .	32
9. Comparison of the circumference/area ratio for three different sized rings.....	39
10. Total number of grasshoppers species (by subfamily) collected in 1988, 1989, 1990 in winter wheat and adjacent field borders	54
11. Grasshopper species occupying winter wheat and adjacent range in 1988, Willow Creek, Montana.....	55
12. Grasshopper species occupying winter wheat and adjacent range in 1989, Willow Creek, Montana.....	56
13. Grasshopper species occupying winter wheat and adjacent range in 1990, Willow Creek, Montana.....	57
14. Grasshopper species composition in the range	59
15. Grasshopper species composition in the crop	60
16. Comparison of the predominant species in range and crop over three years.....	62
17. Population dynamics and dispersal of <i>Aulocara elliotti</i> , 1988	70
18. Population dynamics and dispersal of <i>A. elliotti</i> , 1989.....	71
19. Population dynamics and dispersal of <i>A. elliotti</i> 1990.....	73
20. Comparison of the developmental stages of <i>Melanoplus sanguinipes</i> captured using a drop cage versus a sweep net.....	90
21. Comparison of developmental stages of three <i>Melanoplus</i> species in winter wheat and adjacent range.....	91

LIST OF FIGURES

Figure	Page
1. Sampling design for nearest-neighbor test to measure the spatial pattern of <i>M. packardii</i>	16
2. Ring randomization scheme for density estimate study	18
3. Spatial pattern analysis of <i>Melanoplus packardii</i> using nearest neighbor technique.....	23
4. Index of Dispersion plotted against sub-sample unit size.	26
5. Sample design diagram.....	46
6. Grasshopper temporal density estimate differences in range and crop, 1988....	65
7. Grasshopper temporal density estimate differences in range and crop using a drop cage, 1989.....	66
8. Grasshopper temporal density estimate differences in range and crop using a sweep net, 1989.....	67
9. Grasshopper temporal density estimate differences in range and crop using a drop cage, 1990.....	68
10. Grasshopper temporal density estimate differences in range and crop using a sweep net, 1990.....	69
11. Comparison of the developmental rates of three <i>Melanoplus</i> species in crop versus adjacent range.....	92

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. ellioti* 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 egg-laying 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 two-striped 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 led to the creation of a large number of ecotones 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 ecotones, 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 these 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 0.25m² 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 m² 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 maroccanus* 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.

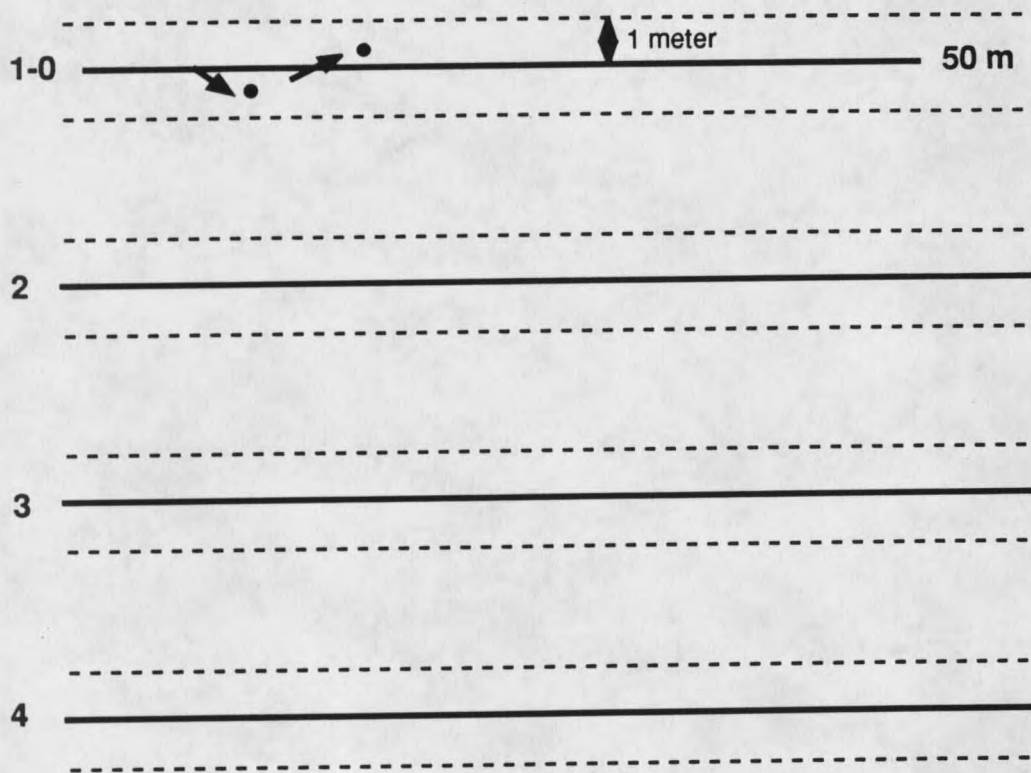
Preliminary Spatial Pattern Study

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

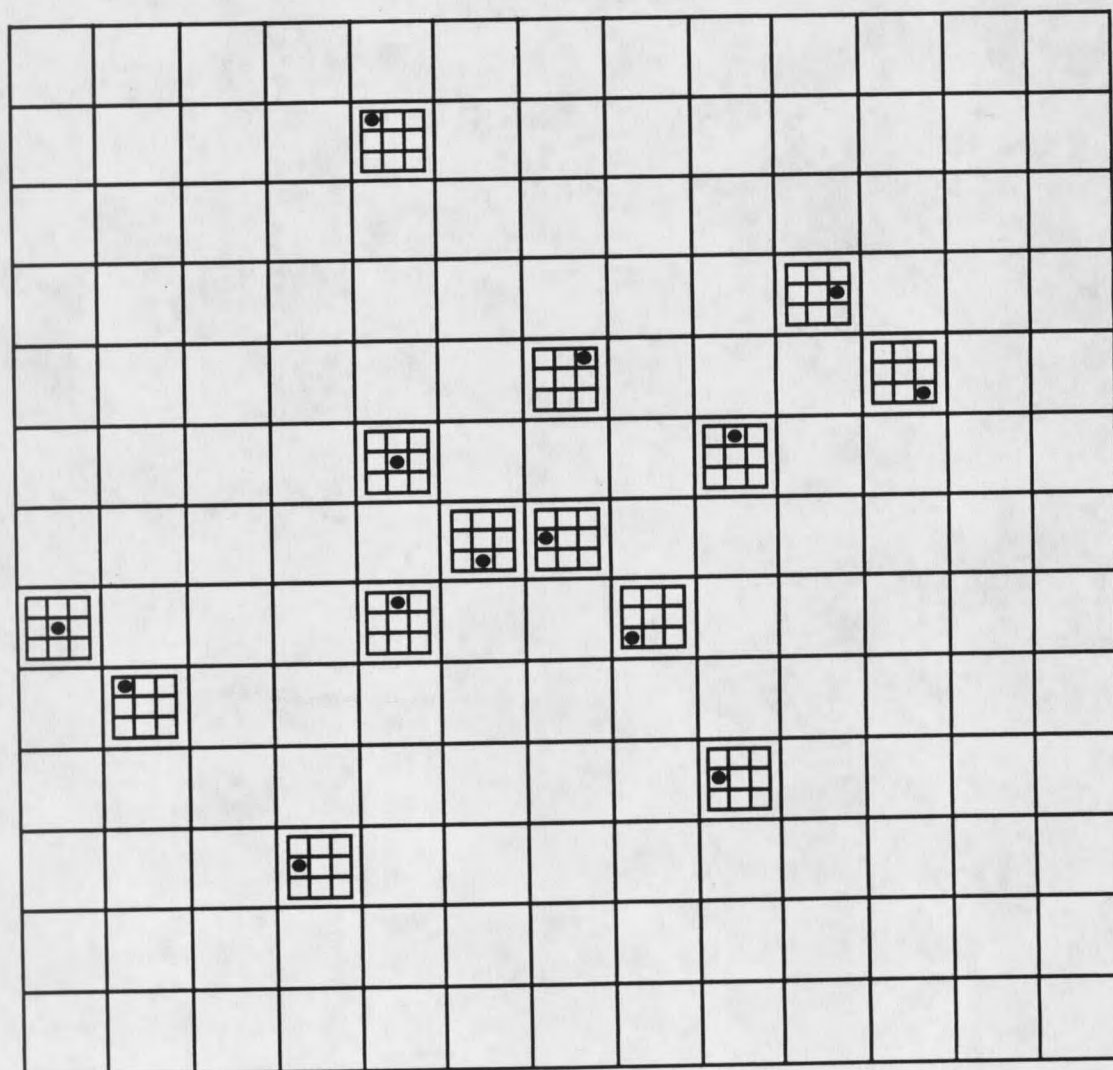
Sample Plot Designs. At the 1990 study site, two sample plots (East Block and West Block) were established. A plot consisted of 169 10 x 10 meter quadrats (Figure 2). One sampling ring made of 3 gauge aluminum wire was placed within a randomly selected quadrat. There were 80, 0.05m² rings, 40 0.10m² rings, and 16, 0.25m² rings (total of 136 rings) for each set of 169 quadrats. The total area encompassed in the three ring size classes was equal (4m²) 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 0620h 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, 0.05m²; 40, 0.10m²; 16, 0.25m² 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-

tribution of grasshoppers was clumped. If the plot of I_d against changing subsample sizes remained constant then distribution was assumed to be random or the sample size of the sample unit was still smaller than the clump size. Subsample unit size was increased by adding grasshopper densities from adjacent rings of identical size. In the case of 0.05m^2 rings, subsample sizes were 0.05, 0.10, 0.25, 0.50, and 0.80m^2 and 0.10, 0.20, 0.50, and 0.80m^2 for the 0.10m^2 rings. The 0.25m^2 rings were not utilized because so few rings were used at each site. The increase in subsample size was limited to 20% of N (Ludwig and Reynolds 1988). The Morisita index of dispersion was computed as follows: $I_d = n/n-1 (x^*/x)$:

where n =total number of individuals in sample, $x^*=x+IC$, IC =Index of clumping $=(s^2/x)-1$, s^2 =variance of the sample, and x =mean number of individuals/ring

Spatial Pattern Analysis Using Distribution Models

Grasshopper densities were compared to determine if they varied significantly within a "block" at two different sample periods or between blocks sampled at the same time period on two consecutive sampling days. For example, East Block R-1 was sampled in early morning on sampling day 1 and mid-morning on sampling day 2, while the West Block R-2 was sampled in mid-morning on sampling day 1 and early morning on sampling day 2. A block of rings was selected randomly at the beginning of each paired sampling date. ANOVA (MSUSTAT-Lund 1991) procedures were used for analysis of density estimates for 0.05m^2 rings. Sample dates and sample periods were used as the equivalent of four treatments for the analysis.

The design was analogous to a "completely randomized design" if this had been an experimental study instead of a sampling study. Grasshopper density estimates for 0.10m^2 and all rings combined were also compared over all sample periods for early morning and mid-morning sample periods.

Vegetation Basal Area and Grasshopper Density Comparisons

I also assessed the possible relationship between grasshopper density estimates and the basal area of vegetation encompassed by rings in each ring class (i.e. 0.05, 0.10m² rings). Basal area estimates were combined across 0.05 and 0.10m² rings as well as across all rings and the density estimates were evaluated in relation to basal area. The sample design was the same as that used for the spatial pattern analysis of grasshoppers. The dominant vegetation in each ring was identified and the basal area of all plants estimated. Basal area was selected instead of aerial cover because the basal area of plants remains fairly constant while foliage cover fluctuates seasonally (Bonham 1989).

The method used to estimate basal area was that of Daubenmire (1959) with the following modifications. Basal area was estimated in the three different sized subsample rings instead of the standard 0.10m² rectangular frame. Also, the rings were divided into quarters to facilitate estimation. Daubenmire's (1959) classes were modified to reflect the difference of measuring basal area rather than aerial cover and to provide more equal number of subsamples within each class. The area covered by the base of the plant in this study was less than the foliage so the number of classes was reduced to three.

Estimates of basal area were placed in the following three categories 2% or less, 2-9% with a midpoint of 5%, and 10%, or more. Grasshopper density estimates in each basal area class were compared to determine if there were significant differences in the estimates among basal area category. The data were analyzed using ANOVA (MSUSTAT-Lund 1991). For this analysis, the basal area categories were the equivalent of treatments. The three categories served as the three treatments for analysis.

Potential Sampling Bias Evaluated Using Three Different Sized Rings

This study evaluated the variability of absolute density estimates when three observers counted grasshoppers simultaneously flushed from three different sized rings. On 11 September 1990, three observers sampled both blocks of rings to evaluate the variability in density estimates among observers using 0.05, 0.10, and 0.25m² rings. Early morning sampling of Block R-2 was initiated at 0710h when ambient temperature, 10 cm above the soil surface, was 7°C and terminated at 0825h when the ambient temperature was 15°C. Mid-morning sampling of R-1 began at 0900h (16°C) and ended 1000h at 19°C. All observers had previous experience using sampling rings. Counts were recorded in secrecy to avoid biasing the estimates. The ring randomization schemes used for the spatial pattern analysis study were also used for this study. Mean density estimates per ring of each observer were compared using ANOVA (MSUSTAT-Lund 1991). Each observer estimated the density of grasshoppers at two sample periods. The six samples (two sample periods by three observers) were analogous to "completely randomized design" and served as six treatments for the analysis.

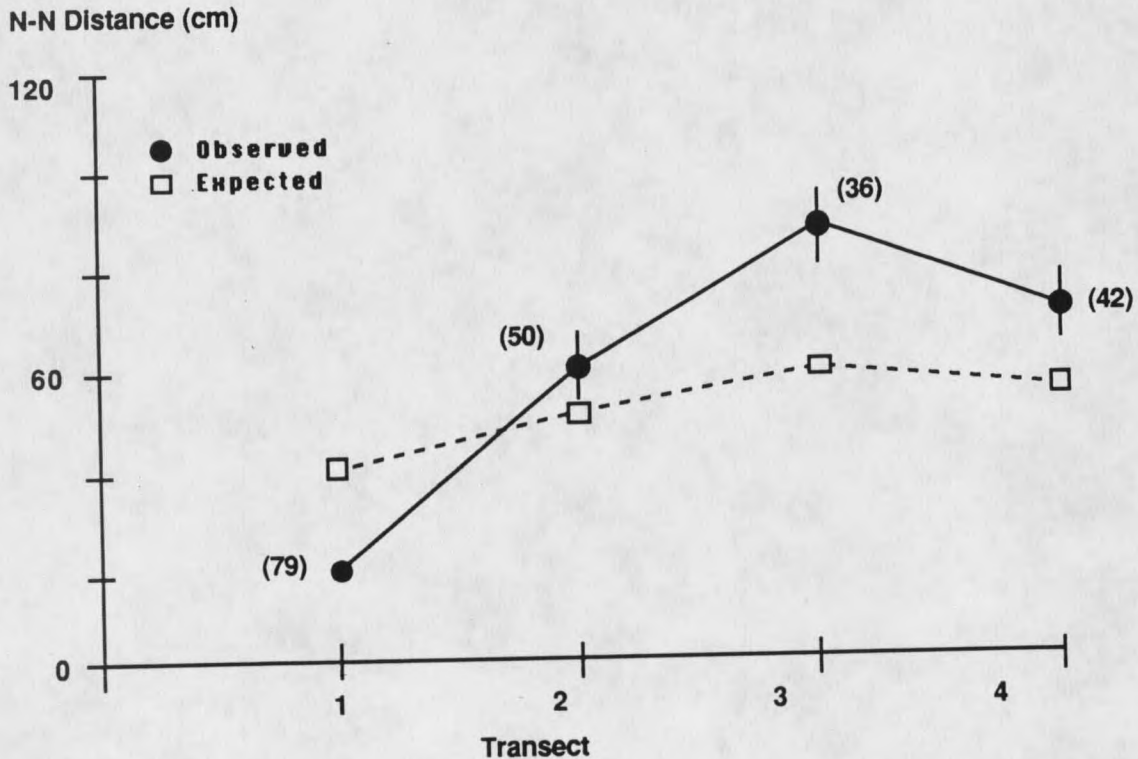
Results

Preliminary Spatial Pattern Analysis

In the preliminary study, *M. packardii* exhibited a clumped distribution along the first transect, where measurements were made between 0547h and 0640h. The ratio *R*, which is a measure of the degree to which a sample population departs from randomness, was 0.510 and the z score was 8.48, $P < 0.001$ (Figure 3). Measurements

along transect 2 began at 0646h and ended at 0728h. The resulting distribution was uniform or regular ($R=1.214$, $z=2.89$, $P<0.05$). Measurements along transect 3 and 4 began at 0735h and ended at 0848h and also resulted in a uniform distribution ($R=1.506$, $z=5.84$, $P<0.001$ and $R=1.282$, $z=3.5$, $P<0.001$ respectively) (Figure 3). Thus, the spatial distribution changed and the nearest neighbor distances increased as morning temperatures and time of sampling increased. Increased activity of *M. packardii* during the later sample period made nearest neighbor measurements progressively more difficult.

Figure 3. Spatial pattern analysis of *Melanoplus packardii* using nearest neighbor technique.



Spatial Pattern Analysis Using Distribution Models

Grasshopper frequency counts for nine early morning and eight midmorning sampling periods were tested for fit to a Poisson and negative binomial distribution models. This resulted in a total of 27 early morning samples. Twenty six out of the 27 (96%) of the early morning samples tested fit a Poisson distribution model (Table 1). One early morning sample using 0.25 m² rings did not fit this distribution. Twenty six early morning samples were tested for fit to a negative binomial distribution, 23 (88%) of these samples fit this distribution model. One sample period using 0.05 m² rings and two using 0.10m² rings did not fit this distribution (Table 1).

There were eight midmorning sample periods in this study for each of three ring sizes. Twenty two of the 24 samples (92%) tested fit a Poisson distribution model. One sample period using 0.10m² rings and one using 0.25m² rings didn't fit the model (Table 1). There were 19 midmorning samples tested for fit to a negative binomial distribution model, 16 (84%) out of the 19 fit this model. One sample period using 0.05m² rings and two using 10.m² rings did not fit this distribution (Table 1). Five samples were not tested for fit to a negative binomial distribution because a "k", a measure of clumping in a negative binomial distribution model, could not be calculated for these samples.

Spatial Pattern Analysis Using Morisita's Index of Dispersion

Plotting Morisita's Index of Dispersion I_d against increasing cumulative sample unit size was the third method used to determine the spatial pattern of individuals occupying nondiscrete habitats (Figure 4). In this study, no abrupt I_d change occurred

Sample Dates 1990		0.05m2				0.10m2				0.25m2			
		Poisson χ^2	df	Neg. Binomial χ^2	df	Poisson χ^2	df	Neg. Binomial χ^2	df	Poisson χ^2	df	Neg. Binomial χ^2	df
8/11	EMS	1.7225	2	1.2101	1	4.938	2	4.917*	1	3.551	4	4.259	4
8/16	EMS	3.999	2	0.2491	1	0.218	2	0.133	1	6.701	4		
	MMS	2.766	2	4.0512*	1	1.564	3	1.904	1	5.802	4		
8/17	EMS	3.358	2	4.268*	1	1.715	3	1.185	1	1.155	4	1.631	3
	MMS	4.551	2	1.699	1	2.075	2	1.357	1	5.661	4		
8/22	EMS	2.29	2	2.469	1	0.31	3	0.277	2	11.187*	4	7.58	5
	MMS	2.115	2	2.72	1	6.314*	2	0.181	1	2.928	4		
8/23	EMS	2.87	2	1.2219	1	2.999	2	0.27	1	3.22	4	2.508	3
	MMS	2.642	2	0.8161	1	0.288	3	0.324	1	3.6361	4		
9/8	EMS	1.0377	1	0.0876	1	2.219	2	4.238*	1	0.6	1	0.055	1
	MMS	4.614	2	0.0196	1	6.28	2	10.309*	1	2.292	4		
9/9	EMS	0.026	1	0.0913	1	0.659	2	0.023	1	5.454	4	0.641	2
	MMS	7.1306*	2	0.3757	1	1.877	2	0.077	1	2.535	4	2.105	2
9/11	EMS	0.1314	1	0.4904	2	0.474	2	0.331	1	1.276	1	1.378	1
	MMS	1.2829	2	0.1841	1	4.626	2	7.435*	1	2.043	3	1.776	2
9/12	EMS	0.3285	1	0.0088	1	0.03	2	0.123	1	2.558	1	0.901	1
	MMS	4.1092	2	3.7162	1	2.265	2	2.406	1	3.987	4	6.045	1

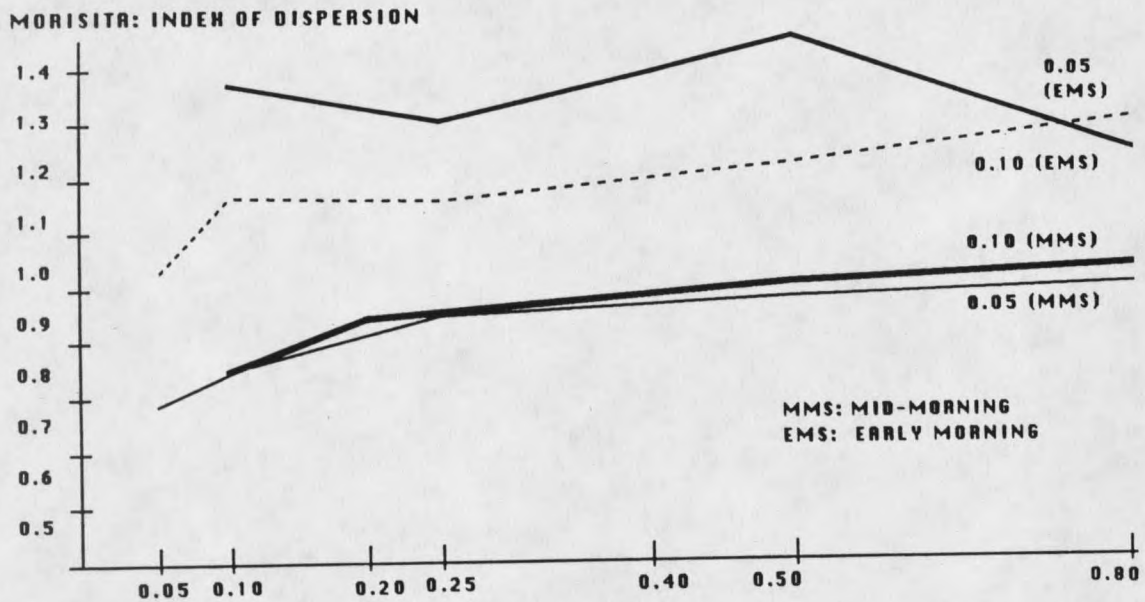
EMS=Early Morning Sampling

MMS=Mid-morning Sampling

25

Table 1. Grasshopper Sample Populations Fit to a Poisson and Negative Binomial Distribution Models

Figure 4. Index of Dispersion plotted against sub-sample unit size.



as the subsample size units were increased to a maximum size of 0.8m². The index of dispersion for all subsample units from the early morning sample period were larger than those from the midmorning sample period and all early morning samples exceeded 1.0 (Table 2). These results suggest that there is a tendency for grasshoppers to aggregate early in the morning when compared to their distribution in midmorning (Figure 4).

Table 2. Cumulative Morisita's Index of Dispersion compared to increasing sample sizes.

	0.05m ² Rings		0.10m ² Rings	
	EMS*	MMS**	EMS*	MMS**
0.05	1.03	0.78		
0.1	1.17	0.88	0.1	0.88
0.25	1.16	0.96	0.2	0.94
0.5	1.23	0.98	0.5	0.99
0.8	1.30	1.01	0.8	1.03

* EMS = Early Morning Sampling

** MMS = Mid-Morning Sampling

Grasshopper Density Estimate Comparisons

The four grasshopper density estimates produced using 0.05m² rings for the first paired sample periods (16-17 August 1990) were not significantly different (Table 3). At paired sample period (22-23 August 1990), the early morning density estimates were significantly lower than those at the mid-morning sample periods (Table 3). In the final two paired sample periods, grasshopper density estimates produced by sampling in the early morning were also significantly lower than those during the mid-morning sample periods (Table 3). When ambient air temperatures were at or below 11°C at the beginning of the early morning sample period the adult grasshopper density estimates were significantly lower than the mid-morning sampling periods (Table 3).

Table 3. Grasshopper density comparisons between early and mid-morning sampling periods utilizing 0.05m² rings.

Sample Dates		8/16-17			8/22-23		
	\bar{X}	SE	Temp°C		\bar{X}	SE	Temp°C
EMS				EMS			
R-1	1.05	0.11 A	14	R-1	0.65	0.11 A	10
R-2	1.05	0.10 A	13	R-2	0.88	0.10 AB	7
MMS				MMS			
R-1	0.98	0.11 A	27	R-1	1.05	0.11 BC	20
R-1	1.08	0.10 A	26	R-2	1.23	0.11 C	17
F=0.1711		MSE=0.8769		P=0.95 *		F=5.218	
				MSE=0.9263		P=0.0004	
Sample Dates		9/8-9			9/11-12		
	\bar{X}	SE	Temp°C		\bar{X}	SE	Temp°C
EMS				EMS			
R-1	0.39	0.07 A	11	R-1	0.21	0.05 A	11
R-2	0.44	0.07 A	8	R-2	0.34	0.07 A	7
MMS*				MMS			
R-1	0.80	0.09 B	16	R-1	0.66	0.08 B	17
R-2	1.00	0.09 B	20	R-2	0.90	0.09 B	19
F=13.85		MSE=0.4983		P<0.0001		F=17.30	
				MSE=0.4504		P<0.0001	
*df=316 all paired sample dates N=80							
EMS=Early Morning Sample Period				MMS=Mid-morning Sample Period			

Comparisons among other ring classes showed results similar to the 0.05m² rings (Table 4). The mean and standard error, SE, was calculated for the 0.10m² and 0.25m² rings (Table 4). Early morning density estimates were compared to mid-morning density estimates across all sample periods for 0.10m² rings and all rings. Combined early morning density estimates were significantly less than mid-morning estimates for both comparisons (Table 5). Thus, density estimates were significantly lower when grasshopper counts were made at ambient temperatures below 11°C for all three ring classes.

Grasshopper Density Estimates Compared to Percent Basal Area Estimates of Vegetation

The total basal cover of plant species encompassed by three different sized rings (0.05, 0.10 and 0.25m²) was estimated for both ring randomization schemes. The mean basal area was estimated to be 7.7% for ring scheme 1 (R-1) and 8.1% scheme 2 (R-2) N=136 for both schemes. *Agropyron cristatum* made up 73% of the total basal cover in R-1 and 79% in R-2. Nineteen percent of the basal cover in R-1 and 9% in R-2 was composed of *Medicago sativa*. *Bouteloua gracilis* was the third most dominant plant species. Five percent of the total basal cover was composed of this plant in R-1, while 11.6% was found in the rings of R-2. Other species, especially *Stipa commata* made up 3% of the total basal cover in R-1 and 0.4% in R-2.

Grasshopper densities for all 0.05m² rings ranged from a low of 2.45 grasshoppers per ring overall paired sample dates in category 1 to a high of 4.23 in category 3 (Table 6). Grasshopper densities for 0.10m² rings, 0.05 and 0.10m² rings combined and all rings combined showed the same significant trend (Table 6). In this study, sampling rings encompassing an area with higher basal cover had higher grasshopper density estimates than rings in areas with lower basal cover.

RING SCHEME #1

Sampling Dates	0.05				0.10				0.25			
	EMS		MMS		EMS		MMS		EMS		MMS	
	$\bar{\chi}$	SE	$\bar{\chi}$	SE	$\bar{\chi}$	SE	$\bar{\chi}$	SE	$\bar{\chi}$	SE	$\bar{\chi}$	SE
8/16-17	1.05	0.11	0.98	0.11	1.78	0.20	1.78	0.20	2.63	0.41	2.50	0.28
8/22-23	0.65	0.11	0.88	0.10	1.08	0.24	1.38	0.14	2.44	0.31	2.56	0.30
9/8-9	0.39	0.07	0.70	0.13	1.18	0.14	0.69	0.18	0.69	0.18	2.31	0.41
9/11-12	0.21	0.05	0.66	0.08	0.40	0.12	1.13	0.14	0.81	0.23	1.94	0.30

RING SCHEME #2

8/11	0.74	0.10			1.05	0.18			2.94	0.54		
8/16-17	1.05	0.10	1.08	0.10	1.33	0.20	1.45	0.23	3.50	0.35	3.30	0.37
8/22-23	1.05	0.11	1.23	0.11	1.63	0.19	1.65	0.21	3.38	0.62	3.13	0.36
9/8-9	0.44	0.07	1.00	0.09	0.95	0.14	1.48	0.15	1.50	0.40	3.13	0.44
9/11-12	0.34	0.07	0.90	0.09	0.48	0.12	1.35	0.15	1.00	0.29	2.94	0.40

EMS=Early Morning Sampling

MMS=Mid-morning Sampling

Table 4. Comparison of grasshopper densities between early morning and mid-morning sampling periods using 0.05, 0.10, and 0.25m² rings.

Table 5. Grasshopper density estimates, early morning (EMS) vs mid-morning (MMS) sampling periods.*

	0.10m ² Rings		0.05, 0.10, 0.25m ² Rings	
	\bar{X}	**	\bar{X}	**
EMS	4.688	A	4.217	A
MMS	5.713	B	5.165	B
F=	4.731		9.413	
MSE =	8.883		13.000	
df=	158.000		542.000	
P-value	0.010		0.0001	

* Ring randomization scheme 1 & 2 combined

** Different letters denote significant differences between means
Grasshoppers/2.5m²

Table 6. Grasshopper densities utilizing three different sized sampling rings for 1990.

Ring Size Sample Date	0.05		0.10		0.25	
	\bar{X} *	SE	\bar{X}	SE	\bar{X}	SE
8/11 EMS 1	14.75	0.57	10.5	0.38	11.75	1.25
8/16 EMS 2	21.0	0.27	13.25	0.24	14.0	0.46
MMS 1	19.5	0.65	17.75	0.42	10.0	0.21
8/17 EMS 1	21.0	0.09	17.75	0.62	10.5	0.63
MMS 2	21.5	0.19	14.5	0.23	13.0	0.37
8/22 EMS 2	21.0	0.60	16.25	0.52	13.5	1.92
MMS 1	17.5	0.37	13.75	0.20	10.25	0.55
8/23 EMS 1	13.0	10.27	10.75	0.71	9.75	0.70
MMS 2	24.5	0.19	16.5	1.02	12.5	0.72
9/8 EMS 1	7.75	0.43	7.0	0.34	2.75	0.31
MMS 2	20.0	0.09	14.75	0.61	12.5	0.75
9/9 EMS 2	8.75	0.69	9.5	0.83	6.0	1.49
MMS 1	16.0	0.33	11.75	0.27	9.25	0.75
9/11 EMS 2	6.75	0.89	4.75	0.60	4.0	0.84
MMS 1	13.3	0.62	11.25	0.60	7.75	0.59
9/12 EMS 1	4.25	0.41	4.0	0.61	3.25	0.38
MMS 2	18.0	0.24	13.5	0.76	11.75	0.66

* \bar{X} density estimates for all ring sizes in grasshoppers/m²

Variation in Density Estimates by Three Observers

The estimates of density from counts made simultaneously by three observers did not vary significantly for any of the different sized rings per sample period (Table 7). However, there was a trend in the effect of ring size on density estimates, during the early morning and mid-morning sample periods. The highest density estimates by the three samplers occurred with the 0.05m² in 5 out of the 6 samples. The density estimates for 0.10m² rings were the second highest in 4 out of 6 samples. The density estimates in the 0.25m² rings were the lowest in 5 out of six samples (Table 8).

Table 7. Plant basal cover compared to grasshopper density.*

Basal Cover Categories	Ring Size (sq. m.)			
	0.05	0.1	0.05 & 0.10	0.05, 0.10, & 0.25
1	2.45 A (126)	4.36 A (47)	2.97 A (173)	3.1 A (179)
2	3.50 B (90)	5.43 AB (60)	4.27 B (150)	5.0 B (174)
3	4.28 C (104)	5.68 B (53)	4.73 B (158)	5.9 C (192)
<i>F</i>	22.28	2.723	21.26	30.98
MSE	4.336	8.899	6.515	11.89
<i>P</i> -value	<0.001	0.0462	<0.001	<0.001

(1) 2% or less basal cover (2) 5% basal cover (3) 10% or more basal cover

Comparisons across four paired sample dates Numbers in () = N

Table 8. Absolute density estimates of three observers sampling rings simultaneously.

0.05m ² rings		EMS		MMS		
Observer	\bar{X} *	SE	N	\bar{X}	SE	N
1	0.20	0.05	80 A	0.58	0.09	80 BCD
2	0.34	0.07	80 AB	0.66	0.08	80 CD
3	0.36	0.07	80 AB	0.80	0.09	80 D
<i>F</i> =9.208		df= 234		MSE=0.8231		<i>P</i> <0.0001
0.10m ² rings		EMS		MMS		
Observer	\bar{X} *	SE	N	\bar{X}	SE	N
1	0.40	0.12	40 A	1.28	0.20	40 B
2	0.48	0.12	40 A	1.13	0.14	40 B
3	0.45	0.09	40 A	1.33	0.17	40 B
<i>F</i> =9.570		df= 234		MSE=0.8231		<i>P</i> <0.0001
0.25m ² rings		EMS		MMS		
Observer	\bar{X} *	SE	N	\bar{X}	SE	N
1	0.69	0.22	16 A	2.44	0.40	16 C
2	1.0	0.29	16 A	1.94	0.30	16 BC
3	1.19	0.29	16 AB	2.06	0.28	16 C
<i>F</i> =5.281		df= 90		MSE=1.441		<i>P</i> =0.0001

* Multiple comparisons of means for each ring size done using a LSD at 0.05 significance.

Discussion

Spatial Pattern of Grasshoppers

Observations and data from studies conducted in 1989 and 1990 strongly suggest that the spatial pattern of adult grasshoppers in northern rangelands, in the United States, reseeded to crested wheatgrass and alfalfa is clumped early in the morning when ambient temperatures are below 13°C. (Figures 3, 4, Tables 3, 5). Support for such a conclusion can be obtained from the following observational information and the results

of studies conducted in 1989 and 1990. It was not uncommon to observe 15 or more adult *Melanoplus sanguinipes*, *M. bivittatus*, and *M. packardii* aggregated in a large clump of alfalfa or crested wheatgrass early in the morning at the beginning of sampling (Gillespie unpub. data). Such behavior has been displayed by other grasshoppers. Ellis (1953) and Chapman (1972) reported that *Locusta migratoria migratoriodes* (R and F) aggregated at the warmest available spots, but they were not necessarily being attracted to each other. Parker (1982) found that *Dactyloptum bicolor* (Thomas) concentrated in the plant canopy where they could maintain the highest body temperatures. Sheltering from cold has also been described in other temperate grasshopper species where they often spend cold nights near the ground in dense vegetation (Uvarov 1977). *Schistocerca* adults exposed to cold winter conditions in Morocco sheltered deep inside low vegetation and in rock crevices when air temperature was about 8°C (Waloff pers. comm. in Uvarov 1977). Grasshoppers, in reseeded range, may aggregate in clumps of vegetation because ambient temperatures in clumps of mature *Medicago sativa* and *Agropyron cristatum* were higher than those found 2 cm above bare ground (Olson and O'Neill unpub. data). Temperature differences between clumps and bare soil occur at a time when daily ambient temperatures were at a minimum, around sunrise (Rosenberg 1974). A study conducted in a mature barley field obtained similar results (Geiger 1965). Temperatures recorded at 10 cm above the soil surface in the plant canopy were 2°C higher than those above bare soil at 0600h (Geiger 1965).

The results of the various spatial pattern analysis studies also tend to support the above conclusion. The results of the nearest neighbor study in 1989 showed that the spatial pattern of *M. packardii* was clumped along transect 1 (Figure 3). Morisita's index of dispersion also suggest that the spatial pattern of adult grasshoppers was

clumped early in the morning when compared to the mid-morning sample period. I_d was always greater than one and exceeded the values of the mid-morning sample periods across all sample unit sizes (Table 2, Figure 4). The observed frequency distributions generated by the ring counts fit both Poisson and negative binomial distribution models (Table 1). Ludwig and Reynolds (1988) concluded that these results suggest that there is a tendency toward aggregation, but such conflicting results illustrated the importance of the careful selection of a null hypothesis and the value of an independent data set to confirm suspected biological pattern.

Thompson (1987) obtained similar results studying the spatial pattern of grasshoppers in short grass prairie, and concluded that grasshoppers in this habitat approximated a Poisson distribution. He also concluded that the perception of nonrandomness increased as sampling rings size was increased from 0.10m^2 to 1.0m^2 . His study was conducted from mid-morning to early afternoon (Thompson 1987). The significant differences in adult grasshopper density estimates when early morning ambient temperatures were below 13°C also support the conclusion that the spatial pattern of grasshoppers was aggregated early in the morning (Table 3). I think the aggregation of adult grasshoppers early in the morning is a behavioral response to ambient temperatures below 13°C . Grasshoppers in a *Agropyron cristatum* / *Medicago sativa* / *Bouteloua gracilis* (AgCr/MeSa/BoGr) rangeland may use mature plant clumps to increase body temperature or prevent loss of body heat. Such behavioral responses to ambient temperatures have been displayed by grasshoppers in other studies discussed previously. This behavior would allow resumption of daily activities earlier than if an individual *M. sanguinipes*, *M. bivittatus* or *M. packardii* spent the night on bare ground. Thermoregulatory behavior would affect the spatial distribution of grasshoppers and more importantly, grasshopper density estimates made at different times of the day.

In two previous studies, Southwood (1978) found that grasshopper movement from one microhabitat to another could have a significant effect on grasshopper density estimates, when sampling was done at different times of the day. Thompson (1987) found that grasshopper density estimates at temperatures below 15°C could be 400% less than those made when temperatures exceeded 25°C.

The lower density estimates in cool mornings could be attributed to observer error. Inactive grasshoppers are difficult to spot in a sampling ring and often do not get included in the grasshopper counts. To increase the detection of inactive adult grasshoppers, I used a 2.5 meter stick and my hands to "tease" grasshoppers out of the vegetation.

Other conclusions that can be drawn from this and past studies are as follows. Studying the spatial pattern of grasshoppers using a nearest-neighbor technique has one draw back, which is the requirement that grasshoppers remain relatively inactive while measurements are taken. Sampling near sunrise while grasshoppers were relatively inactive met the inactivity criteria, but increasing activity by *M. packardii* due to increasing ambient temperatures and observer disturbance while sampling transect 2, 3, and 4 must have had a marked effect on the precision and accuracy of the results (Gillespie and O'Neill unpub. data).

The use of ring subsamples, to develop observed frequency distributions that can be compared to the expected frequency distribution of models for goodness of fit presents some problems. First, if an observer is interested in accurate grasshopper counts, the area of visual concentration is limited to a maximum ring size of approximately 0.10m² (Onsager 1977, 1991). Secondly, counting grasshoppers when densities are high can also place limitations on ring size. At high grasshopper densities, large number of grasshoppers can be flushed rapidly from a ring. This burst of

movement can confuse the observer and produce erroneous counts. Limiting the size of rings is a way to reduce such errors. This limitation in ring size also tends to limit the number of grasshoppers which will occupy a ring and ultimately, reduces the number of frequency classes which can be produced by such density counts. A lower number of frequency classes also limits the detection of spatial patterns (Thompson 1988). It appears that using different sized rings to assess the spatial pattern of grasshoppers is not the most effective way to study this aspect of grasshoppers. This study confirms Ludwig and Reynolds (1988) precautions with regard to using arbitrary sample units to assess the spatial patterns of organisms. The use of Morisita's index of dispersion may be a more effective technique to identify the patterning of grasshoppers both at a given point in time and at different times of the day.

Plotting Morisita's index of dispersion against increasing sample unit size did not produce any distinct spatial patterns (Figure 1). There are two plausible explanations for such results. First, the distribution of grasshoppers is truly random both in the early and mid-morning sampling periods, because there was no abrupt change in the graph of Morisita's index of dispersion (I_d) over changing sample unit size (Figure 1). Second, the distribution of grasshoppers may be clumped during one or both sampling periods, but the size of the sample unit never approximated the clump size of grasshoppers. Therefore, the spatial pattern appeared random.

It is unfortunate that the number of sampling rings in this study limited the systematic increase of the sample unit size to only 0.80m^2 . This method is a viable way to study the spatial pattern of grasshoppers, and increasing the number of rings in the study would have allowed me to plot I_d against sample unit sizes in excess of 0.80m^2 . If an aggregation of grasshoppers was larger than 0.80m^2 , this method might have detected it.

I think a spatial analysis of plants at the study sites would have provided added insight into the spatial pattern of grasshoppers and may have helped in the selection of subsample unit sizes for such a study. If the spatial pattern of plants at the study site were clumped, subsample unit sizes could be selected to determine if the spatial pattern of grasshoppers was related to the spatial pattern of plants.

The results of this study and those conducted by Parker (1930), suggest that the morning ambient air temperature thresholds for activity in North American grasshoppers, such as *Camnula pellucida*, *M. sanguinipes*, and *M. packardii* lie in a range of 9-16°C. Chapman (1972) found that male and female *Locusta migratoria migratoriodes* (R and F) were incapable of locomotion at temperatures below 15°C. Therefore, the results of this study suggest that adult grasshopper density estimates in AgCr/MeSa/BoGr habitat using ring subsample units should not be initiated until ambient temperatures exceed at least 12°C to insure that grasshoppers have resumed daily activities. Parker's (1930) study would suggest that sampling should not begin until air ambient temperatures exceed 16°C.

A second factor affecting grasshopper activity may be changing light intensity. Ellis and Ashall (1957) and Kennedy (1939) found that rapid changes in light intensity also stimulated grasshopper activity. Roosting *Schistocera* began descending from plant roost 20 minutes before sunrise. Morning observations of adult grasshopper activity could not be accounted for by only changing ambient temperatures in this study. Activity may be affected by some interaction between increasing temperature and changing light intensity (Gillespie pers. obs.). However, at our latitudes temperatures closely track light and it may not be necessary to use light intensity to assess grasshopper activity (Kemp 1986).

Grasshopper Density and Ring Basal Cover

The mean basal area of plants at the study site was 7.7% and 8.1% for ring scheme 1 and 2, respectively. These estimates were in close agreement with previous studies conducted in similar rangeland habitats. In mixed grass prairie in Canada, Coupeland (1960) estimated the basal cover of grasses to be 9% and Smoliak et. al (1971) estimated a *Stipa / Bouteloua* rangeland to be 6.7%. Estimated basal cover from each sampling ring was placed into three classifications, less than 2% (1), 5% (2), more than 10% (3). When grasshopper densities were compared across these three categories, density increased with increasing basal cover (Table 6). Grasshopper populations may be higher in denser vegetation because these areas provide a more concentrated supply of a specific food plant or set of food plants, or a microhabitat to reduce thermal stress, and/or predation or improve oviposition success (Isley 1937, Anderson and Wright 1952, Anderson 1964, 1973, Joern 1979, 1982).

These results may have some important implications for sampling. A stratified random sampling design taking into account the basal area or aerial cover of plants might produce more accurate grasshopper density estimates and provide better insights into the spatial pattern of grasshoppers. Further study will be required to answer the question, whether grasshopper density estimates are always higher in areas of higher basal cover or whether their daily or seasonal shifts in density estimates from areas with high basal cover to areas with low basal cover.

Variation in Density Estimates by Three Samplers

The estimates of density made simultaneously by three observers did not vary significantly among ring sizes or sample periods (Table 7). In a study conducted in

AgCr/BoGr prairie, Onsager (1991) found that 0.05m² rings resulted in the most repeatable density estimates. Onsager (1991) also found that grasshopper density estimates were consistently higher using the 0.05m² than 0.10m² rings and that 0.10m² rings produced higher density estimates than 0.25m² rings. A similar trend occurred in this study when I sampled rings by myself and with two other observers (Tables 5, 7). Thompson (1988) also found that density estimates decreased as ring size increased. One factor which may contribute to increasing density estimates in smaller rings when compared to larger rings, is the ratio of the circumference to area. The smaller the ring the more perimeter there is per unit area (Table 9). This may make it more difficult to decide if a grasshopper is truly encompassed in the ring or outside of it. The greater number of small (0.05m²) rings used in this study and earlier studies plus the increased perimeter per area may contribute to higher density estimates, because decisions about the location of grasshoppers must be made more often using a larger number of small rings vs. fewer larger rings.

A counter argument can be made for increased accuracy using smaller ring sizes. An observer may be able to concentrate on the area encompassed by a small ring much better than a large ring. A small ring will generally contain fewer grasshoppers than a large ring, making it easier to count the grasshoppers flushed from the rings. This leads to higher density estimates because fewer grasshoppers go uncounted. Onsager (1991) offered a similar explanation for the consistently higher density estimates.

Table 9. Comparison of the circumference/area ratio for three different sized rings.

Area (m ²)	Circumference	CIA Ratio*
0.05	0.3956	7.912
0.10	0.5589	5.589
0.25	0.8855	3.530

* C/A = circumference/area

CHAPTER THREE

HABITAT ASSOCIATIONS AND TEMPORAL SHIFTS IN DENSITIES OF GRASSHOPPER SPECIES (ORTHOPTERA:ACRIDIDAE) BETWEEN WINTER WHEAT (*TRITICUM AESTIVUM* L.) AND ADJACENT RANGELAND

Introduction

Movements of organisms, which include dispersal, migration, and local movement between microhabitats, has always been of interest to ecologists because it provides insight into why the distributions and abundances of organisms fluctuate through time (Krebs 1985). Efforts to quantify grasshopper movement fall into two broad categories. First, a number of dispersal studies were conducted to quantify directed movement between habitats. A second group of smaller scaled studies attempted to quantify local movement between microhabitats. This study was concerned with the dispersal of grasshopper species between a winter wheat and adjacent rangeland habitat. For the purposes of this study, dispersal is defined as the spreading of individuals from the immediate environment of parents and neighbors in order to escape unfavorable conditions, such as drought, and reduced food availability (Begon et. al. 1990, Joern and Gaines 1990).

The majority of the past dispersal studies consisted of releasing a large number of marked individuals from a single location. These individuals were marked by paint or a

radioactive isotope and their dispersal followed through time. For example, Post and Anderson (1950) reported that nymphs of *Melanoplus* species dispersed up to 35 m in 24 hours. Munro and Telford (1942) found that third to fifth instar grasshoppers moved up to 100 m in 2.5 h on barren cultivated soil. In Australia, Clark (1962) followed the dispersal of adult *Phaulacridium vittatum* (Sjost) from a mass release site. He reported that the adults dispersed from the initial release site for 2 days to a week. After this period of time, dispersal ceased and travel was restricted to local movement between microhabitats. Riegert et. al. (1954) used a radioactive tag, Phosphorus-32, to mark adults and nymphs of *C. pellucida* and *M. sanguinipes* for a dispersal study. They reported that mixed populations of fifth instar nymphs and adults of *M. sanguinipes* dispersed up to 220 meters in 6 days when released on bare cultivated soil. Lastly, Baldwin et. al. (1958) recovered 80% of the P-32 tagged third and fourth instar nymphs of *M. sanguinipes*, released in the middle of alfalfa *Medicago sativa* L. and weeds, within 18 meters of the release site after 20 days.

A second group of studies, conducted by Richards and Waloff (1954) and Dempster (1955), attempted to quantify the localized, small scale movement of grasshoppers between microhabitats, rather than their directed dispersal between habitats. They reported that *Chorthippus parallelus* (Zett.) and *Chorthippus brunneus* (Thumb.) third and fourth instar nymphs, released in cages, moved from an area of short sparse vegetation to an area of taller dense vegetation. They also found that movement from short vegetation was accentuated following a drought. In a study that simulated more natural conditions, Joern (1983) located and marked individuals of four coexisting grasshopper species in their "chosen" microhabitat and then followed their movement within a 95 x 95 meter grid system. In this study, the maximum movement per day for those individuals remaining in the study site was 35 meters per day.

Overall, studies designed to quantify grasshopper movement (either dispersal or localized movement of individuals) within or across habitats have had inherent problems. In studies where large populations of marked grasshoppers were released from a central point or were released in suboptimal habitats (Munro and Telford 1942, Post and Anderson 1950, Riegert et. al. 1954, Baldwin et. al. 1958, Clark 1962) such as the middle of a barren cultivated field, dispersal rate estimates are artificial and may be due to the initial crowding of grasshoppers (Joern 1983). Additionally, studies that rely on mark-recapture techniques have disadvantages, in that marks may be lost during molting, or mortality and dispersal rates may be high. Loss of individual tags or increased mortality would reduce recapture rates and incorrectly suggest smaller dispersal distances. The use of a radioactive tag surmounts some of these problems (Reigert et. al. 1954, Baldwin et. al. 1958), but again, low recapture rates make statements concerning dispersal quite tentative. The use of a grid to follow grasshopper species within a microhabitat, (Joern 1983), was designed to alleviate problems of mass release and release in artificial habitats. Unfortunately, small recapture sample sizes at many sample periods also produced tentative conclusions (Joern 1983).

In spite of the problems, such methods have merit because they may help determine which environmental factors are related to the dispersal of grasshoppers (Begon et. al. 1990). Also, knowledge of individual movement might explain the heterogeneity of population abundance and species distribution typically seen in natural systems (Roughgarden 1977, Kemp et. al. 1990a, 1990b).

If grasshopper density estimates were compared between two adjacent habitats and the differences between these estimates fluctuated through time, one may hypothesize that such fluctuations were due in part to individuals moving between the two habitats. For example, Shotwell (1941) studied grasshopper dispersal by comparing sweep net

grasshopper density estimate changes between sample plots over a six day period. In his study, he reported increases in densities in 6 out of 10 study sites. At the ten sites, density estimate changes ranged from a low of 52% to a high of 245% when they were compared to the initial estimate of density at the beginning of the study. However, there were only five modified sweep samples taken at each study plot. Also, the study was only conducted over a 6 day period so no conclusions could be drawn concerning seasonal dispersal of grasshoppers at these plots. In a second study, conducted by Richards and Waloff (1954), they suggested that differences observed in the age structure of nymphs between two habitats was due to the dispersal of older nymphs from a grass-heath habitat to a dense grass habitat. However, conclusive evidence of grasshopper dispersal would still require following a group of individuals through time.

During the 1985-1987 grasshopper outbreak in Montana, we lacked dispersal information for grasshoppers in winter wheat and adjacent rangeland. This lack of information limited control recommendations during this outbreak. If the populations of grasshopper species of economic importance are to be suppressed before they exceed economic injury levels, then such dispersal information must be incorporated into a grasshopper integrated pest management program.

In an effort to provide a basis for the sound pest management of grasshoppers in dryland crops, I established a study to assess the temporal shifts in density estimates of grasshoppers at the interface between a selected crop and adjacent rangeland. The first objective was to develop a grasshopper association list in winter wheat and adjacent reseeded range, composed mainly of crested wheatgrass, *Agropyron cristatum* (L.) Gaertn. and alfalfa, *Medicago sativa* L. and determine if the predominant species in both habitats are as equally likely to occur in range versus the crop. The second

objective was to assess the reliability of grasshopper density estimates produced by different sampling methods in both habitats. The third objective was to determine if such a sampling method could detect the dispersal of grasshopper species between the crop and adjacent rangeland. The last objective was to determine if the predominant species in "newly" reseeded rangeland are the same as those in "old" reseeded rangeland.

Methods and Materials

Study Site

Ten study sites, located near Three Forks and Willow Creek in Gallatin County, Montana USA., were sampled for grasshopper populations during 1988 through 1990. A study site was composed of a field planted to winter wheat and an adjacent rangeland characterized as a *Stipa comata* Trin. and Rupr. and *Bouteloua gracilis* (H.B.K.) Lag. (STCO/BOGR) rangeland habitat (Mueggler and Stewart 1980, Kemp et. al. 1990 a,b) which was reseeded to crested wheatgrass and alfalfa. The study sites had to be relocated every year because there was no crop to sample the following year. The winter wheat fields used in the study were left fallow the following year and then planted to spring wheat during the third year of sampling.

Sampling Design, Equipment, and Regime

At three sites in 1988, three 110 meter transects were established perpendicular to a winter wheat field and the adjacent rangeland. Half of the transect was located in the wheat field and half was located in the rangeland. There were six sample sites per transect in the crop and six in winter wheat for a total of twelve. There were a total of 36

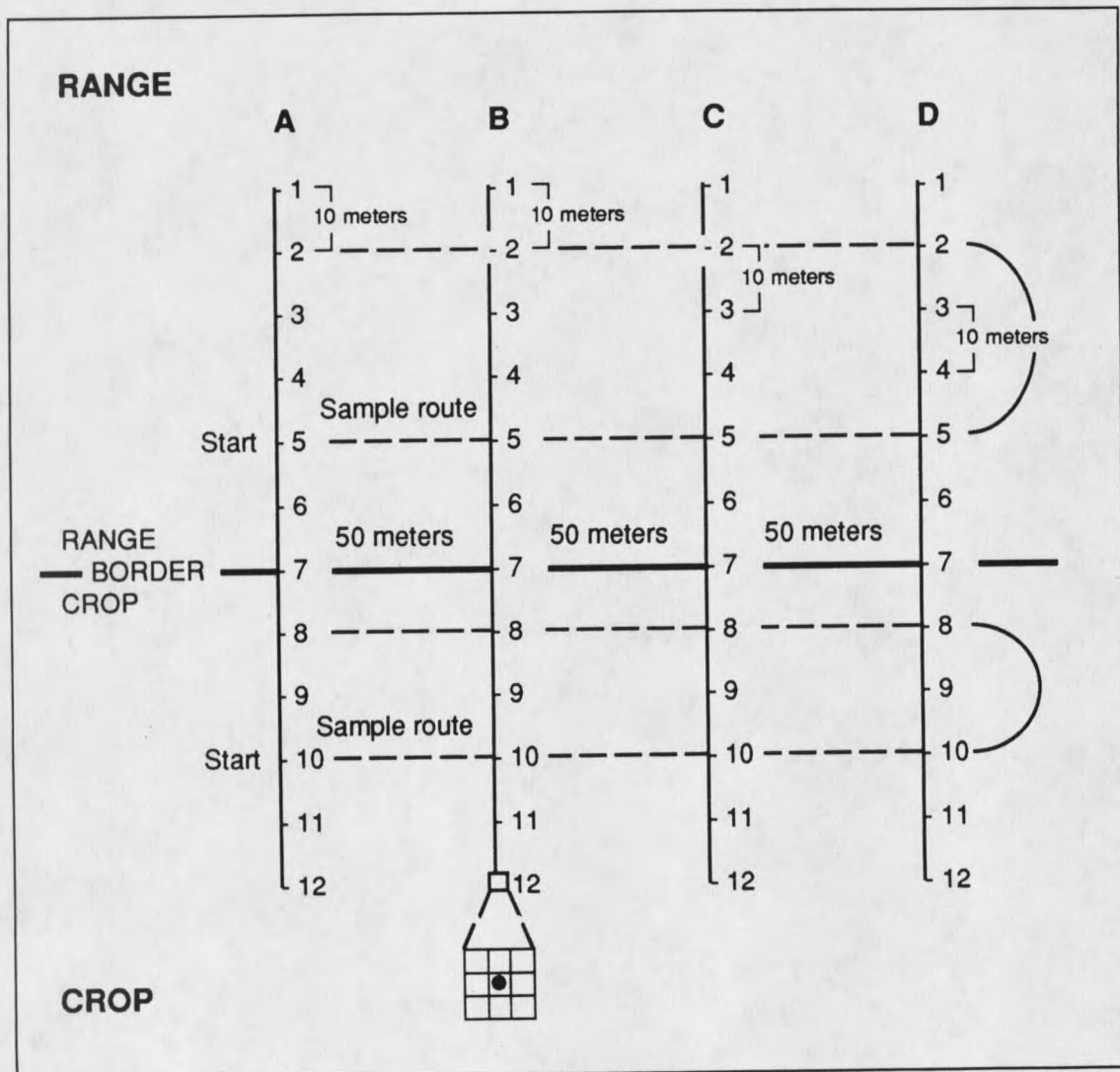
subsample sites per study site. The twelve subsample sites were systematically located 10 m apart in order to avoid disturbing grasshoppers in adjacent subsample sites.

The first and third transects were located at least 50 meters from the edge of any adjacent field to avoid any "edge effect" (Figure 5). Transects were spaced 50 meters apart to reduce disturbing grasshoppers located along adjacent transects and the recounting of disturbed individuals that may have moved into the adjacent transects. Further, the resulting size of the study site was limited to 150 meters by 120 meters in order to increase grasshopper and plant community homogeneity and reduce sampling time in the crop and rangeland. Subsample sites along each transect were numbered one through twelve and each transect was designated by a letter (Figure 5). This was done so that subsample sites could be identified while sorting insects.

A grid system in which subsample sites were selected randomly for sampling was not used because such a design would have made subsample site location more difficult and thus, increased sampling time. In 1988, areas to be sampled at a subsample site were selected haphazardly each week and sampling occurred along a transect instead of across transects as in 1989 and 1990.

In 1989 and 1990, the sampling design was modified in an attempt to minimize sampling biases, which will be explained with each modification. A fourth transect was added to each study site and a grid of nine blocks was staked out over the center of each subsample site. This grid of nine blocks allowed the investigator to randomly select one block for sampling at each sample period. The area within each block was approximately 0.5m^2 . The elimination of haphazard selection of subsample sites and the addition of a transect was implemented to help reduce the variance and sampling biases in these years, such biases may have been introduced using the sample design of 1988.

Figure 5. Diagram of sample design for all sites in 1989 and 1990. In 1988 only three transects were used. Subsample site 6 and 7 were 5 meters from border, subsample sites selected haphazardly. Sampling across transects at randomly selected subsample sites. Twelve subsample sites per transect. Range sampled first at all weekly sample periods. In 1989, 1990 a grid of nine blocks laid over center of each subsample site, one block randomly selected at each weekly sample period. 1988 area to be sampled at subsample site selected haphazardly.



In 1988, sampling occurred along a transect, in order to increase sampling speed and avoid damaging the crop with sampling equipment. Unfortunately, this meant that the second and third like numbered subsample sites on adjacent transects could be sampled 1/2 to 1 hour later than the first (Figure 5). If grasshopper activity reduced capture rates, such reductions might increase the variance of a density estimate produced for like number subsample sites for a sample period (Figure 5). In 1989 and 1990, variation in ambient temperatures at the time of sampling like numbered subsample sites was reduced by sampling these sites consecutively, across transects rather than sampling different subsample sites consecutively along a transect (Figure 5). The method of sampling across transects will be explained in more detail in the sampling regime section. There were a total of 48 subsample sites at a study site, 26 in the field border and 22 in the crop. There were fewer sites in the crop because the seventh group of four subsample sites was located at the crop-field interface. Two subsample sites were located in the rangeland and two sites in the crop (Figure 5).

A drop cage and a vacuuming device were used to capture insects at the study sites. The drop cage was made of canvas stretched over a cylinder which enclosed 0.5m² area (Onsager 1990). Cage height was increased to 80 cm in order to enclose mature winter wheat plants while allowing the investigator to bend over the cage to collect insects using a cart-mounted vacuum device. A muslin sock was placed at the end of the suction hose furthest from the vacuum to collect insects before they could be sucked through the vacuum fan. A lid on the cage kept insects from escaping during sampling. To reduce crop damage produced by pushing a cart through the field, a hand-held leaf blower was modified to vacuum up sample insects. This device was used in 1989 and 1990 in conjunction with the cart-mounted vacuuming device to sample insects. A 37.5 cm diameter sweep net was used in 1989 and 1990 to take ten

sweeps adjacent to each subsample site. Insects and plant debris collected at each subsample site using both sampling devices were placed in individual paper sampling bags. These bags were placed in a cooler at the termination of sampling and then placed in a lab freezer for later sorting and identification.

Sampling Regime

The 1988 sampling began in the first week of June and continued until the end of August when grasshopper populations declined. In 1989 and 1990, inclement weather delayed emergence of first instars and study site selection and postponed sampling until the second week of June. Sampling was terminated the second week of September.

In all three years, sampling began in early morning between 0615h and 0630h when ambient temperatures were between 11-13°C. At this range of temperatures, grasshopper activity was limited to movement from the base of the vegetation onto plants and bare soil. Grasshopper movement actually enhanced the speed of sampling because insects could be collected more efficiently and quickly from the plant and soil surface rather than from the base of the vegetation.

The first subsample site investigated in 1988 was located furthest from the crop (Figure 5). Sampling proceeded along that transect until all the sites in the rangeland were sampled. Sampling of the second transect began in the rangeland at the subsample site nearest the crop and continued through the furthest. The third transect was sampled the same as the first. Subsample sites in the crop were immediately sampled upon finishing the rangeland sites. The crop subsample site nearest the rangeland on the first transect was sampled first followed by the second until all sites on the first transect were completed. The crop subsample sites on the second and third transect were sampled in like manner. In all three years, I decided to sample the crop

sites last because the taller, denser vegetation of winter wheat and cooler temperatures in the crop canopy (Geiger 1965) restricted the movement of grasshoppers for a longer period of time than in the rangeland. I assumed that capture efficiency of the drop cage was maintained at higher ambient temperatures in the crop than in the rangeland.

Sampling within one habitat and then the second was also done to increase sampling speed. At many of the sites, the rangeland and crop were separated by a fence, and pulling equipment back and forth through the fence to sample all subsample sites randomly across both habitats would have resulted in considerable lost sampling time.

At the beginning of sampling in 1989 and 1990, temperatures were measured by placing a glass tube thermometer, enclosed in a narrow white rectangular holder, 10 cm above the soil surface. To avoid excessive heating of the thermometer it was placed so that the widest portion of the thermometer holder was parallel to sun rays. Temperatures were also recorded at the end of each sample period. Before sampling numbers between one and twelve were randomly selected and the subsample sites corresponding to those numbers were sampled in the order the random numbers were selected (Figure 5). Upon completion of sampling in the rangeland the crop was sampled following the same procedure.

In all three years, the sampling routine for all subsample sites involved rapidly approaching a site and quickly dropping a cage over the subsample site. Travel time, sampling and the placement of plant debris and insect specimens in paper sampling bags was limited to approximately 2 min and 30 s, in order to maintain sampling speed. Drop cage sampling of the 48 subsample sites was completed between 0830h and 0900h. Insect specimens and plant material were placed in a cooler upon completion of sampling in each habitat. At the end of this sample period, the relative humidity was measured using a sling psychrometer.

Sweep sampling was initiated following the completion of drop cage sampling in 1989 and 1990. The side of the transect swept was randomly selected at each sample period. Insects collected per ten sweeps at a subsample site were placed in a paper sampling bags. As soon as sweeping was completed at each subsample site, the stage of development of crested wheatgrass or winter wheat was recorded on the paper sampling bag. Upon completion of sweep sampling in each habitat, sampling bags were placed in a cooler. At the end of a sample period all insect samples were transferred to a freezer to await sorting of insects in the lab.

At the lab, insects were removed from the plant material of each subsample site and the grasshoppers were sorted from the other arthropods. Grasshoppers were then sorted by species, stage of development, and sex (in the adult stage).

Data Analysis

Upon completion of grasshopper sorting a list of grasshopper species by subfamily occupying winter wheat and the adjacent rangeland was generated for all three years. A second list identifying the species collected in the winter wheat and in rangeland was generated for each year. Sorting of data also provided a list of the predominant species in each habitat and the percentage each species contributed to the species complex at each of ten study sites and over all sites. The mean number of grasshoppers per species collected over the three year study was calculated along with a standard error (SE) for the four predominant species in each habitat and for all other species lumped into one group. An overall mean and SE for the three years was calculated for all grasshoppers collected in rangeland and winter wheat.

To determine if there was a significant difference in the number of species collected in rangeland and winter wheat, the Mann-Whitney U-test was conducted using

(MSUSTAT-Lund 1991). The same tests were used to determine if there was a significant difference in the number of species collected in "newly" reseeded rangeland vs "old" reseeded rangeland. A Mann-Whitney U-test was also used to determine if there was a significant difference in the number of *M. sanguinipes* (Fabricius) and *A. elliotti* Thomas specimens collected in "newly" reseeded rangeland when compared to "old" reseeded rangeland.

A Kruskal-Wallis test was used to determine the existence of an overall significant difference in the number of specimens collected at all ten study sites for *M. sanguinipes*, *M. bivittatus* (Say), *M. packardii* Scudder, *A. elliotti*, and all other species combined in rangeland and crop (MSUSTAT-Lund 1991). The same test was used to determine if there was an overall significant difference in number of specimens collected per year for the four species and all other species combined. The Mann-Whitney U-test was used to make pairwise comparisons between species and other species combined to determine if there was a significant difference in specimens collected in rangeland and the crop for each year and over all three years.

A comparison was made to determine if the number of species collected using a sweep net was significantly different from those using a drop cage in both habitats. A Mann-Whitney U-test was used to determine if a different sampling method captured significantly more or less species in either habitat (MSUSTAT-Lund 1991).

To follow the seasonal trends in grasshopper density estimates in the two habitats by the four predominant species, means and standard errors (SEs) were calculated (MSUSTAT-Lund 1991). These summary statistics were used to graphically display the density estimates of the four predominant grasshopper species (*M. sanguinipes*, *M. packardii*, *M. bivittatus*, and *A. elliotti*) in both habitats for each sample period. Wilcoxon Sign-Rank tests were conducted to determine if the densities estimates of

these four species in adjacent habitats were significantly different during each sample period. The statistical program utilized was NPAR1WAY which performs analysis of variance on ranks of independent groups (SAS 1985).

Sample populations of *M. bivittatus* and *M. packardii* were combined for data analysis for the following reason. It was observed that while sampling at a given site if *M. bivittatus* was prevalent *M. packardii* was not and vice versa. At a site where one species was scarce there were never enough individuals captured to do density estimate comparisons for the scarce species in both habitats. The behavior of these two species also appeared similar enough during observations and sampling in 1988, to group samples for analysis.

Density estimates were also summarized into three sample periods and analyzed per year instead of by site in an attempt to identify possible trends over three years. Mann-Whitney U-tests were used to compare density estimates in rangeland and winter wheat for *M. sanguinipes*, *M. packardii*, *M. bivittatus*, and *A. elliotti*, and all four species (MSUSTAT-Lund 1991).

A 2x2 contingency table was used to determine if there were significant differences in the pattern of temporal density estimates produced using a sweep net as compared to a drop cage. The two columns were non-significant differences and significant differences between habitats. The rows were the two sampling methods.

Results

Grasshopper Species Occupying Winter Wheat and Adjacent Field Borders

During the three year period of the study, a total of thirty-one grasshopper species were identified from sampling both habitats. Eleven species were collected in the

subfamily Melanoplineae, the spur-throats, seven species in the Gomphocerinae, the slant-face, and thirteen species of Oedopodinae, the banded-wings (Table 10). Sixteen grasshopper species were collected in both habitats and the four most prevalent species were *M. sanguinipes*, *M. packardii*, *M. bivittatus*, and *A. elliotti* (Table 10).

Nineteen grasshopper species were identified from three study sites in 1988 (Table 11). Of the nineteen species identified from these sites only 5 to 7 were collected in the crop. Only two species at any one site could be considered abundant in the crop. At site 1, *M. sanguinipes* and *M. packardii* were the most abundant species in the sample population, whereas at site 2 and 3 *M. sanguinipes* and *M. bivittatus* were predominant (Table 11).

In 1989, 25 species were collected at four study sites (Table 12). Fourteen of the 25 species were also collected in the crop. At site 4, *M. sanguinipes* and *M. bivittatus* were the most prevalent species while at site 5 and 6 only *M. sanguinipes* was collected in large numbers. At site 7, *M. bivittatus* was the dominant crop species followed by *M. sanguinipes* and *Camnula pellucida* (Table 12).

In 1990, 22 species of grasshoppers were collected at three study sites (Table 13). Eleven of these species were collected in the crop. *Melanoplus sanguinipes* was the most abundant species at all three sites in both habitats. The second most abundant species at all three rangeland sites and two of the crop habitats was *M. packardii*. *Melanoplus bivittatus* was the second most abundant species in the crop at Site 10 (Table 13).

Over the three year study period, *M. sanguinipes*, *M. packardii*, and *M. bivittatus* were consistently the most abundant crop species at all study sites. *Aulocara elliotti* was an abundant species as well as the three *Melanoplus* species in rangeland *Camnula pellucida* was abundant in both the crop and rangeland at Site 7, in 1989 (Table 13).

Table 10. Total number of grasshoppers species (by subfamily) collected in 1988, 1989, 1990 in winter wheat and adjacent field borders.

SUBFAMILY	• Dominate species	Range	Crop
Melanoplineae			
1.	<i>M. sanguinipes</i>	•	•
2.	<i>M. packardii</i>	•	•
3.	<i>M. bivittatus</i>	•	•
4.	<i>M. infantilis</i>	0	0
5.	<i>M. confusus</i>	0	0
6.	<i>M. femurrubrum</i>	0	0
7.	<i>M. dawsonii</i>	0	
8.	<i>Melanoplus gladstoni</i>		0
9.	<i>Hesperotettix viridis</i>	0	
10.	<i>Aeloplides turnbulli</i>	0	0
11.	<i>Phoetaliotes nebrascensis</i>	0	0
Oedipodinae			
1.	<i>Opeia obscura</i>	0	
2.	<i>Amphitornus coloradus</i>	0	0
3.	<i>Philobostroma quadrimaculatum</i>	0	
4.	<i>Aeropedellus clavatus</i>	0	0
5.	<i>Aulocara ellioti</i>	•	•
6.	<i>Ageneotettix deorum</i>	0	0
7.	<i>Psoloessa delicatula</i>	0	
Gomphocerinae			
1.	<i>Arphia pseudonietana</i>	0	
2.	<i>Arphia conspersa</i>	0	
3.	<i>Encoptolophus costalis</i>		0
4.	<i>Hadrotettix trifasciatus</i>	0	0
5.	<i>Spharagemon equale</i>	0	0
6.	<i>Spharagemon campestris</i>	0	
7.	<i>Camula pellucida</i>	0	0
8.	<i>Dissosteira carolina</i>	0	0
9.	<i>Xanthippus corallipes</i>	0	0
10.	<i>Metator pardalinus</i>	0	
11.	<i>Trachyrhachis kiowa</i>	0	
12.	<i>Circotettix carlinianus</i>	0	
13.	<i>Circotettix rabula</i>	0	

Species	Site 1		Site 2		Site 3	
	Range	Crop	Range	Crop	Range	Crop
1. <i>Melanoplus sanguinipes</i> (Fabricius)	✓✓	✓✓	✓✓	✓✓	✓	✓
2. <i>M. packardii</i> Scudder	✓✓	✓✓	✓	✓	❖	✓
3. <i>M. bivittatus</i> (Say)	✓	✓	✓✓	✓✓	✓	✓✓
4. <i>Aulocara elliotti</i> Thomas	✓	❖	✓	❖	✓	❖
5. <i>Ageneotettix deorum</i> (Scudder)	❖	❖	✓	✓	❖	❖
6. <i>Aeropedellus clavatus</i> (Thomas)	✓		✓	❖	✓	
7. <i>Amphitornus coloradus</i> (Thomas)	❖	❖	❖		❖	
8. <i>Spharagemon equale</i> (Say)	❖		❖		❖	
9. <i>Arphia pseudonietana</i> (Thomas)					❖	
10. <i>M. infantilis</i> Scudder	❖				❖	
11. <i>Trachrhachys kiowa</i> Thomas			❖		❖	
12. <i>Dissosteira carolin</i> (L.)	✓				❖	
13. <i>Metator pardalinus</i> (Saussure)			❖		❖	
14. <i>Psoloessa delicatula</i> Scudder					❖	
15. <i>Camula pellucida</i> Scudder			❖			
16. <i>Xanthippus corallipes</i> Halderman			❖			
17. <i>Arphia conspersa</i> Scudder			❖			
18. <i>Phoetaliotes nebrascensis</i> (Thomas)		❖				
19. <i>Opeia obscura</i> (Thomas)	❖					

Subsample Totals: Range: 18
 Crop: 18

LEGEND:

✓✓

100 or more specimens collected in a habitat per season

✓

10 or more specimens collected in a habitat per season

❖

1 or more specimens collected in a habitat per season

Table 11. Grasshoppers species occupying winter wheat and adjacent field borders in 1988, Willow Creek, Montana.

Species	Site 4		Site 5		Site 6		Site 7	
	Range	Crop	Range	Crop	Range	Crop	Range	Crop
1. <i>Melanoplus sanguinipes</i> (Fabricius)	✓✓	✓✓	✓✓	✓✓	✓	✓✓	✓	✓
2. <i>M. packardii</i> Scudder	✓	✓	✓✓	✓	✓	✓	✦	✦
3. <i>M. bivittatus</i> (Say)	✓✓	✓✓	✓	✓	✓	✓	✓✓	✓✓
4. <i>Aulocara elliotti</i> Thomas	✓✓	✓	✓✓	✓	✓	✦	✦	
5. <i>Ageneotettix deorum</i> (Scudder)	✦	✦						
6. <i>Aeropedellus clavatus</i> (Thomas)	✓	✦	✓	✦	✦			
7. <i>Amphitornus coloradus</i> (Thomas)	✓				✦			
8. <i>Spharagemon equale</i> (Say)	✓	✦	✦	✦	✦			
9. <i>Arphia pseudonietana</i> (Thomas)	✦							
10. <i>M. infantilis</i> Scudder	✦		✦		✦			
11. <i>Trachyrhachis kiowa</i> Thomas	✦							
12. <i>Dissosteira carolina</i> (L.)	✓	✦	✦		✦			
13. <i>Metator pardalinus</i> (Saussure)	✦							
14. <i>Psoloessa delicatula</i> Scudder	✦		✦		✦			
15. <i>Camula pellucida</i> Scudder	✓	✓	✦	✦			✓	✓
16. <i>Xanthippus corallipes</i> Halderman	✦	✦	✦					
17. <i>M. confusus</i>	✦	✦	✦	✦				
18. <i>M. femurrubrun</i>		✦	✦	✦	✦			
19. <i>Hadrotettix trifasciatus</i>	✦	✓						
20. <i>Circotettix carlinianus</i> (Thomas)					✦			
21. <i>Spharagemon campestris</i> (McNeill)					✦			
22. <i>Encoptolophus costalis</i> (Scudder)						✦		
23. <i>M. dawsonii</i> (Scudder)					✦			
24. <i>Circotettix rabula</i> Rehn & Hebard							✦	
25. <i>Aeloplides turnbulli</i> (Caudell)							✦	✦
Subsample Totals:	Range:	26	Site 7:	Range:	15	LEGEND: See Table 11.		
Sites 4,5,6:	Crop:	22		Crop:	15			

Table 12. Grasshoppers species occupying winter wheat and adjacent field borders in 1989, Willow Creek, Montana.

Species	Site 8		Site 9		Site 10	
	Range	Crop	Range	Crop	Range	Crop
1. <i>Melanoplus sanguinipes</i> (Fabricius)	✓✓	✓✓	✓✓	✓✓	✓✓	✓✓
2. <i>M. packardii</i> Scudder	✓✓	✓✓	✓✓	✓	✓	✓
3. <i>M. bivittatus</i> (Say)	✓	✓	✓	✓	✓	✓✓
4. <i>Aulocara ellioti</i> Thomas	✓✓	❖	✓	❖		
5. <i>Ageneotettix deorum</i> (Scudder)	❖		❖	❖		
6. <i>Aeropedellus clavatus</i> (Thomas)	✓		✓	❖	✓	
7. <i>Amphitornus coloradus</i> (Thomas)	✓		❖		❖	
8. <i>Spharagemon equale</i> (Say)	✓		❖		❖	
9. <i>M. infantilis</i> Scudder	❖		❖			
10. <i>Trachrhachys kiowa</i> Thomas	✓					
11. <i>Dissosteira carolin</i> (L.)	❖	❖				
12. <i>Psoloessa delicatula</i> Scudder	❖				❖	
13. <i>Camula pellucida</i> Scudder	❖	❖	❖	❖		
14. <i>Xanthippus corellipes</i> Halderman	❖		❖	❖	❖	
15. <i>Arphia conspersa</i> Scudder	❖					
16. <i>Phoetaliotes nebrascensis</i> (Thomas)			❖			
17. <i>M. confusus</i>					❖	
18. <i>M. femurrubrum</i>						❖
19. <i>Sphragemon campestris</i> (McNeill)			❖			
20. <i>Hesperotettix viridis</i>	❖		❖		❖	
21. <i>Philobostroma quadrimaculatum</i> (Thomas)	❖					
22. <i>Melanoplus gladstoni</i>		❖				

Subsample Totals: Range: 26
 Sites 8,9,10 Crop: 22

LEGEND: See Table 11.

Table 13. Grasshoppers species occupying winter wheat and adjacent field borders in 1990, Willow Creek, Montana.

Predominant Grasshopper Species in Rangeland Over the Entire Study Period

Overall, 57% of the grasshopper specimens collected in rangeland were *M. sanguinipes* (Table 14). This species was the major component of the species complex in six of the ten rangeland study sites (Table 14). *Aulocara ellioti* was also an important component of this species complex. This species made up 23% of the sample population collected in rangeland (Table 14). Additionally, *A. ellioti* was the predominant species at two study sites. *Melanoplus packardii* made up 9.7% of the species complex compared to 5.6% for *M. bivittatus* (Table 14). *Ageneotettix deorum* and *C. pellucida* were important components of the species complex at two sites (Table 14). The other 25 species collected in rangeland made up 4.7% of the sample population.

Over the three years, 63% of sample population in winter wheat was composed of *M. sanguinipes*. *M. sanguinipes* was the predominant species in 8 out of 10 study sites (Table 15). Overall, 24.5% of the sample population was composed of *M. bivittatus* (Table 15). This species was the most abundant at two study sites (Table 15).

The number of individual *M. packardii* and *A. ellioti* captured per site represented 8.7% and 2.4% of the sample population, respectively (Table 15). The number of individuals captured in the "other species" category (1.4%) included, *C. pellucida* which was prevalent at one study site (Table 15).

Comparison of the Number of Species Collected Between Habitats

Overall, there were 13.5 ± 1.04 species collected per site in rangeland (N=10) compared to 7.9 ± 1.03 per site for winter wheat (N=10). The results of a Mann-Whitney U-test suggested that the rangeland sites supported a greater average species richness than the crop sites ($P = 0.013$).

Date	Site	<i>M. sanguinipes</i>	<i>M. packardii</i>	<i>M. bivittatus</i>	<i>A. ellioti</i>	<i>A. deorum</i>	<i>C. pellucida</i>	Other
1988	1	38	40	4	14	0	0	4 = 100%
	2	67	4	17	3	5	0	4 = 100%
	3	37	6	30	8	0	0	19 = 100%
1989	1	29	2	11	48	0	0	10 = 100%
	2	21	10	1	63	0	0	5 = 100%
	3	64	9	12	8	0	0	7 = 100%
	4	23	2	48	2	0	25	1 = 100%
1990	1	50	21	1	19	0	0	9 = 100%
	2	94	3	0.5	1	0	0	1 = 100%
	3	78	5	10	0.2	0	0	7 = 100%
OVERALL:								overall
	\bar{X} /site	615.50	104.20	60.60	247.10		52.10	\bar{X} /site:
	SE	309.74	47.20	15.15	151.78		14.37	1079.50
	%	57	9.71	5.6	23		4.7	350.06

- * = Numbers designate percentages
- 0 = Boldface indicates majority of population
- 0 = Outline indicates second most numerous species

Table 14. Grasshopper species composition in the range.*

Date	Site	<i>M. sanguinipes</i>	<i>M. packardii</i>	<i>M. bivittatus</i>	<i>A. ellioti</i>	<i>A. decorum</i>	<i>C. pellucida</i>	Other
1988	1	40	35	23	1	0	0	1 = 100%
	2	55	2	40	1	1	0	1 = 100%
	3	31	5	64	0	0	0	0 = 100%
1989	1	49	4	38	6	0	0	3 = 100%
	2	40	21	21	14	0	0	4 = 100%
	3	46	14	26	3	0	0	11 = 100%
	4	18	0	55	0	0	26	0 = 100%
1990	1	74	15	9.5	1	0	0	0.5 = 100%
	2	94	4	1	0.5	0	0	0.5 = 100%
	3	62	9	28	1	0	0	0 = 100%
OVERALL:								overall
	\bar{X} /site	344.10	47.20	133.4	13.30		7.5	\bar{X} /site:
	SE	122.74	13.07	31.65	6.30		2.5	545.50
	%	63.00	8.70	24.50	2.40		1.40	128.29

8

- * = Numbers designate percentages
- 0** = Boldface indicates majority of population
- 0 = Outline indicates

Table 15. Grasshopper species composition in the crop.*

Species Comparison at Reseeded Sites

When the number of species collected in "newly" reseeded range, 11.25 ± 1.70 , (N=4) was compared to those collected in "old" reseeded range, 16.00 ± 1.53 , (N=3) there was no significant difference ($P = 0.216$). At 4 "newly" reseeded sites *A. ellioti* averaged 19.5 ± 9.11 (N=4) specimens while at "old" reseeded sites (N=3) this species averaged 742 ± 410.6 , ($P = 0.05$). This suggests that significantly more *A. ellioti* were supported by "old" reseeded vs. "newly" reseeded sites. In contrast, *M. sanguinipes* averaged 996 ± 792.12 (N=4) specimens at newly reseeded sites vs. 428 ± 62.85 , (N=3) at "old" reseeded sites, ($P = 0.38$).

Comparison of Predominant Species Between Habitats

The most abundant species collected in both rangeland and winter wheat over the three year study was *M. sanguinipes* (Table 16). In the crop, *M. bivittatus* was the next most prevalent species followed by *M. packardii*, and *A. ellioti*. There was no significant difference in the *M. sanguinipes* and *M. bivittatus* specimens collected per site, while their numbers were significantly different from those collected for the other two species and all other species categories (Table 16). On a yearly basis, *M. sanguinipes* was the most prevalent species in winter wheat and rangeland in 1988 and 1990. In 1989, both *A. ellioti* and *M. sanguinipes* were the most prevalent species collected in rangeland (Table 16). The predominance rank of species in crop remained the same over the three years (Table 16). In range, there was more variation in the ranking of species (Table 16). The species which varied the most in its ranking was *A. ellioti* (Table 16).

Table 16. Comparison of the predominant species in range and crop over three years.

Range			Crop		
All three years	\bar{X}	SE		\bar{X}	SE
<i>M. sanguinipes</i>	615.50±309.74	A	<i>M. sanguinipes</i>	344.10±122.74	A
<i>A. ellioti</i>	247.10±151.78	B	<i>M. bivittatus</i>	133.40±31.65	A
<i>M. packardii</i>	104.20±406.67	B	<i>M. packardii</i>	47.20±13.07	B
<i>M. bivittatus</i>	60.60±15.15	B	<i>A. ellioti</i>	13.30±6.28	C
Other Species	50.10±14.37	B	Other Species	7.50±2.50	C
Kruskal Wallis	$\chi^2 = 14.45, P = 0.0006 N = 10$		$\chi^2 = 33.57, P = < 0.0001 N = 10$		
Range			Crop		
1988	\bar{X}	SE	1988	\bar{X}	SE
<i>M. sanguinipes</i>	26.09±4.92	A	<i>M. sanguinipes</i>	19.47±4.03	A
<i>M. packardii</i>	12.79±3.35	B	<i>M. bivittatus</i>	16.73±3.57	A
<i>M. bivittatus</i>	6.27±1.30	B	<i>M. packardii</i>	6.33±1.82	BC
<i>A. ellioti</i>	5.06±1.47	B	<i>A. ellioti</i>	0.55±0.20	C
Other Species	3.00±0.51	B	Other Species	0.33±0.11	C
Kruskal Wallis	$\chi^2 = 36.08, P = < 0.0001 N = 34$		$\chi^2 = 61.28, P = < 0.0001 N = 34$		
Range			Crop		
1989	\bar{X}	SE	1989	\bar{X}	SE
<i>A. ellioti</i>	64.91±15.71	A	<i>M. sanguinipes</i>	20.97±4.65	A
<i>M. sanguinipes</i>	35.31±6.94	A	<i>M. bivittatus</i>	18.69±4.58	A
<i>M. bivittatus</i>	10.16±2.91	B	<i>M. packardii</i>	4.19±0.82	B
<i>M. packardii</i>	9.22±2.11	B	<i>A. ellioti</i>	3.28±0.76	BC
Other Species	8.91±2.53	B	Other Species	1.69±0.47	C
Kruskal Wallis	$\chi^2 = 25.53, P = < 0.0001 N = 32$		$\chi^2 = 45.62, P = < 0.0001 N = 32$		
Range			Crop		
1990	\bar{X}	SE	1990	\bar{X}	SE
<i>M. sanguinipes</i>	147.79±41.09	A	<i>M. sanguinipes</i>	75.29±13.52	A
<i>M. packardii</i>	11.61±2.61	B	<i>M. packardii</i>	6.96±1.35	B
<i>A. ellioti</i>	8.11±2.47	BC	<i>M. bivittatus</i>	6.57±1.55	B
Other Species	4.86±0.98	C	<i>A. ellioti</i>	0.64±0.29	C
<i>M. bivittatus</i>	2.64±0.60	C	Other Species	0.39±0.17	C
Kruskal Wallis	$\chi^2 = 62.30, P = < 0.0001 N = 28$		$\chi^2 = 90.83, P = < 0.0001 N = 28$		

Means are significantly different if separated by different letters. Mann Whitney U-Test used for pairwise comparisons

Comparison of Species By Sampling Methods

There was no significant difference in the number of species captured using a sweep net (11.0 ± 1.55 , $N=6$) when compared to using a drop cage in rangeland (8.5 ± 1.06 , $N=6$, $P=0.20$) or winter wheat, $P=0.52$. The mean number of species captured using a sweep net was 6.33 ± 1.28 and 5.0 ± 0.63 using a drop cage.

Comparison of Temporal Density Estimates Using a Sweep Net versus a Drop Cage

A 2x2 contingency table was used to compare the number of non-significant and significant density estimates in rangeland and crop using a drop cage versus a sweep net. The test resulted in no significant difference between sampling methods ($\chi^2=0.413$, $df=1$, $P=0.19$, $N=118$).

Density Estimate Comparison Between Habitats

When weekly density estimates for *M. sanguinipes* from 9 study sites were compared between the two habitats the following results were obtained. In 4 out of the 9 sites significant shifts in density estimate differences occurred between the two habitats during the sample season (site 1, 2, 4, and 10, Figure 6, 7, 9, 10). At site 1, 2, and 10 density estimates in the rangeland were significantly different than those in the crop in one or more early sample periods (Figure 6, 9, 10). At site 4, rangeland density estimates during the early sample periods were not significantly greater (Figure 7). In the middle sample periods density estimate differences changed between habitats. Density estimates in the crop were significantly greater than those in the rangeland at sites 1, 4, and 10, but not significantly different at site 2 (Figures 6, 7, 9, 10). During the late sample periods density estimates in the rangeland were again

significantly different than those in the crop at most sample periods at site 1 and 2 (Figure 6). At site 4 and 10 density estimates in the rangeland never exceeded those in the crop at the late sample periods (Figures 7, 8, 9, 10). At site 9, density estimates for *M. sanguinipes* remained significantly higher in the rangeland than the crop until the final two sample periods (Figures 9, 10). At site 3, 5, 6 and 8 density estimates in the two habitats were either never significantly different or were significantly greater in one habitat only sporadically, and no clear trend was evident (Figures 6, 7, 9, 10).

The combined weekly density estimates of *M. bivittatus* and *M. packardii* were also compared between the two habitats to determine if there were any patterns in density estimate differences within the nine study sites. At study sites 1 and 2, significant differences in density estimates did occur during the sampling season. Densities of these two species at site 1 were greatest in the rangeland during the early sample periods while at site 2 they were greatest in the crop (Figure 6). The density estimate difference pattern in the mid and late sample periods was similar to those of *M. sanguinipes* (Figure 6). At sites 3 and 4, they were always greatest in the crop (Figures 6, 7, 8). At sites 5, 6, 8, 9, and 10 generally no significant differences in density estimates occurred between habitats at any sample periods (Figures 7, 8, 9, 10). Occasionally, significant density differences occurred between habitats but there was no consistent pattern (Figures 7, 8, 9, 10).

Density estimates of *Aulocara elliotti* in the crop rarely exceeded those in the range and when they were greater in the crop there was no consistent pattern as occurred at some study sites with the other three species, discussed previously (Tables 17, 18, 19).

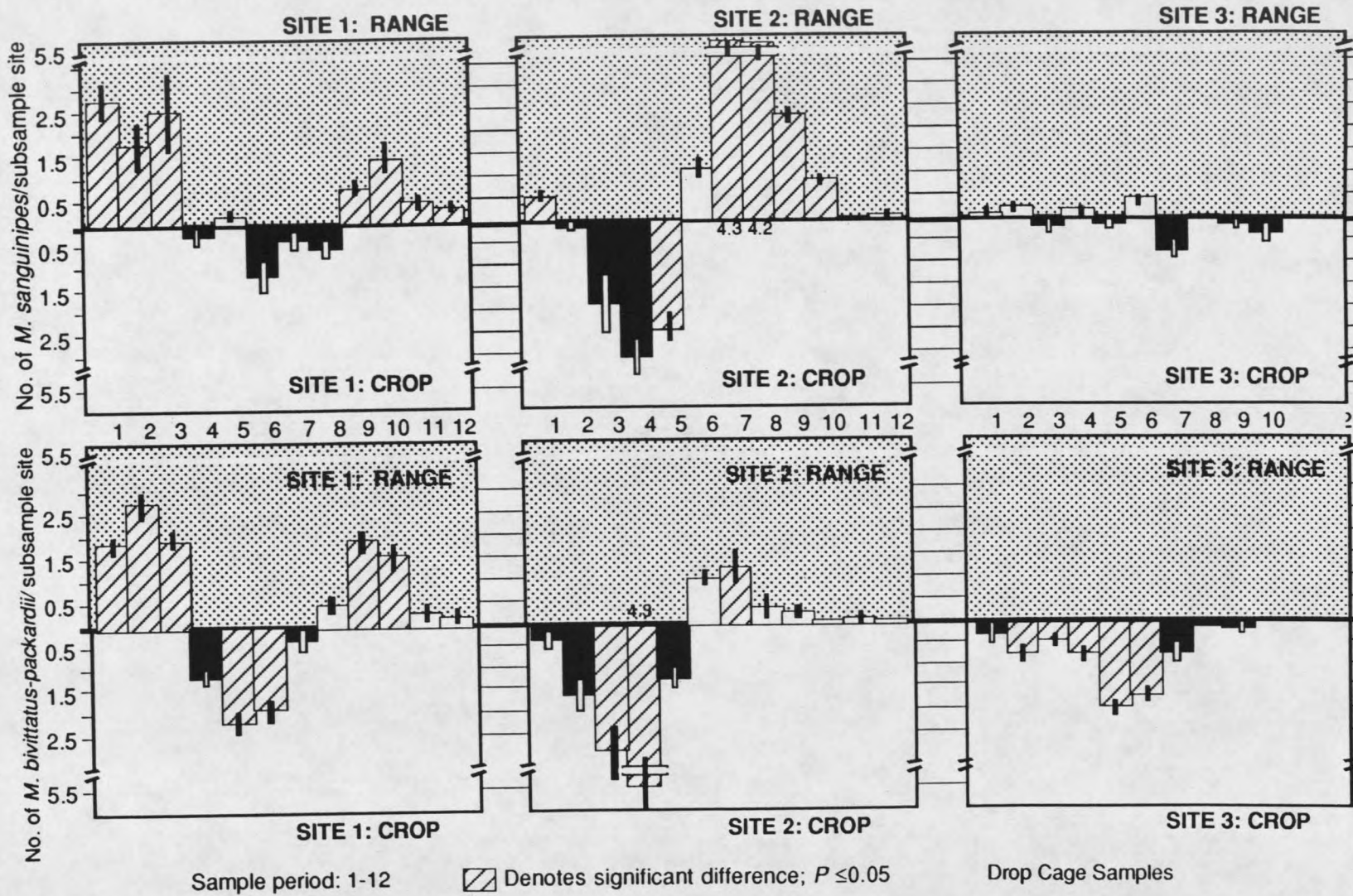


Figure 6. Temporal density estimate differences in rangeland and winter wheat crop; 1988.

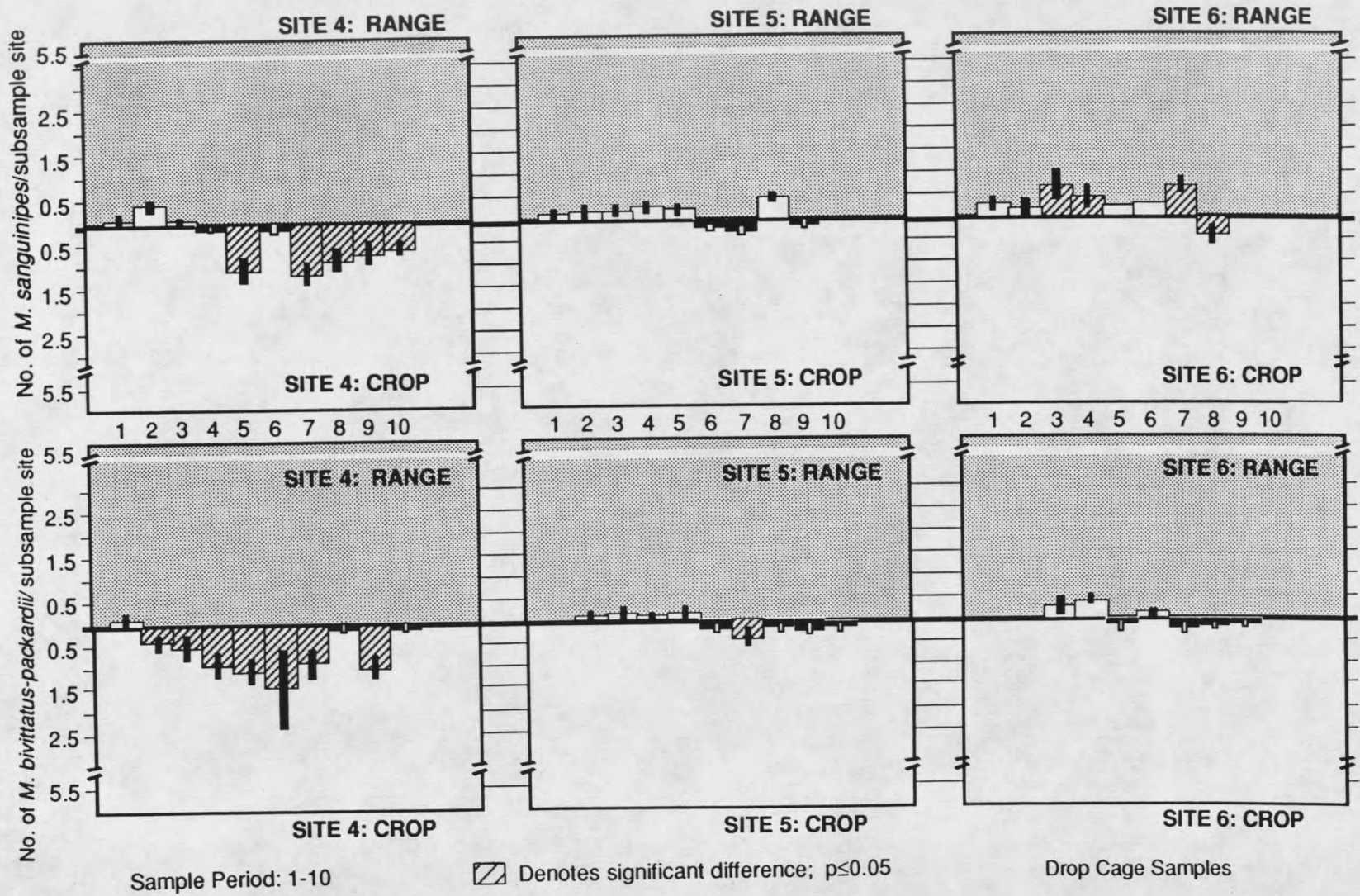


Figure 7. Temporal density estimate differences in rangeland and winter wheat crop; 1989

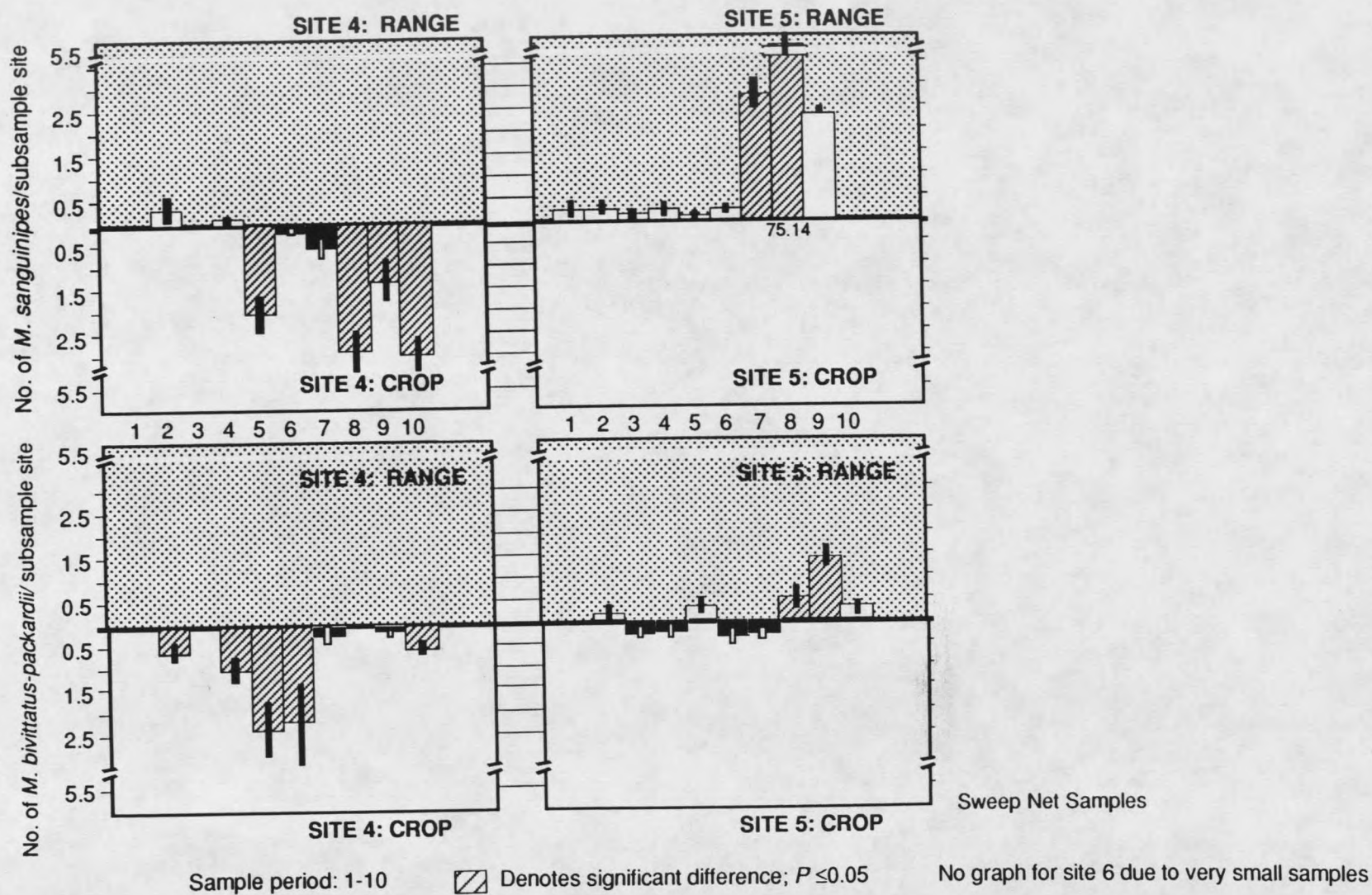


Figure 8. Temporal density estimate differences in rangeland and winter wheat crop; 1989

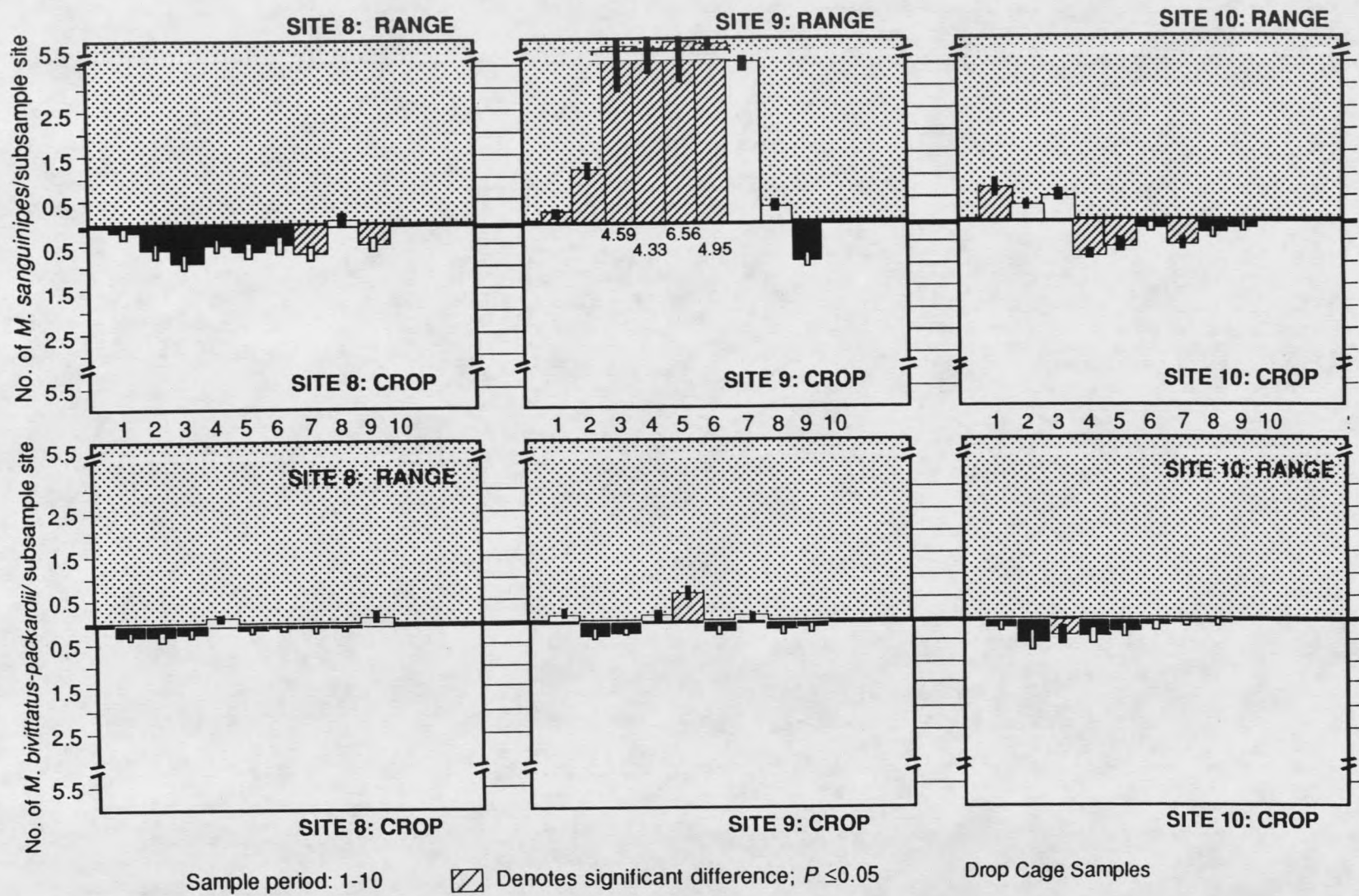


Figure 9. Temporal density estimate differences in rangeland and winter wheat crop; 1990

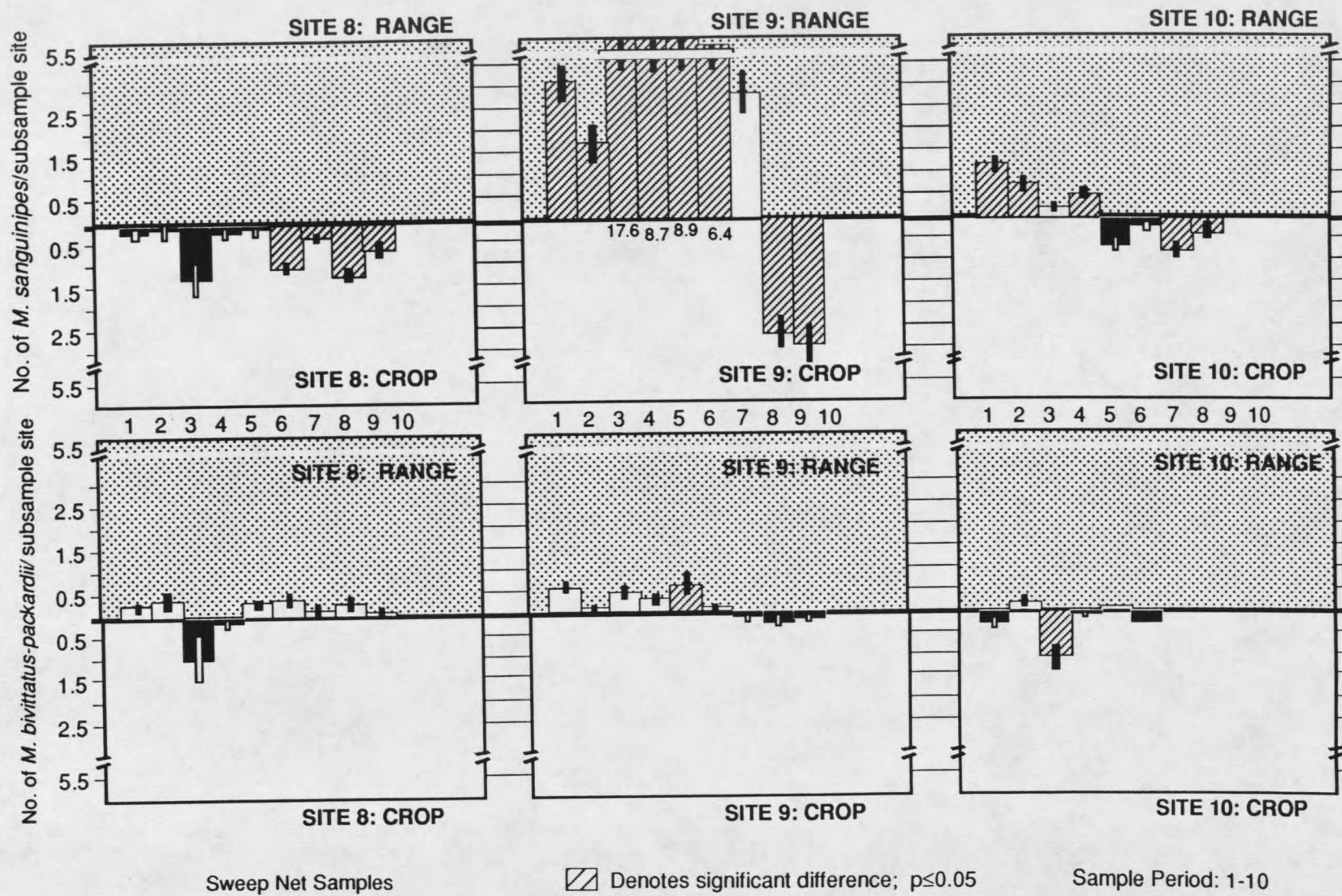


Figure 10. Temporal density estimate differences in rangeland and winter wheat crop; 1990.

Table 18. SITE 4 - Population dynamics and dispersal of *A. elliotti*; 1989.

	Drop Cage					Sweep				
	Range		Crop		<i>P</i> -value	Range		Crop		<i>P</i> -value
	\bar{X}	SE	\bar{X}	SE		\bar{X}	SE	\bar{X}	SE	
1.	0.50	0.13	0.06	0.06	0.003	No Sample				
2.	2.23	0.47	0.06	0.06	0.003	3.92	0.59	0.11	0.08	0.0001
3.	0.88	0.19	0.17	0.12	0.006	No Sample				
4.	0.38	0.15	0.05	0.05	0.05	0.69	0.15	0.41	0.32	0.41
5.	0.42	0.14	0.04	0.04	0.019	1.54	0.32	0.41	0.16	0.003
6.	0.81	0.22	0.06	0.06	0.008	1.31	0.24	0.18	0.14	0.0004
7.	0.85	0.16	0	0	0	2.19	0.39	0.22	0.22	0.0004
8.	0.96	0.20	0	0	0	1.42	0.28	0.17	0.09	0.001
9.	0.19	0.10	0.11	0.08	0.54	0.73	0.18	0.22	0.22	0.08
10.	0.23	0.08	0.17	0.09	0.61	0.69	0.19	0.17	0.09	0.035

SITE 5 - Population dynamics and dispersal of *A. elliotti*; 1989.

	Drop Cage					Sweep				
	Range		Crop		<i>P</i> -value	Range		Crop		<i>P</i> -value
	\bar{X}	SE	\bar{X}	SE		\bar{X}	SE	\bar{X}	SE	
1.	No Sample					No Sample				
2.	0.11	0.06	0.05	0.05	0.51	0.22	0.13	0	0	0
3.	0.12	0.08	0	0	0	0.46	0.16	0.22	0.13	0.28
4.	0.15	0.07	0.05	0.05	0.32	0.12	0.10	0.11	0.08	0.97
5.	0.31	0.11	0.17	0.09	0.35	0.27	0.10	0.05	0.05	0.12
6.	0.27	0.12	0.11	0.08	0.32	0.54	0.24	0.56	0.22	0.96
7.	0.62	0.18	0.66	0.18	0.85	1.73	0.34	1.50	0.63	0.73
8.	0.88	0.13	1.17	0.20	0.24	2.85	0.43	0.05	0.05	0.0001
9.	1.38	0.22	0.89	0.27	0.16	5.31	0.53	0.17	0.09	0.0001
10.	0.62	0.26	0.72	0.21	0.77	3.58	0.44	1.22	0.50	0.001

Table 18. Continued on following page.

Table 18. Continued.

SITE 6 - Population dynamics and dispersal of *A. elliotti*; 1989.

	Drop Cage					Sweep				
	Range		Crop		<i>P</i> -value	Range		Crop		<i>P</i> -value
	\bar{X}	SE	\bar{X}	SE		\bar{X}	SE	\bar{X}	SE	
1.	No Sample					No Sample				
2.	0.27	0.09	0.09	0.06	0.12	No Sample				
3.	0.19	0.10	0	0	0	0.19	0.08	0.05	0.05	0.13
4.	0.77	0.05	0	0	0	0.77	0.05	0	No Sample	
5.	0.15	0.12	0.05	0.05	0.43	No Sample				
6.	0.04	0.04	0	0	0	No Sample				
7.	0.04	0.04	0	0	0	No Sample				
8.	0.08	0.05	0	0	0	No Sample				
9.	0	0	0	0	0	No Sample				
10.	No Sample					No Sample				

Table 19. SITE 8 - Population dynamics and dispersal of *A. elliotti*; 1990.

	Drop Cage					Sweep				
	Range \bar{X}	SE	Crop \bar{X}	SE	P-value	Range \bar{X}	SE	Crop \bar{X}	SE	P-value
1.	1.27	0.28	0	0	0	1.15	0.20	0	0	0
2.	0.08	0.05	0	0	0	0.81	0.24	0	0	0
3.	0.04	0.04	0	0	0	0.46	0.17	0	0	0
4.	0.23	0.10	0.05	0.05	0.39	0.46	0.13	0.18	0.11	0.20
5.	No sample					0.62	0.18	0.05	0.05	
6.	0.31	0.11	0	0	0	0.58	0.16	0	0	0
7.	0.15	0.07	0	0	0	0.31	0.09	0	0	0
8.	0.27	0.09	0	0	0	0.27	0.14	0	0	0
9.	0	0	0	0	0	0.12	0.07	0	0	0
10.	No sample					No sample				

SITE 9 - Population dynamics and dispersal of *A. elliotti*; 1990.

	Drop Cage					Sweep				
	Range \bar{X}	SE	Crop \bar{X}	SE	P-value	Range \bar{X}	SE	Crop \bar{X}	SE	P-value
1.	No Sample					No Sample				
2.	0.15	0.09	0	0	0	0.19	0.12	0.05	0.05	0.31
3.	0.04	0.04	0	0	0	0.23	0.17	0	0	0
4.	0	0	0	0	0	0	0	0	0	0
5.	0.04	0.04	0	0	0	0.08	0.05	0	0	0
6.	0	0	0	0	0	0.19	0.10	0.05	0.05	0.23
7.	0.04	0.04	0	0	0	0.38	0.27	0	0	0
8.	0.04	0.04	0.18	0.14	0.46	No Sample				
9.	No Sample					0.08	0.05	0.04	0.04	0.99
10.	0	0	0.09	0.09	0	No Sample				

Discussion

Grasshopper Species Occupying Winter Wheat and Adjacent Range

Thirty one species were collected at ten sites over a three year period. Twelve of these species were collected, exclusively in the rangeland while none of the 31 species were collected only in the crop (Tables 10, 11, 12, 13). Also, there were significantly more species of grasshoppers collected in the rangeland than crop (13 ± 1.04 vs 7.9 ± 1.03). In an earlier study, 25 species in three subfamilies were collected in the same plant community type (Agcr/Mesa) in the Gallatin Valley (Kemp et. al 1990a, b). There was considerable overlap in the grasshopper species collected in both studies even though sampling occurred at different sites and during different years. The predominant species in the crop for all three years was *M. sanguinipes* followed by *M. bivittatus*, *M. packardii*, and *A. elliotti* (Table 14). Only the first three of these species were abundant in winter wheat (Table 16). A fifth species *C. pellucida* was abundant, at only Study Site 4, 1989 (Table 14). Over the same three year sample period, *M. sanguinipes*, *M. packardii*, *M. bivittatus*, and *A. elliotti* were also the predominant species in the rangeland study sites. The most abundant species in the rangeland was *M. sanguinipes* followed by *A. elliotti*, *M. packardii*, and *M. bivittatus* (Table 16). *Camnula pellucida* was a common in the rangeland of Site 7, 1989 (Table 12).

Historically, *M. sanguinipes*, *M. bivittatus*, *M. packardii* and *C. pellucida* are considered economically important species in the Northern Great Plains (Brooks 1958). Populations levels of these species can be very high during outbreaks (Shotwell 1941, Parker et. al. 1955, Reigert et. al. 1965, Bird et. al. 1966, Bird and Romanov 1966,

Gillespie 1985, 1987, Harris 1985, Hantsbarger 1986). During 1985 through 1987 it was not uncommon to receive reports of grasshopper densities in excess of 50 m² in Montana (Gillespie 1987, and pers. obs.). It is important to note, that this study was conducted when the grasshopper densities in Montana were low compared to those of 1985 through 1987 (Kemp 1992).

At "newly established" sites, the proportion of the population composed of *M. sanguinipes* was quite high, ranging from 64% to 94%. In "older" reseeded sites 21 to 50% of the sample population was composed of *M. sanguinipes* (Table 14). At "newly" reseeded sites, the number of *A. ellioti* specimens collected were significantly lower than those collected at "old" reseeded sites. In a study, in which alfalfa and milkvetch, *Astragalus cicer* L., was reseeded into native rangeland, densities of *M. sanguinipes* increased 3 fold over a three year period (Hewitt and Onsager 1988). In a second study, densities of *M. sanguinipes* increased 1000% over three years when western wheatgrass *Agropyron smithii* Rydb. and green needle grass *Stipa viridula* Trin. was interseeded into native rangeland (Hewitt and Rees 1983). Thus, results to date, suggest that populations of *M. sanguinipes* may benefit from plant community disturbances produced by reseeded and the addition of forbs such as alfalfa.

The study of the insect fauna in Agcr/Mesa habitat type should become increasingly important as small grain acreages are enrolled in the Conservation Reserve Program (CRP)(USDA/ASCS pers. comm.). In Montana, approximately 80% of the small grains fields established on highly erodible land have been planted to crested wheatgrass. It is a common practice to also plant a legume such as alfalfa, *Medicago sativa*, with this grass species (USDA/ASCS pers. comm.). Based on my results, grasshopper species communities at CRP sites are considerably less diverse than the native rangeland that existed before the introduction of agriculture (Kemp et. al.

1990a). In my study 9%, 10%, and 19% of the species complex was composed of other species in "old" reseeded sites when compared to 1%, 1%, 7% and 7% in "newly" reseeded sites. Many of these CRP acres will be composed of a plant community very similar to the reseeded rangeland surrounding small grain fields at Three Forks and Willow Creek.

Very little research has been done concerning the effect these new CRP habitats will have on the grasshopper species complex surrounding small grain fields. However, Spangler and MacMahon (1990) found that a grass monoculture of crested wheatgrass supported higher populations of pest populations of grass feeding mirids than surrounding polycultures.

The effect that such reseeding programs will have on the populations of economically important grasshopper species is unknown. The results of my study suggest that the grasshopper species complex in "newly" reseeded rangeland may be composed of a greater proportion of pest species than those in "old" reseeded rangeland. During an outbreak these simple plant communities surrounding the crop may support populations of *M. sanguinipes*, *M. bivittatus*, *M. packardii* and *C. pellucida* which can disperse the short distances to small grain fields to feed on the crop. Hopefully, this study will begin to form a baseline of information for future studies in small grains bordered by CRP.

Density Estimate Comparisons Between Two Habitats

There were seasonal shifts in the density estimate differences between the rangeland and crop for *M. sanguinipes*, at four study sites (Figures 6, 7, 9). Similar shifts in density estimate differences of *M. bivittatus*-*M. packardii* occurred at two study sites (Figure 6). The changes in density estimates of these grasshopper species

between habitats support the hypothesis, that these estimate shifts are largely due to dispersal of grasshoppers from the rangeland habitat into the adjacent crop habitat. In most cases (4 out of 6), the abundance data suggest that the grasshopper populations dispersed into the rangeland when the crop matured. Results from these sites would support the use of temporal density estimates to quantify movement of *M. sanguinipes*, *M. bivittatus*-*M. packardii* between habitats.

Results of this study support earlier observations of grasshoppers dispersing between rangeland and crops during grasshopper outbreaks (Shotwell 1941, Smith 1954, Parker et. al. 1955, Dempster 1963, Bird et. al. 1966, Bird and Romanov 1966, Uvarov 1977, and Gillespie 1987), and work in Britain, where *C. brunneus* and *C. parallelus* nymphs dispersed from sites of oviposition to taller grass to feed. Later, adult females moved to shorter grass and bare soil to oviposit (Richards and Waloff 1954).

There are other plausible hypotheses to explain temporal changes in density estimates across habitats. There may be fluctuating rates of mortality within a habitat. Variable rates of predation, parasitism, or shifting habitat quality or conditions may produce such shifts (Begon et. al. 1990). Also, sampling biases associated with sampling methods may affect grasshopper surveys. However, sampling bias was probably not a factor in this study, because sweep net and drop cage samples tended to capture grasshoppers at similar stages of development during a given sample period, Chapter 4, and there was no significant difference in detection of density estimate patterns at a given sample period using the two sampling methods.

Temporal shifts in density estimates of *M. sanguinipes* between habitats did not occur at five study sites (Tables 6, 7, 9). Similarly, there were no shifts in *M. bivittatus*-*M. packardii* density estimates at seven sites (Tables 6, 7, 9). The lack of a

temporal shift in density estimates may be due to extremely low densities of *M. sanguinipes* and *M. bivittatus*-*M. packardii* at these sites compared to those where shifts occurred. Fewer grasshoppers at these sites may have made it more difficult to detect any trends in the density estimates between habitats. However, this was not the case at study site 9. The density estimates of *M. sanguinipes* were highest at this site and no dispersal was detected until the last two sample periods (Figure 10).

I expected *M. sanguinipes* to move readily between habitats at site 9, but this did not occur (Figure 10). I suspect the reason for such a result at this one site may be explained in part by the interaction of the following site specific factors. There was abundant rangeland forage at site 9, more abundant than any other study site. The abundant forage at this site may be due to the increased spring rainfall in 1990, when compared to 1988 (USDA/SCS 1987-1990). Secondly, in 1990, the crop and crested wheatgrass and alfalfa matured at nearly the same rate, while in 1988, the year when dispersal between the crop and rangeland was most evident (Figure 6), the plants in the crop and rangeland matured at different rates (pers. obs.). At this site, I concluded that the quality and quantity of the rangeland forage was adequate to support the development of a greater density of *M. sanguinipes* for a longer period of time than at the other study sites and this species was not forced to disperse into winter wheat for food until after the crop had matured.

Grazing may also reduce the amount of forage in rangeland and affect the rate of dispersal of some grasshopper species. At site 10, the maturation rates of crested wheatgrass, alfalfa, and winter wheat were the same as at site 9, but at site 10 the rangeland was intensively grazed before sampling began. A lack of rangeland forage, due to grazing may have created conditions which promoted the dispersal of lower densities of the three *Melanoplus* species into winter wheat when compared to site 9

(Figures 9, 10). Capinera and Sechrist (1982) studying short grass prairie and Jepsen-Innes and Bock (1989) studying semi-desert rangelands found that ungrazed and lightly grazed pastures generally supported a higher total number of grasshoppers than heavily grazed areas.

In this study, dispersal of *M. sanguinipes*, *M. packardii*, and *M. bivittatus* from rangeland to a crop may have required a certain set of environmental conditions at a rangeland/crop interface and sufficient grasshopper densities in order for detectable dispersal to occur between habitats. I think these conditions occurred at several study sites over the three year study period.

Price (1975) and Wellington (1980) provide a good working hypothesis for the study of grasshopper dispersal. They found that the three main factors which influence the dispersal of insects, include the dispersal strategy of the insect, population density of the insect, and nutritional factors (Price 1975, Wellington 1980). All three conditions occurred at sites where dispersal was detected (sites 1 and 2, 1988, site 4, 1989, and site 10, 1990) (Figures 6, 7, 8, 9). At these sites, there were grasshopper species with good dispersal capabilities (Parker et. al. 1955, Shotwell 1941, and Smith 1954), population densities appeared to be high enough for dispersal to occur, and the quantity and quality of nutrition was reduced by grazing and/or reduced precipitation in 1988.

Low annual precipitation in 1988 reduced the quantity of forage and resulted in the early maturation of crested wheatgrass and alfalfa. The annual precipitation at a Snow Survey Site near the study sites were approximately 8.75 cm less than 1987 and 5.75 cm and 3.75 cm lower than 1989 and 1990 respectively (USDA/SCS 1987-1990). Early maturation of rangeland plants also reduced the quality of rangeland forage for the three grasshopper species. Lack of forage for *M. sanguinipes*, *M. packardii* and *M.*

bivittatus, likely resulted in dispersal of these species into the crop to exploit winter wheat and weeds for food and shelter (Smith 1949, 1959, Smith et. al. 1952, Pickford 1962, 1963).

Conversely, early maturation of winter wheat led to reinvasion of the rangeland by the bulk of the grasshopper populations. Rangeland grasses were maturing when sampling began the first week in June as opposed to July in 1989, 1990. Winter wheat also matured early, harvest occurred 10 to 14 days earlier than 1989 and 1990. Grasshopper populations also declined early resulting in the termination of sampling the third week in August.

Grasshoppers may have reinfested the rangeland to feed and/or to lay eggs in the undisturbed soils. Two grasshopper species in Britain, *Chorithippus brunneus* and *C. parallelus*, displayed such behavior dispersing to shorter grass and bare soil to oviposit (Richards and Waloff 1954). The range/crop interface at Three Forks and Willow Creek may provide oviposition sites for these species as proposed by Uvarov (1977) and Pickford (1963). It is important to note that dispersal between habitats occurred at four out of the nine sites studied during a period when regional grasshopper densities were at a low point (Kemp 1991).

In 1989 and 1990, grasshoppers may have remained in the rangeland because plants in the rangeland matured at the same rate as those in the crop, and forage was adequate enough to support the bulk of the grasshopper populations in this habitat. Nutrition may not have been as important a factor as it was in 1988, but further study is needed to determine what role nutrition plays in the dispersal of grasshoppers. It would be interesting to follow density estimate differences between rangeland and winter wheat during grasshopper outbreak to determine if dispersal could be quantified more easily using these sampling methods during periods of elevated grasshopper

densities (those exceeding USDA/APHIS's economic threshold for rangeland and crops).

If movement is an important factor in the production of fluctuating density estimates in adjacent habitats then some interesting questions arise. Do grasshopper species move back and forth between habitats every season? Data from this study would support that either dispersal does not occur, or is not always detectable using density estimate differences between habitats at reduced grasshopper densities. Further, are there conditions in the environment and the population dynamics of grasshoppers which are correlated with more or less dispersal in a given season? The final important question becomes what are the environmental conditions and factors in the population dynamics of grasshoppers which are correlated to more or less dispersal in a given season. I think the next step would be to track certain nutrients in rangeland and crop plants to determine if they fluctuate within and between seasons as the three *Melanoplus* species populations fluctuate between rangeland and winter wheat.

CHAPTER FOUR

COMPARISON OF DEVELOPMENTAL DIFFERENCES AMONG THREE *MELANOPLUS* SPP. (ORTHOPTERA:ACRIDIDAE) IN WINTER WHEAT AND ADJACENT RANGELAND.

Introduction

The developmental rate of an organism is affected by numerous factors. Begon et. al. (1990) classified these environmental factors into two broad categories termed conditions and resources. Conditions are defined as environmental factors which vary in time and space (Begon et. al. 1990). These factors include temperature, relative humidity, pH, salinity, and concentration of pollutants. Resources are environmental factors which can be reduced by the activity of an organism. Resources include, CO₂, solar radiation, water, space, and nutrients (Begon et. al. 1990). The conditions and resources affecting the developmental rates of grasshoppers that have received the most research attention are temperature, relative humidity, and nutrients.

Results of laboratory and field cage studies have shown that elevated temperatures increase the rate of development in grasshoppers (Parker 1930, Hamilton 1936, 1960, Shotwell 1941, Brett 1947, Pepper and Hasting 1952, Dempster 1963, Putman 1963, Kemp and Sanchez 1987, Kemp and Dennis 1989). However, such developmental increases occur only between critical minimum low and critical maximum high temperatures (Chapman 1982, Begon et. al. 1990). Individuals exposed to temperatures below or above this range die by either, freezing or desiccation.

Relative humidity at optimum levels can also increase the rate of development (Parker 1930, Shotwell 1941, Dempster 1963). Relative humidities below optima lead to desiccation and those above may promote the development of diseases that can lead to the death of the organism. Generally, when the effects of relative humidity on development are studied they are done in conjunction with temperature studies (Parker 1930, Hamilton 1936, 1960, Shotwell, 1941, Dempster 1963).

The quantity and nutritional quality that plants and minerals have on the developmental rates of grasshoppers have been commonly studied resources (Brett 1947, Smith 1949, 1959, Smith et. al. 1952, Pickford, 1958, 1962, 1963, Barnes 1965, and Reigert et. al. 1965). In these studies, survival and nymphal developmental rates were fastest when *Melanoplus sanguinipes* (Fabricius) and *Camnula pellucida* Scudder were provided a straight or mixed diet of winter wheat, *Triticum aestivium*, as opposed to western wheatgrass, *Agropyron smithii* Rydb. The specific diets for these studies included winter wheat and barley *Hordeum vulgare* L. or a combination of wheat and weeds, such as mustard *Brassica kaber* (DC.) L.C. Wheeler or dandelion, *Taraxacum officinale* Web. and western wheatgrass (Smith 1949, 1959, Smith et. al. 1952, Pickford 1962, 1963). *Melanoplus sanguinipes*, when reared on an exclusive diet of native plants which included, needle and thread grass, *Stipa comata* Trin. and Rupr. junegrass, *Koeleria cristata* (L.) Pers., blue grama, *Bouteloua gracilis* (H.B.K.) Lag and moss phlox *Phlox hoodii* Richards and *C. pellucida* reared on the same grasses with the addition of western wheatgrass, *A. smithii*, experienced reduced survival and extended developmental rates when compared to a diet containing a combination of wheat and weeds. (Putman 1962, Pickford 1963).

Scientists have also provided grasshoppers with diets containing different levels of mineral nutrients to determine how such differences will affect the developmental rates

of grasshoppers. Smith (1960) found that the nymphal development of *M. sanguinipes* was shorter on a diet of winter wheat containing a low level of phosphorus than nymphs provided a diet of winter wheat with a high phosphorus level. Similarly, *M. sanguinipes* nymphs developed more rapidly on winter wheat receiving a higher level of nitrogen than nymphs feeding on wheat of a lower nitrogen level (Smith 1949, Smith and Northcott 1951).

One limitation of the above studies is that they have been conducted either in the lab or in field cages in one habitat. Few field studies have compared the developmental rates of grasshopper species occupying adjacent habitats. For example, Waloff and Richards (1954) studying *Chorthippus brunneus* and *C. parallelus* found that there were more first instar nymphs in an area of sparse vegetation, referred to as an oviposition site, than in an adjacent habitat. The second habitat, composed of taller denser vegetation, had a larger number of second and third instars than expected by chance. They concluded that this difference in apparent developmental rates was due to dispersal by the older instars into the denser vegetation to feed.

The location of winter wheat adjacent to rangeland offers an opportunity to conduct a field study comparing the developmental stages of selected grasshopper species in proximate habitats. It is unlikely that, at any point in time, the aggregate of conditions such as ambient temperatures and relative humidities or resources such as solar radiation, space or nutrient quantity and quality would ever be the same in different habitats (Gieger 1965, Rosenberg 1974). Such variation in environmental factors between habitats could have significant effects on the developmental rates of grasshopper species occupying both habitats.

For pest managers, it is important to know if grasshopper age structure differences occur between habitats and what factors might be correlated to these

differences. If differences occur, pest managers might recommend that producers manipulate the plant community at the interface between rangeland and crops to keep pest species in these areas longer, thus reducing the time grasshoppers feed on a crop.

The objectives of this study included the following: First, I wanted to determine if a sampling scheme could be developed to compare the age structure of grasshoppers in adjacent habitats. Secondly, determine if the age structure of grasshopper species occupying winter wheat and the adjacent rangeland varies between the two habitats.

Methods and Materials

Study Site

Ten sites located near the communities of Three Forks and Willow Creek (longitude 111° 30' latitude 45° 45') Gallatin County, Montana USA. were sampled for grasshopper populations during 1988, through 1990. A study site was composed of a field planted to winter wheat and an adjacent field border characterized as a *Stipa comata-Bouteloua gracilis* (STCO/BOGR) rangeland habitat (Mueggler and Stewart 1980, Kemp et. al. 1990 a,b) which was reseeded to crested wheatgrass, *Agropyron cristatum* (L.) Gaertn. and alfalfa, *Medicago sativa* L. The study sites were at different locations in different years because winter wheat fields were fallowed every other year. Fallowing and crop rotation have been used to conserve soil moisture and enhance weed and disease control in small grains in Montana.

Sampling Design

The sample design, equipment, and regime for this study was similar to that used for the study in Chapter 2. In 1988, at three study sites, three transects were laid out so

they bisected the rangeland/crop border. Twelve subsample sites, 10m apart, were located along each transect. Six transects were in rangeland and 6 were in the crop. There were a total of 36 subsample sites at each study site. In 1989, and 1990, 4 transects were laid out so they bisected the rangeland/crop border. Subsample site 7, on each transect was located at the crop rangeland border. Two were in the crop and 2 were in the rangeland. There were a total of 48 subsample sites at a study site, 26 in rangeland and 22 in the crop. In 1989 there were 4 study sites and 3 in 1990.

Sampling began between 0615h and 0630h and consisted of slamming a 0.05m² drop cage over the surface of the vegetation and soil at each subsample site. Arthropods were collected from the plants and soil surface using a cart-mounted modified vacuuming device. Specimens were captured in a muslin sock before they were damaged by the vacuum fan. The rangeland subsample sites were sampled first followed by subsample sites in the crop.

In 1989 and 1990, 10 sweep samples were taken at each subsample site following drop cage sampling. Arthropod specimens and plant debris from each subsample site were placed in a paper sampling bag and then placed in a cooler at the end of each sample period. At the end of each sample day sampling bags were placed in a lab freezer to await sorting of insects from plant debris. In the laboratory, grasshoppers were removed from the plant debris and other arthropods, and sorted by species, stage of development and sex. For more details of the sample design, equipment, and regime consult the methods and materials section in Chapter 2.

Data Analysis

In order to obtain sufficient specimens to compare stages of development of grasshoppers collected in rangeland to those in winter wheat at each sample period,

specimens from drop cage and sweep net samples were pooled. Before pooling samples, a comparison of developmental stages of *M. sanguinipes*, collected by each sampling device within a habitat, was made to determine if different stages of development were captured by the two sampling devices at any given sampling period. Comparisons were made using *M. sanguinipes* from the 1990 samples. Only in this year and with this species were enough grasshoppers captured by both methods in both habitats to allow such a comparison.

A 2xc contingency table was used to analyze the data within both habitats. The rows of the table consisted of the two sample methods in a habitat and the columns were composed of the stages of development collected using a sweep net, and developmental stages collected using the drop cage at a sample period.

A Fisher's Exact Test was used to determine if significant differences in the collection of developmental stages, between sampling devices, occurred more often in one habitat than the other. In this test the 2 rows were the habitats and the 2 columns were total number of sample periods and the sample periods with significant differences in age structure (MSUSTAT-Lund 1991).

A 2xc contingency table was also used to compare the stage of development of *M. sanguinipes*, *M. packardii* and *M. bivittatus* between the two habitats. Three comparisons were made, one using all three species combined, a second using *M. sanguinipes* alone, and a third, combining *M. bivittatus* and *M. packardii*. All comparisons were made using a program called Loglinear (MSUSTAT-Lund 1991). This program estimates the expected cell counts in a rxc contingency table and compares them to observed cell counts. Rows of the contingency table were the two habitats and the columns were the individual grasshoppers collected in each developmental stage at a particular sample period.

A 2x3 contingency table was used to determine if the proportion of the population of *M. sanguinipes* and *M. packardii* + *M. bivittatus* in both habitats varied between the three sample periods. The rows for this table were the two habitats and columns were the three sample periods. If there was a significant variation in the proportion of the population in the two habitats for one or more sample periods a second contingency table was constructed. This 2x2 contingency table was used to determine if there was a significant difference in the proportions of the population collected in both habitats for the most similar sample periods. If there was no significant difference, the cells for both sample periods were collapsed to form one column of a 2x2 contingency to determine if there was a significant variation between the two similar sample periods and the third dissimilar sample period. If there was a significant difference between the two most similar sample periods, a 2x2 contingency table was analyzed using the sample period with the population proportions most like the dissimilar sample period.

Results

Twenty three sample periods were compared to determine if there was a difference in the collection of developmental stages in winter wheat and rangeland using a sweep net and drop cage. Of the thirteen comparisons made in range, only one (8%) revealed a significant difference in stages of development collected by the two sampling methods (Table 20). Similarly, ten sample periods in the crop were compared to determine if there was a significant difference in developmental stages collected between sampling methods in this habitat. Only one of ten (10%) comparisons was significantly different, $P \leq 0.05$ (Table 20).

Only in two out of 23 samples (9%) was there a significant difference in stages of development collected using a sweep net versus a drop cage (range, 1 in 13 and crop, 1

in 10). Using the results of a Fisher Exact Probability Test, I concluded that there was no significant difference ($P \leq 0.61$) in stages of development collected by the two methods across the twenty three sample periods.

In 1988, there were significant differences in developmental stages collected between habitats at the early and late sample periods (Table 21). In the early sample period more fourth and fifth instars of *M. packardii* + *M. bivittatus* were collected in the crop than rangeland (Table 21, Figure 11). In the early and mid sample periods 56% of the sample population of *M. packardii* + *M. bivittatus* was collected in the crop, while at the late sample periods only 12% of these two species was collected in this habitat. There was a significantly smaller proportion of the population occupying the crop in the late sample period when compared to the two earlier sample period ($\chi^2=80.88$, $P \leq 0.0001$, $df=1$). The results suggest that, later developmental stages were collected in the crop versus the rangeland when a greater proportion of the sample population was collected in the crop.

There was no difference in the developmental stages of *M. sanguinipes* collected between habitats at the early and mid sample periods (Table 20, Figure 11). In the late sample period significantly more *M. sanguinipes* adults were captured in the rangeland than in the crop (Table 20). A significantly greater proportion of the sample population was collected in the rangeland (80%) during the late sample period than was collected in the two previous sample periods (54%) ($\chi^2=41.85$, $P < 0.0001$, $df=1$).

STUDY LOCATION: SITE 3

Date: 1990	6/26	7/5	7/17	7/17	7/24	7/24	7/31
Habitat:	Range Border	Range Border	Range Border	Crop	Range Border	Crop	Range Border
Dev. Stage:	1-4	1-5	2-A	3-A	3-A	5-A	5-A
χ^2 :	1.234	4.563	2.164	5.506	4.818	5.775	0.1048
df:	3	4	4	3	3	1	1
P value:	0.7488	0.3348	0.7088	0.1367	0.1841	0.0163*	0.7462

STUDY LOCATION: SITE 2

Date: 1990	7/11	7/11	7/22	7/22	7/28	7/28	8/2-3	8/2-3	8/9	8/9
Habitat:	Range Border	Crop	Range Border	Crop	Range Border	Crop	Range Border	Crop	Range Border	Crop
Dev. Stage:	1-A	1-A	3-A	2-A	2-A	2-A	3-A	4-A	4-A	4-A
χ^2 :	8.272	3.452	4.52	4.475	12.72	6.859	7.161	13.52	2.273	3.223
df:	5	5	3	4	4	4	2	2	2	2
P value:	0.1410	0.6332	0.2091	0.3454	0.0128*	0.1424	0.271	0.0016	0.3211	0.1976

96

STUDY LOCATION: SITE 1

Date: 1990	7/8	7/8	7/12	7/12	7/18	7/18
Habitat:	Range Border	Crop	Range Border	Crop	Range Border	Crop
Dev. Stage:	1-A	1-5	3-A	2-A	2-A	2-A
χ^2 :	7.600	3.313	5.209	4.990	2.849	5.268
df:	5	4	6	4	4	4
P value:	0.1787	0.5019	0.3913	0.2875	0.5862	0.2599

1-A stage of development (1, 2, 3, 4, 5, A)

Table 20. Comparison of capture efficiency of grasshopper developmental stages in *Melanoplus sanguinipes* using drop cage and sweepnet; 1990.

Table 21. Comparison of developmental stages of three *Melanoplus* species captured in winter wheat and adjacent range.

SAMPLE PERIODS 1988

Combined Species		Early	Mid	Late
<i>M. sanguinipes</i>	χ^2 :	16.33	6.38	12.40
<i>M. packardii</i>	P value:	0.006	0.170	0.025
<i>M. bivittatus</i>	df:	5	4	2
<i>M. sanguinipes</i>	χ^2 :	2.55	3.32	12.29
	P value:	0.77	0.51	0.015
	df:	5	4	4
<i>M. bivittatus</i>	χ^2 :	26.46	7.86	5.19
<i>M. packardii</i>	P value:	<0.0001	0.096	0.27
	df:	5	4	4

SAMPLE PERIODS 1989

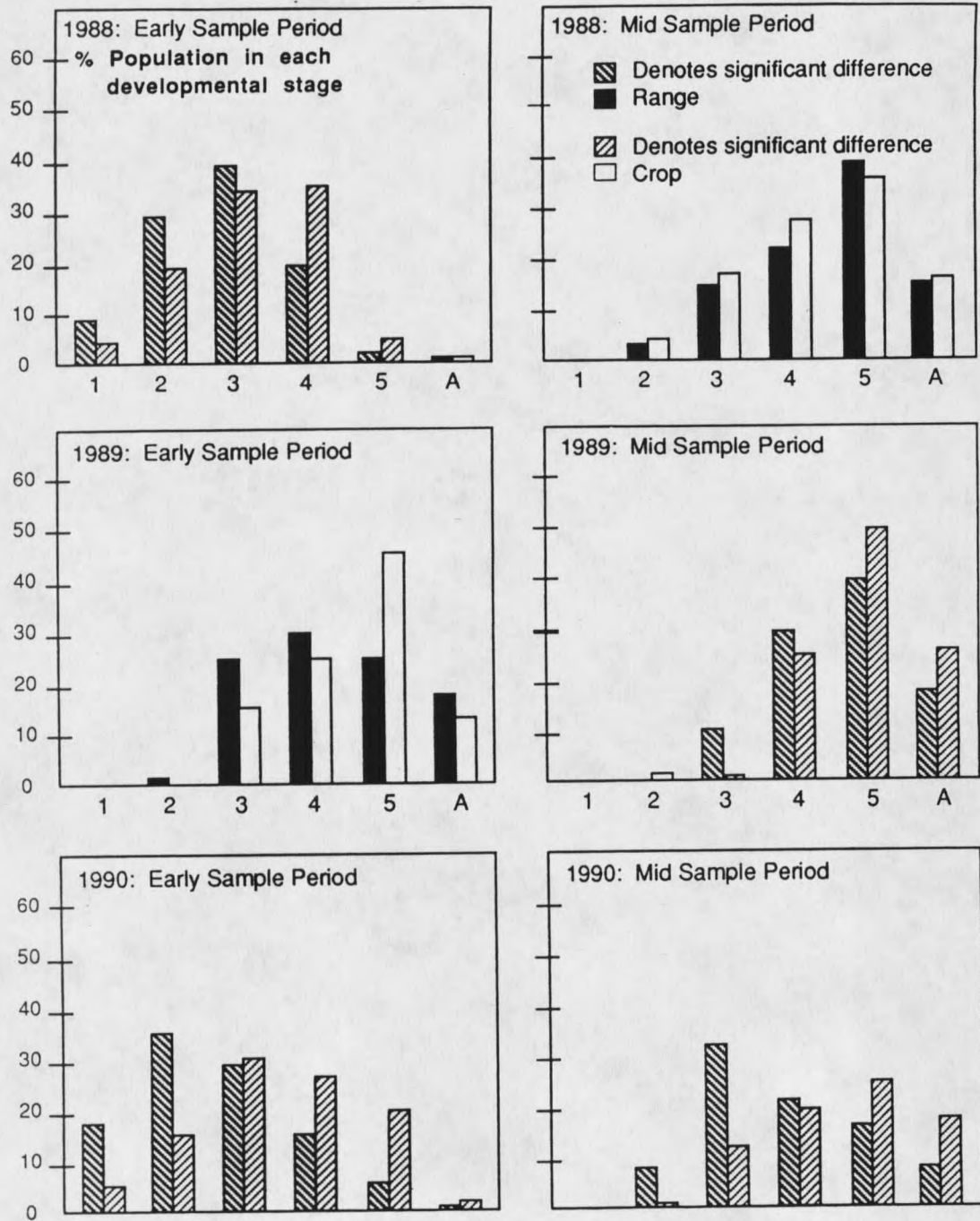
Combined Species		Early	Mid	Late
<i>M. sanguinipes</i>	χ^2 :	8.15	8.81	3.53
<i>M. packardii</i>	P value:	0.085	0.031	0.06
<i>M. bivittatus</i>	df:	4	3	1
<i>M. sanguinipes</i>	χ^2 :	1.18	10.47	*
	P value:	0.88	0.015	
	df:	4	3	
<i>M. bivittatus</i>	χ^2 :	6.93	2.55	*
<i>M. packardii</i>	P value:	0.073	0.47	
	df:	3	3	

SAMPLE PERIODS 1990

Combined Species		Early	Mid	Late
<i>M. sanguinipes</i>	χ^2 :	108.30	327.80	12.67
<i>M. packardii</i>	P value:	<0.0001	<0.0001	0.006
<i>M. bivittatus</i>	df:	5	4	3
<i>M. sanguinipes</i>	χ^2 :	63.95	215.3	4.22
	P value:	<0.0001	<0.0001	0.24
	df:	5	5	3
<i>M. bivittatus</i>	χ^2 :	43.81	56.77	14.49
<i>M. packardii</i>	P value:	<0.0001	<0.0001	0.003
	df:	5	4	3

* Sample too small.

Figure 11. Comparison of the developmental rates of three *Melanopus* species ** in crop vs. adjacent range.

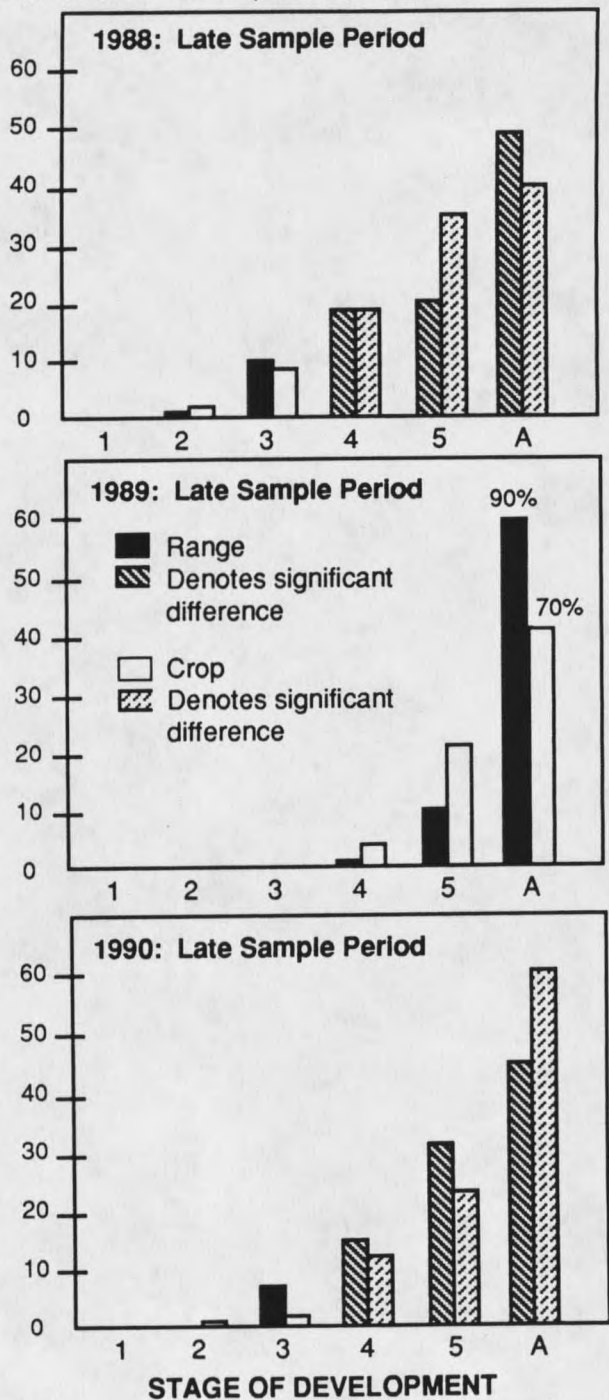


* Sample period when there was a significant difference in stage of development collected in range vs. winter wheat.

** *Melanopus sanquinipes*, *Melanopus bivittatus*, *Melanopus packardii*.

Figure 11. Continued.

% Population in each developmental stage



In 1989, only at the mid-sample period were significantly greater number of older developmental stages collected in the crop when compared to the rangeland (Table 20, Figure 11). At this sample period 48% of the sample population of *M. sanguinipes* was collected in the crop versus 17% and 35% at the early and late sample periods. There was a significantly greater proportion of the sample population collected in crop at the mid-sample period when compared to the early and late sample period ($\chi^2=76.98$, $P < 0.0001$, $df=2$). I think that this decline in the proportion of the population occupying rangeland during the mid-sample period can be attributed to dispersal of the older developmental stages of *M. sanguinipes* into the crop. At all sample periods in 1990, later developmental stages were captured in the crop when compared to rangeland (Table 20, Figure 11). These significant differences occurred for all three species combined, for *M. sanguinipes* alone, and *M. packardii* + *M. bivittatus* combined, even though the bulk of the grasshopper population remained in the rangeland at all sample periods (Table 20, Figure 11). Across the three sample periods approximately 72% of the specimens of *M. sanguinipes* collected, were collected in the rangeland (early 72%, mid 70%, and late 72%) ($\chi^2=3.77$, $P = 0.15$, $df=2$). During the early sample period 49% of the specimens of *M. packardii* + *M. bivittatus* were collected in range, while 58% were collected in the mid-sample period and 54% in the late period. There was no difference in the proportion of the sample population collected across sample periods in the rangeland ($\chi^2=5.58$, $P = 0.06$, $df=2$). I think it is interesting to note that *M. sanguinipes*, *M. bivittatus* and *M. packardii* displayed the same trend in 1990.

Discussion

In this study, the developmental stages of *M. sanguinipes* collected, at any given sample period, using a sweep net were not significantly different than those collected

