



The ecology of selected grasshopper species along an elevational gradient
by David Harrison Wachter

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in
Entomology

Montana State University

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Abstract:

The extent to which grasshopper communities along an elevational gradient change in southwest Montana was studied. In addition to this, four species were chosen to examine changes in phenology along the gradient. This thesis examines the hypothesis that species assemblages change with elevation and that intraspecific variation in phenology occurs with changes in elevation.

I used detrended correspondence analysis to evaluate changes in grasshopper and plant species across eleven sampling sites of varying elevation and aspect. Weekly sampling of each site allowed for the plotting of phenologies for *Melanoplus sanguinipes*, *Melanoplus bivittatus*, *Chorthippus curtipennis*, and *Melanoplus oregonensis*.

The results showed non-random distribution of grasshopper species along the gradient. Grasshopper species distribution was significantly correlated to elevation, precipitation, proportion of grasses and forbs, and the total number of plant species. Phenological studies showed that nymphal emergence was later at sites greater in elevation. Adults from higher elevation sites appeared at collection dates nearly equal to those from lower elevation sites.

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APPROVAL

of a thesis submitted by

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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.

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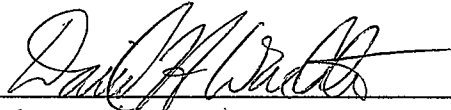
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ABSTRACT

The extent to which grasshopper communities along an elevational gradient change in southwest Montana was studied. In addition to this, four species were chosen to examine changes in phenology along the gradient. This thesis examines the hypothesis that species assemblages change with elevation and that intraspecific variation in phenology occurs with changes in elevation.

I used detrended correspondence analysis to evaluate changes in grasshopper and plant species across eleven sampling sites of varying elevation and aspect. Weekly sampling of each site allowed for the plotting of phenologies for Melanoplus sanguinipes, Melanoplus bivittatus, Chorthippus curtipennis, and Melanoplus oregonensis.

The results showed non-random distribution of grasshopper species along the gradient. Grasshopper species distribution was significantly correlated to elevation, precipitation, proportion of grasses and forbs, and the total number of plant species. Phenological studies showed that nymphal emergence was later at sites greater in elevation. Adults from higher elevation sites appeared at collection dates nearly equal to those from lower elevation sites.

INTRODUCTION

Importance of Grasshopper Studies

Southwest Montana is composed of regions of steppe and mountain ranges (Price, 1981). Grasslands within these regions are distributed within a complex topography. This regional variation creates environmental gradients that affect plant and animal assemblages at the landscape and community scale (Senft et al. 1987). These gradients also provide ecologists with opportunities to study the spatial and temporal aspects of insect diversity and abundance.

In the temperate grasslands of North America, grasshoppers (Orthoptera: Acrididae) are among the most abundant and economically important grazing herbivores (Otte 1981). Their abundance and food preferences occasionally make them strong competitors with humans because they consume food crops and livestock forage. For this reason, they are a relatively well-studied group (Alexander and Hilliard 1969, Evans 1988, Joern 1979, 1982, Kemp et al. 1989,1990, Uvarov, 1931). However, researchers have only recently addressed the factors that influence grasshopper distribution (Evans 1987, Kemp et al, 1990a,b). In this thesis, I present the results from studies of grasshopper distribution along an environmental gradient from the steppe regions in the Gallatin Valley of southwest Montana to alpine regions of surrounding mountain ranges.

Climate of Southwestern Montana

The climate of southwestern Montana is influenced by latitude, continentality, and altitudinal variation. The climate is characterized by low annual precipitation, large quantities of solar radiation, and wide daily and annual temperature fluctuations. The steppe habitat of this region (1400-1600 m altitude) is characterized by hot dry summers and cold winters with precipitation amounts increasing with higher elevations. Precipitation in the region typically ranges from 20 to 35 cm annually depending on the local elevation.

The mountain ranges surrounding the Gallatin Valley of southwest Montana begin at elevations around 1800 m and rise to heights from 2800 to 3500 m. Mean annual precipitation in the mountains varies from 25 cm at lower elevations to 50 cm at higher elevations. Most of the precipitation comes in the form of snow. Tree line in the mountains begins around 2700 to 2800 m depending on the local conditions. Conditions, which create such variable climates, include elevation, slope angle, and aspect. For example, mountainsides facing southwest tend to be the warmest and driest slopes because earlier evaporation of dew allows the sun to more rapidly heat the soil surface; in contrast north-facing slopes tend to be wetter and cooler (Shreve 1924, Greg 1963). At any time, there can be great variation in weather conditions over short distances.

Vegetation of Southwest Montana

Grasslands composed mainly of native vegetation were chosen for this study. Sampling sites were chosen from four regional or landscape vegetation categories: steppe, piedmont, montane, and alpine (Price, 1981). The piedmont or foothill zone generally represents an integration of steppe and montane vegetation, and is an area where precipitation tends to increase most abruptly.

The steppe zone is found in the central portion of the Gallatin Valley, a sinking block between faults from which rise the Bridger and the Gallatin mountain ranges to the east and south, respectively. The elevation of the valley varies from 1200 m to 1600 m. In the western portion of the valley, grassland sites are relatively hot and dry with some vegetation characteristics similar to those found in the Great Basin desert (Mueggler and Stewart 1983).

As the valley floor rises to the east into the foothills of the Bridger Mountains and Gallatin Range (1400 m to 1800 m), there is a corresponding increase in mean annual precipitation from 35 to 50 cm. The steppe/montane interface or foothill zone occurs at an elevation between 1500 m and 1700 m.

The montane region is characterized by cool, moist coniferous forest. Montane grasslands occur at elevations between 1800 m to 2700 m with vegetation varying dramatically within this area due to local differences in conditions governed by slope angle, aspect, soil type, and elevation.

The alpine regions in the Bridger and Gallatin ranges are found at elevations

between 2700m and 3100m. In this region, we see a shift from the coniferous forest to alpine tundra. The growing season is extremely short and plants possess adaptations to survive the harsh climate. These adaptations include a bunched and shortened morphology and increased plant hair to increase insulation.

Many of these sites, including the montane and alpine sites, have been grazed by both domestic and wild animals, but their precise grazing history is unknown. During the course of the study, grazing was observed on the steppe sites, one foothills site, and one montane site.

Grasshoppers in Steppe and Mountain Environments

In mountainous regions, the effect of altitude on the evolution of insect morphology is similar to that of latitude. A number of insect traits vary with increasing altitude (Mani 1968, Alexander and Hilliard 1968, Somme 1982). First, the reduction in body size with increasing altitude is one of the most striking forms of variation within and between species (Mani 1968). Second, insects tend to exhibit increased aptery with increasing altitude. Uvarov (1977) suggested that wing reduction in alpine grasshoppers was an important adaptation to the alpine environment arising from the selection pressure of the climate. Uvarov felt that given the short growing season, it is more important to put more of the energy stores toward reproductive structures rather than wings.

Third, some insect species exhibit increased melanism with increased altitude. Kingsolver (1983, 1985b) documented the importance of melanism in pierine butterflies at high elevations and its relation to thermoregulation.

Fourth, insects exhibit increased cold-hardiness with increasing elevation (e.g. Salt 1961, Duman et al. 1982, Somme 1982). Physiological cold-hardiness seems to come from one of two methods (e.g. Salt 1961, Duman et al. 1982, Somme 1982). Freezing-tolerant species are able to survive the formation of ice crystals in their tissue. In contrast, freezing-susceptible insects rely on supercooling to survive. In addition to these processes, insects inhabiting higher elevations can perform their daily activities at temperatures lower than those of their lowland counterparts (Gillis and Smeigh 1985).

Lastly, due to cooler temperatures, the rate of development may be retarded at higher altitudes. This may result in a need for two or more years to complete the life cycle. It may also result in the compression of the length of each instar or a reduced number of instars. For example, White (1978) found that three species of grasshoppers in the Craigieburn Range of New Zealand had two-year life cycles.

Distribution of Acrididae

Approximately 200 species of Acrididae have been identified in the grasslands of the western United States, (Pfadt, 1968). Kemp et al. (1990a)

identified more than forty species inhabiting steppe and foothill regions in the Gallatin Valley of Montana. Unfortunately, the economic impact of most of these species is unknown, because they have not been studied in enough detail to understand their true status as pests. However, two grasshopper species frequently considered as pests of Montana agriculture include Melanoplus sanguinipes (Fabricius) and Aulocara ellioti Thomas.

Alexander and Hilliard (1969), working in the Colorado Rocky Mountains, cataloged 94 species of Orthoptera, including 73 species of Acrididae along an altitudinal gradient from 1530 m to 4265 m. The gradient was divided into 1000 ft bands. Each band was placed in one of nine vegetation zones, based on vegetation patterns and dominant plant species. (The results showed a clear segregation of particular grasshopper species into distinct zones along the gradient and a reduction in species numbers with increasing elevation. There was also evidence that some species showed compressed life cycles during development from nymph to adult and an expanded duration of the egg phase. This study was descriptive in nature and did not quantitatively examine how factors other than vegetative zones influenced distribution or phenology.

Scoggen and Brusven (1973), in a study to detect grasshopper species association with plant communities, used several biotic and abiotic factors in a cluster analysis. Their study included an altitudinal gradient of 2000 m. Their findings showed that, out of 10 plant communities, five vegetation communities

were significant indicators of certain assemblages of grasshopper species.

However, their analysis was not based on quantitative data using grasshopper abundance. Rather, they used the arbitrary terms "accidental", "occasional", or "common".

Evans (1987) examined how fire, topography, and vegetation influenced grasshopper communities on tall grass prairie. The scale of study was defined and smaller than most previous work (Alexander and Hilliard 1968; Scoggen and Brusven 1973). Using detrended correspondence analysis (DCA), Evans showed that grasshopper distribution was most strongly related to the frequency of burn and the soil type. He suggested that this was probably due to the effect of these factors on the local plant communities. However, Evans noted that his study could not differentiate whether grasshopper assemblages were being influenced by plant species or by the physical structure of the environment.

Work by Kemp et al. (1990a) revealed non-random distributions of grasshopper species existed along a rangeland environmental gradient. This gradient consisted of changes in elevation, moisture, and plant communities. The vegetation communities analyzed were chosen based on the concept of habitat type (Mueggler and Stewart 1980). These gradients appeared to play a role in structuring grasshopper community composition. Grasshopper community composition was found to vary both between habitat type patches and within habitat type patches. Significant associations were found between the

number of species as represented by subfamily within a given habitat type, suggesting that, given information on patch resources, one could generally predict species distribution. Yet it remains unknown how dynamic these associations are in space and time.

Phenology of Acrididae

Knowledge of life cycle variation has both applied and theoretical ramifications for ecologists and pest managers. Kemp (1991) discussed the value of understanding phenological patterns for pest control purposes. First, understanding how environmental gradients affect life history patterns can lead to more cost efficient and timely pest control. Second, studying life history variation, particularly within species, may illuminate factors that influence adaptation and speciation.

Early studies of grasshopper development noted that low temperatures accelerated the development of eggs (e.g. Uvarov 1931, Moore 1945, Parker 1930, Bodine 1928). These low temperatures were below what was considered the lower threshold of development (sometimes below 0° c), but above a level that was injurious. Researchers from this period also noted that these thresholds seemed to vary with each life stage (Uvarov 1931). This phenomena suggested to Uvarov that the use of a mean daily temperature was inappropriate for analyzing questions regarding development.

Few studies have examined intraspecific variation in development at different altitudes. Handford (1961), found that mean instars of Camnula pellucida (Scudder) for a given date were lower at higher elevation sites in the 900 foot elevation gradient study. Handford also calculated degree-days above 60° F from air temperatures recorded from a nearby airport. He chose 60° F because the lower threshold for Camnula pellucida (Scudder) was unknown at the time.

Dingle et al. (1990) studied how the life cycle of M. sanguinipes varied with altitude in the Sierra Mountains of California. They sampled six populations from sites at coastal elevations of 90 m to mountain elevations of 2700 m. They computed degree-days from air and soil temperatures using weather stations on each site, with 15° C the lower developmental threshold temperature. Phenologies were calculated as percent instar composition by date. At higher altitudes, they found later spring emergence and a more rapid passage through the instars to maturity. They attributed these differences to the length of the growing seasons based on soil temperatures. They believe that air temperatures do not produce enough degree-days to complete nymphal development. If, however, soil temperatures are used there is adequate heat available for full grasshopper development to occur.

Using laboratory experiments, Dingle's study also showed all populations of M. sanguinipes to be univoltine, but populations varied in their intensity of

egg diapause and rates of growth. At high altitudes females laid diapausing eggs. At mid-altitude females laid a mixture diapausing and nondiapausing eggs. They believed these differences reflected genetic variation among populations.

Objectives of distribution and phenology studies

First, using the methods of Kemp et al. (1990a) as a model, I examined local variation within mountain ranges by sampling mountain slopes of different elevation and aspect to determine local grasshopper species variation. My null hypothesis was that there was no variation in species assemblages between sites of different elevation and vegetation. Second, I examined how grasshopper species varied from steppe elevations to the highest elevations of the surrounding mountain ranges. Third, I examined variation between the Bridger and Gallatin mountain ranges to see how species varied between mountains.

The objectives of the development study were, first, to examine intraspecific variation in phenology of grasshopper species from sites of varying altitude and aspect. My null hypothesis was that there was no intraspecific variation in grasshopper phenology between patches. Second, I wanted to use the concept of degree-days to measure intraspecific and interspecific variation in phenology. Third, I wanted to examine interspecific variation in grasshopper phenology between species inhabiting local patches or having divergent ranges.

MATERIALS AND METHODS

Study Sites

The study area was located in the northern part of Gallatin County, Montana (longitudes $111^{\circ}40'$ - $111^{\circ}41'$ east-west, latitudes $46^{\circ}00'$ - $45^{\circ}30'$ north-south). Sites were chosen from four regional vegetation zones (Price, 1981): steppe, montane, alpine, and the transition between steppe and montane often known as the foothill zone. At each site an area of 50 m x 80 m was laid out. Within this area, 9 linear transects were constructed using flags as markers. I chose two steppe sites from those sampled by Kemp et al. 1990a near Three Forks, Gallatin County, MT. Steppe sites were between 1400 m and 1500 m in elevation and were flat in their aspect. Two foothill sites located on the western front of the Bridger and Gallatin ranges were sampled. The first, located at the entrance of North Cottonwood Creek in the Bridger range at an elevation of ¹⁸⁰⁰~~1650~~ m (longitude 111° - east-west, latitude $45^{\circ}07'$ north-south). The second western foothill site was located at the entrance of Hyalite Canyon near the Gallatin range at an elevation of approximately 1850m (longitude $111^{\circ}01'$ east-west, latitude $45^{\circ}33'$ north-south). A third site, located on the eastern slopes of the Bridgers, at approximately 1950 m in the Brackett Creek drainage was sampled (longitude $110^{\circ}52'$ east-west, latitude $45^{\circ}50'$ north-south). The montane and alpine sites were selected from the

Bridger Mountain Range and the Gallatin Mountain Range. In the Bridger range two sites were selected for weekly sampling. On the west side of the range at an elevation of 2270 m a west-facing meadow was chosen located between Corbly Gulch and Limestone Canyon (Longitude 111°00' east-west, latitude 45°52' north-south. On the east side of the range, located near Fairy Lake a mountain meadow that was relatively flat in aspect and approximately 2350 m in elevation was selected (Longitude 111°02' east-west, latitude 45°55' east-west). An east-facing montane site located in the Gallatin range was sampled. It is located in the Lick Creek drainage at an elevation of 2275 m (longitude 111°01' east-west, latitude 45°33' north-south). Two Bridger alpine sites were selected. The west-facing site is located on a western slope directly below Sacagawea Peak at an elevation of 2950 m (longitude 111°02' east-west, latitude 45°53' north-south). The east-facing Bridger alpine site is located on the north-east side of Hardscrabble Peak at approximately 2850 m (longitude 111°01' east-west, latitude 45°55' north-south). In the Gallatin range, an east-facing alpine site was chosen on the slopes of Mt. Blackmore, at an elevation of 3050 m (longitude 111°00', latitude 45°32').

Sampling Techniques

Grasshoppers

Sampling methodology consisted of two hundred sweeps each traversing

an arc of 180° with a 40 cm diameter sweep net, along permanent linear transects. These 200 sweeps were divided into 50 sweeps along four transects randomly chosen each sampling period. In 1991, the sampling period was between 0900 h and 1600 h. In 1992, the sampling period was shortened compressed to three hours from 1200 h to 1500 h. The period was shortened in an attempt to increase relative abundance, particularly in the mountains. Samples were collected from each site every 7-10 days. In 1991, the seasonal sampling period ran from 15 June to 25 August. In 1992, the sampling period ran from 5 May to 25 August. Samples were placed on ice until they could be delivered to a laboratory freezer.

Plants

Vegetation was sampled from mid-June through August of 1992. Twenty to thirty quadrants (20 cm x 50 cm) were sampled for cover (Daubenmire 1959) and species type along a transect within the area of the grasshopper sampling site. In addition to percent canopy coverage for each plant species, litter, and bare ground coverage were estimated. The variation in the number of quadrants sampled was due to traveling and weather constraints.

Temperature Data and Phenology

Temperature data was collected from stations located at six of the eleven sites (see Table 1 for specific sites). The foothill station was located on the

western front of the Bridger range. The other stations that I installed consisted of two on the west side of the Bridgers and the two on the east side of the Gallatins located in the Hyalite region. Stations were erected in the central portion of each site. A Omnidata two channel Li-cor device was used to take hourly air (5cm) and subsurface (-5mm) temperatures.

Temperature data was reduced to daily maximums and minimums. From this data, degree days were calculated from 5 May to dates on which only adults were collected in samples. Degree days were calculated only for M. sanguinipes and M. oregonensis. This choice was due to their abundance across sites and thermoregulatory studies, that I carried out. The base temperature chosen for calculating degree days for M. sanguinipes was 17°C (Kemp and Dennis 1991). The base temperature chosen for Melanoplus oregonensis Thomas was 5°C. There is no available research data on M. oregonensis developmental thresholds. I chose 5°C for two reasons, first, from thermoregulatory studies of M. oregonensis, I found that alpine populations were able to walk and jump at temperatures in this range. Second, I found nymphs in the alpine regions at temperatures below 10°C.

Degree days were calculated beginning with the installation date of the temperature recording devices. For the 1991 field season, installation occurred after hatch particularly at the lower elevation sites. In 1992, all stations were installed prior to hatch (i.e. approximately julian date 125) (Kemp and Dennis

1991).

Four species were chosen for phenological analysis. These choices reflected three factors: 1) their collection from early nymph stages through adulthood across two or more vegetation zones or at sites of different aspect, 2) their occurrence in numbers high enough to analyze, and 3) my ability to make accurate identifications of nymphs.

Identification of Acrididae

Most of the Acrididae found from these sites are well-documented species, particularly those in the subfamilies Gomphocerinae, Acridinae, and Oedipodinae (Otte 1981). Adults from the steppe and foothill regions were identified using keys from Pfadt (1989), Capinera and Sechrist (1982), Hebard (1928), and Brooks (1958). Nymphs from these regions were identified using Brusven (1972), Scoggan and Brusven (1972), and Hebard (1928). Mountain species, except for certain species of Melanoplus adults and nymphs, could often be identified using the above keys. The subfamily Melanoplinae is a poorly understood group taxonomically (Otte 1993). Few taxonomic keys even refer to certain alpine Melanoplus, in particular M. oregonensis and Melanoplus montanus (Thomas). To aid in the identification of these, Brooks(1913) and Alexander (1948) were used extensively. Information on the nymphs of these problematic species is even more difficult to find. Typically, adult male

characteristics are well enough developed by the fourth instar to allow identification. Identification of the early instars was possible by comparing them with later instars and adults and male morphology was distinguishable often by the fourth instar.

Data Analysis

Given that species along the gradient dropped out of samples with changes in elevation and aspect, I used detrended correspondence analysis (DCA) (ter Braak 1988). DCA is an ordination technique that can summarize count data and arrange it into two-dimensional space. Within these dimensions most of the variation among sites will be accounted for. Increasing distance between samples along the axis shows a decrease in similarity. The axis scores were correlated to site variables using Spearman rank correlation (r_s).

RESULTS

Species DistributionGrasshoppers

I collected twenty-five species of Acrididae from the eleven sites during two field seasons (Table 1). The number of species tended to decrease with increasing elevation ($r_s = -0.72$, $P = 0.012$) (Fig. 1). The total number of individuals collected also decreased with increasing altitude ($r^s = -0.68$, $P = 0.021$, Fig. 2). The montane elevation sites (2250 - 2350 m), showed a slight increase in species numbers and individuals, before decreasing again at the alpine elevation sites.

I found an uneven distribution of grasshopper subfamilies along the environmental gradient (Table 1). The most obvious trend was the increase in the percent of Melanoplineae (all Melanoplus spp.) with an increase in altitude: steppe 31%, foothills 56%, montane 64%, and alpine 88% (chi-square 2x4 contingency table analysis, $\chi^2 = 6.99$, $P = 0.07$). In fact, only 1 of 102 grasshoppers collected on the alpine sites was not a Melanoplus.

Melanoplus comprised a minority of species only on the steppe sites. However, even here they made up the majority of grasshoppers collected, because of the great abundance of Melanoplus infantilis Scudder and M. sanguinipes (74% at the 1400 m site and 69% at the 1500 m site). Other species

Table 1. Grasshopper (Orthoptera: Acrididae) Species Collected. Number of Individuals Collected by Elevation(meters) and Aspect. Superscript key: 1 - Only nymphs collected, 2 - Only adults collected, 3 - Both nymphs and adults collected. Asterisks(*) indicates sites with temperature recording stations.

	Steppe		Foothills			Montane			Alpine		
	1400* Flat	1500* Flat	1800* W	1850 SW	1950 E	2250* SW	2275* E	2350* SE	2850 NE	2950* W	3050* E
Oedipodinae											
<i>Arphia pseudoneatoma</i> ¹	-	-	2	-	-	-	-	-	-	-	-
<i>Arphia conspersa</i> ²	-	-	-	-	-	1	-	-	-	-	-
<i>Camnula pellucida</i> ²	-	-	1	2	2	4	-	5	1	5	- 7
<i>Spharagemon collare</i> ¹	2	30	-	-	-	-	-	-	-	-	-
<i>Trachyrhachys kiowa</i> ³	19	-	-	-	-	-	-	-	-	-	-
<i>Trimerotropis suffusa</i> ¹	-	-	-	-	-	7	4	4	-	-	-
<i>Xanthippus corallipes</i> ³	3	6	-	-	-	-	-	-	-	-	-
Subtotal	24	37 36	4 7	2	4 2	8 12	4	9	1	5	-
Gomphocerinae & Acridinae											
<i>Aeropedellus clavatus</i> ³	11	25	5	-	-	-	-	-	-	-	-
<i>Ageneotettix deorum</i> ³	98	54	-	-	-	-	-	-	-	-	-
<i>Amphitornus coloradus</i> ³	20	44	-	-	-	-	-	-	-	-	-
<i>Aulocara eliotti</i> ³	111	48	-	-	-	-	-	-	-	-	-
<i>Chorthippus curtippennis</i> ³	-	-	-	2	17	25	70	103	-	-	-
<i>Psoleossa delicatula</i> ²	2	14	-	-	-	-	-	-	-	-	-
Subtotal	240 242	185	5	2	17	25	70	103	-	-	-
Melanoplinae											
<i>Melanoplus alpinus</i> ²	-	-	-	-	-	3	-	3	-	-	-
<i>Melanoplus bruneri</i> ³	-	-	15	7	13	-	6	14	-	1	-
<i>Melanoplus bivittatus</i> ³	-	-	92	24	11	9	21	12	-	1	1 6 8
<i>Melanoplus confusus</i> ²	1	-	7	-	-	-	-	-	-	1	-
<i>Melanoplus dawsonii</i> ³	-	-	90	11	-	-	8	-	-	-	-
<i>Melanoplus fasciatus</i> ³	-	-	-	-	-	2	5	-	-	-	-
<i>Melanoplus huroni</i> ²	-	-	-	-	-	-	-	3	-	-	-
<i>Melanoplus infantalis</i> ³	38	260	-	-	-	-	-	-	-	1	-
<i>Melanoplus montanus</i> ²	-	-	-	-	-	-	1	-	-	-	2
<i>Melanoplus oregonensis</i> ³	-	-	12	-	2	75	44	188	20	87	22 8
<i>Melanoplus packardii</i> ³	82	46	-	-	-	-	-	-	-	-	-
<i>Melanoplus sanguinipes</i> ³	649	168	50	-	-	-	-	1	-	-	1 5
Subtotal	770	474	266	42	26	89	88	218	20	91	26

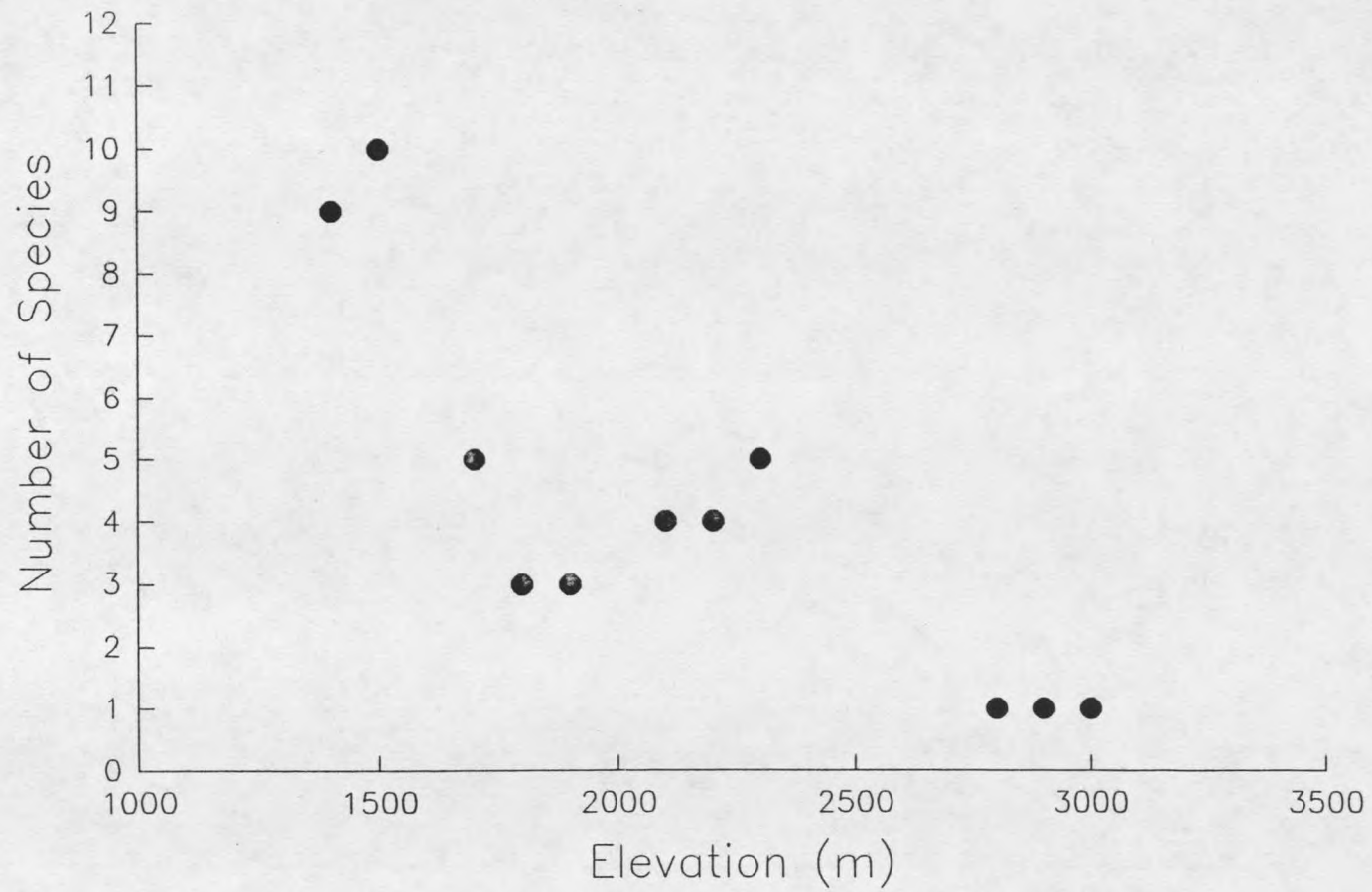


Figure 1. Number of Species as a function of elevation.

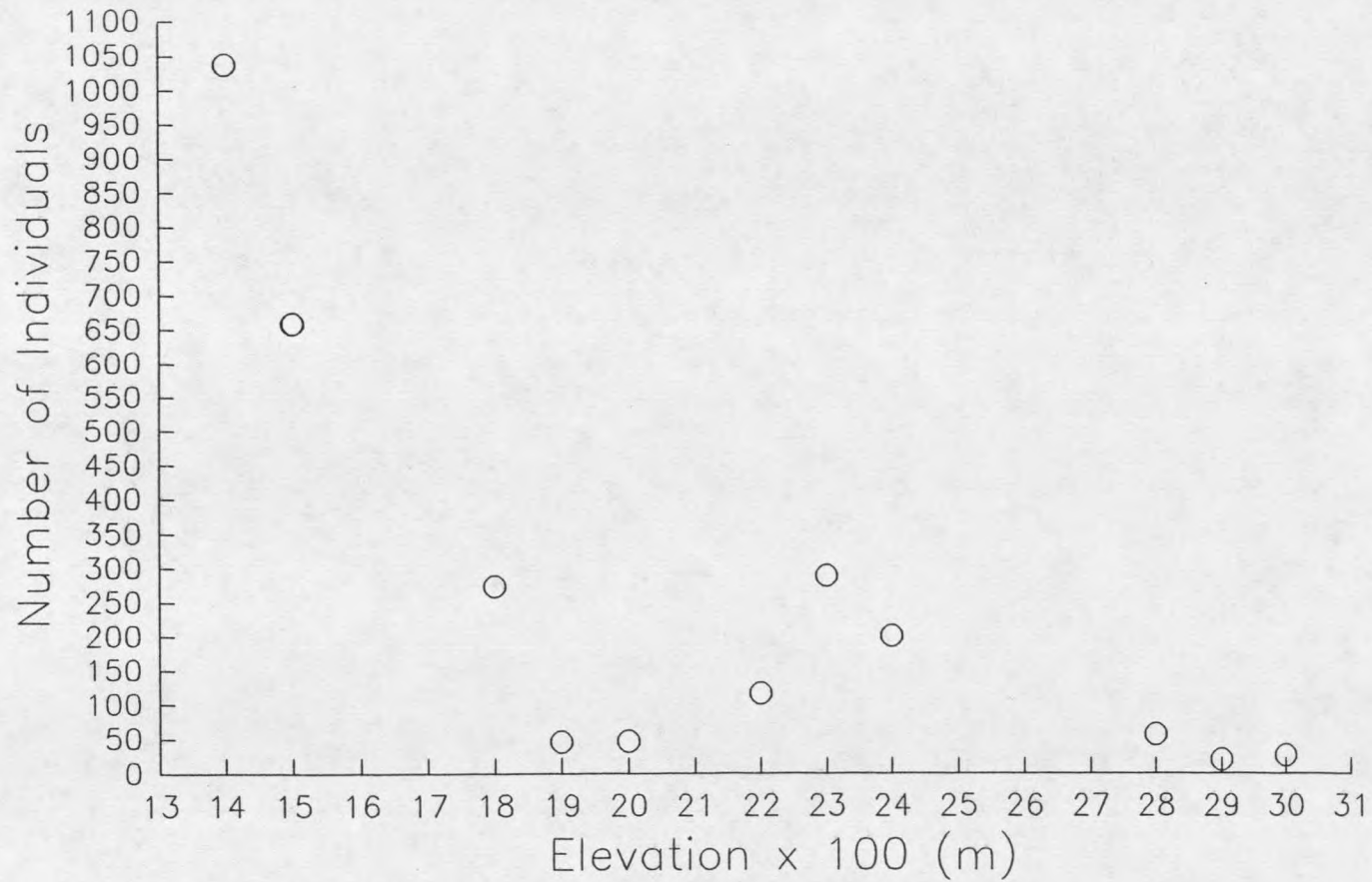


Figure 2. Number of Individuals collected from each sampling site as represented by elevation.

replaced these two as the most abundant Melanoplus in other zones. Melanoplus bivittatus (Say) (35%) and Melanoplus dawsonii (Scudder) (28%) were most abundant in the middle of the gradient (foothills and montane). Melanoplus oregonensis predominated at highest altitudes (montane and alpine), where it made up 91% of the grasshoppers collected.

The fact that nymphs of Melanoplus alpinus Scudder, Melanoplus bruneri Scudder, M. bivittatus, and M. oregonensis were collected on the montane sites suggests that adults of these species oviposit in this zone. Only M. oregonensis was collected throughout its life cycle in the alpine zone.

The greatest diversity of non-melanoplins also occurred on the steppe sites. I found adults of only one gomphocerine on the foothill and montane sites. Although low in abundance at all sites, Camnula pellucida was the only oedipodine collected in all four zones. In contrast, others occurred only on the steppe sites and Trimerotropis suffusa was collected only in the montane zone. No species of Gomphocerinae were widely distributed across the gradient. The most commonly collected species, Chorthippus curtipennis (Harris) was found at five sites in two zones.

Comparisons between the two mountain ranges showed montane species numbers ranging between 6 and 10. The west-facing montane site in the Bridgers (2250 m) contained seven species. The east-facing montane Bridger sites contained six species, while the east-facing montane Gallatin site produced

10 species. The Bridger alpine site (east-facing) contained only one species (M. oregonensis), while the east-facing Gallatin alpine site yielded four species. Melanoplus oregonensis also predominated at this site. Table 2 shows the first collection dates of second instars (1992 data only) from sites of different aspects. Chorthippus curtipennis, found predominantly in the montane zone, was collected 9 days earlier (JD181) at the east-facing Gallatin site and the west-facing Bridger site than the east-facing Bridger site (JD190). This Bridger site is approximately 100 meters higher than the other 2 sites. A similar situation is seen for M. bivittatus in the montane zone. All collection dates were within a four day range. M. oregonensis showed a greater range of variation within vegetation zones. At montane elevations, the Bridger west-facing site was the earliest (JD145) while the Gallatin east-facing site was the latest (JD158). In the alpine region, the Gallatin east-facing site was the earliest (JD180), while the Bridger east-facing site was much later (JD210). The Bridger east-facing site had large amounts of snow until early July.

Grasshopper DCA Results

The DCA on grasshopper study sites, showed that a high proportion of variation in the samples is accounted for by the first DCA axis (Fig. 3). Ninety-four percent of the variance in species data was accounted for in axis 1. Spearman rank correlations showed that axis 1 scores were significantly

