Rangeland Grasshoppers (Orthoptera: Acrididae) of Concern to Management of the Columbia River Basin

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Biogeography and habitat associations of grasshoppers as a functional group

RANGELAND GRASSHOPPERS (Orthoptera: Acrididae) represent a very complex collection of herbivores that interact in space and time. Of the hundreds of grasshopper species present in North America, roughly 200 inhabit grasslands. Further, at a given location, it is not uncommon to find as many as 15 or more grasshopper species over the course of the spring and summer months. Although some species are separated to an extent by differences in phenology, there is considerable overlap of species at a given site during the course of the summer. In spite of the volume of studies conducted on individual species of Acrididae (e.g., Uvarov 1966, 1977; Chapman & Joern 1990), little work has been done on macroscale grasshopper species associations (see Joern [1982] for microhabitat selection).

There has been much historical debate in ecology concerning the organization of communities, and arguments have focused on two divergent concepts. Following the work of Clements (1916), a number of studies have argued that communities are highly integrated and that species are interdependent (e.g., MacArthur 1972, Diamond 1986, Grant 1986). Alternatively, there are a number of studies that follow the general model developed by Gleason (1917, 1926), which suggest that communities are merely a facultative mix of unrelated, yet coexisting, species (e.g., Whittaker 1956, 1960). The arguments about nonrandom versus random species distributions (e.g., Strong et al. 1984, Diamond & Case 1986) can also be viewed within this context. Highly nonrandom patterns of coexistence, however, do not necessarily mean interdependence in species distributions. Studies conducted on desert rodent faunas (Brown & Kurzius 1987) suggest that, although rodent species exhibit highly nonrandom patterns, they are very individualistic in terms of resources used and thus appear to follow the Gleasonian concept of communities consisting of facultative species associations. To address the questions concerning rangeland grasshopper community organization, I conducted a three-year (1988–1990) study where grasshopper communities were monitored over a vegetation gradient in the Gallatin Valley of Montana (Kemp 1992a). Results from the first year of study suggested that vegetation type influenced not only species presence but also relative abundance (Kemp et al. 1990a; but see also Anderson 1964, 1973; Parmenter et al. 1991; Quinn et al. 1991). However, the study of species associations requires data from more than a single year (Wiens 1981). In a study convering the three year span, I examined whether grasshopper species are equally distributed across vegetation type over a 3-yr period (extending the results of Kemp et al. 1990a). Also, I evaluated whether patterns observed at the valley level were consistent across grasshopper communities inhabiting a gradient of vegetation types. Clearly, the grasshopper/vegetation type associations of the Columbia River Basin (CRB) deserve separate study in and of themselves, but a summary review of the Montana results to date can serve as a starting point for panel discussions.

Study Area and Collections. Specific details of sampling methods used to characterize grasshopper communities can be found elsewhere (Kemp et al. 1990a, Kemp 1992a), although selected aspects are repeated here. The study area was located in the northern part of the Gallatin Valley, Gallatin County, Mont. (111°00' - 111°40'N, 46°00' - 45°45'W) in the Agropyron spicatum (Pursh) Scribn. & Smith province of the steppe region (Daubenmire 1978) of the western United States.

Using terms defined by Kotliar & Wiens (1990), it is possible to view the entire landscape as a hierarchy of patch structure. Within this environmental hierarchy, the patch in my study ("a surface area different from its surroundings" [Kotliar & Wiens 1990]) is the basic level of perception of the observer. Patches can be grouped within habitat type, and habitat types can be grouped into a valley. Because habitat type reflects environmental variables such as soil characteristics, precipitation, and elevation, one could expect to observe a high degree of aggregation among patches within habitat type (see Daubenmire 1959, Mueggler & Stewart 1980, Kotliar & Wiens 1990).

Thirty-five patches were selected for study during 1988 and through 1990. Ten of these patches in two native habitat types that had been plowed and replanted were selected to contrast replanted and native patches within the same habitat type. Replanted patches were not recent disturbances and were treated as distinct habitat types. Vegetation transects were used to characterize each patch (Daubenmire 1959). The order of habitats studied represented a gradient of elevation and precipitation, with STCO-BOGR lower and drier and FEID-AGSP higher and more mesic (Mueggler & Stewart 1980; see Fig. 2 in Kemp et al. 1990a, and Kemp 1992a). This range in plant communities encompasses a large proportion of the available grassland habitat types in the Gallatin Valley.

Sweep net collections were made at each patch, in the same area as the vegetation transects, three times (late May-early June, late July, late August) during 1988 and four times (mid-June, early July, early August, mid-September) in 1989 and 1990. In a given year, insect sampling was initiated based on the estimated time of hatching and the presence of nymphs. Springtime hatching from year to year can vary by as much as 4 wk (Kemp & Dennis 1991). Two hundred sweeps per patch were made at each sampling period between 0930 and 1600 hours (MDST) under sunny skies (< 15% cloud cover), and light winds (< 25 km h^{-1}). Each sweep consisted of traversing an arc of 180° through the vegetation with a net as described by Evans (1984, 1988).

Grasshoppers were collected over the course of both spring and summer periods to insure detection of species with different phenological patterns; some species overwinter as eggs and emerge in the spring, whereas others spend the summer months as eggs and overwinter as nymphs. Previous studies of grasshoppers in tallgrass prairie found that in comparison with night trapping, sweep samples provided good estimates of relative abundance and species composition (Evans et al. 1983; Evans 1984, 1988). Therefore, sweep sampling was suitable for discriminating potential differences in grasshopper species composition and relative abundance (from pooled samples comprising 2,200 sweeps at each site over 3 yr) across the selected habitat types.

This study was conducted during years (1988–1990) when regional rangeland grasshopper densities were relatively low. Recent work (Kemp 1992b) showed that, during the period of this study, grasshopper densities throughout Montana declined from outbreak densities in 1986–1987 to nonoutbreak densities in 1989–1 990, with 1988 apparently a transition year (see section on factors influencing grasshopper abundance, below).

Species Associations. Although a total of 44 rangeland grasshopper species was collected throughout the valley during this study, average species richness at the habitat type level ranged from ≈ 10 to 17. For the three years of this study, drier habitat types had greatest species richness values. Replanted habitat types at both ends of the gradient had species richness values similar to their native habitat type associations. The total number of species was significantly different between habitat types, but not between years, nor for the interaction between habitat type and year.

There was incomplete overlap among grasshopper species with respect to habitat type use. For the 33 species considered in one test (those present at >2% of the site-years) the estimate of one eccoligical index led to the conclusion that the habitat type utilization curves for the individual species could not be drawn from some "common" utilization curve for all grasshoppers inhabiting Gallatin Valley and that grasshopper species were nonrandomly associated with habitat type. This suggests that, based on individual species frequencies, the habitat types monitored in this study differed in terms of which grasshopper species were likely to be encountered.

Comutation of other ecological association indicies on the presence–absence data for all 44 grasshopper species collected over the 3 yr for the six habitat typessuggested an overall "positive association" (Schluter 1984). This implied that at least some species among the 44 collected in this study were encountered together more often than would be expected by chance alone. However, examination of pairwise species contrasts revealed no significant associations. Ludwig & Reynolds (1988) point out that this occurrence is not uncommon. Thus, with additional study it may be possible to detect associations among species occurring in groups of greater than two. However, the lack of significance among pairwise species associations showed that the presence of any one grasshopper species was not highly dependent on the presence of other species.

The lack of significant pairwise species associations and the result that grasshopper species used the range of habitat types differently suggest that grasshopper species, in general, are independent resource trackers as follows from the habitat-based models (Hanski 1982, Brown 1984, Brown & Kurzius 1987, Kolasa & Strayer 1988, Kolasa 1989). Additionally, the apparent maintenance of habitat type level species richness (of grasshoppers) to 25–50% of that present at the valley level (above and the results of Kemp et al. [1990a]) indicates that species replacement occurs over the gradient of habitat types. Communities consisting of independent resource trackers and that exhibit species replacement over resource gradients are more likely to be facultative associations of species (Gleason 1917, 1926; Brown & Kurzius 1987) than highly interdependent species assemblages (Clements 1916, MacArthur 1972, Diamond 1986, Grant 1986).

Additional support for the hypothesis of facultative species associations in grasshopper communities comes from studies of host plant use patterns (e.g., Mulkern 1967, Mulkern et al. 1969, Joern 1979, Joern & Lawlor 1980, Otte & Joern 1977, and others) where patterns could be explained equally by factors other than direct competition for specific plant species. Further, detailed manipulation studies conducted by Evans (1989) failed to show exploitive or interference competition among cooccurring grasshopper species during years of moderate forage production. Therefore, although it is possible that rangeland grasshoppers, as resource trackers, interact interspecifically to varying degrees along resource dimensions such as microhabitat (Isely 1937, Joern 1982, Kemp et al. 1990a), preferred oviposition patches (Kemp & Sanchez 1987), and food types (Anderson & Wright 1952; Joern 1979, 1983, 1985; Mulkern 1967; Mulkern et al. 1969; Parmenter et al. 1991; Quinn et al. 1991), evidence thus far suggests that species assemblages at the habitat type level are not highly interdependent.

Species Distribution Hierarchy. With the arbitrary break points that were selected in the Kemp (1992a) study for the rangeland grasshopper species distribution hierarchy for Gallatin Valley (similar to discrete groupings suggested by Kolasa [1989]), results suggest that there are 3 broadly, 19 intermediately, and 22 narrowly distributed species. From a phylogenetic perspective, the subfamily Oedipodinae showed strong representation in the narrowly and intermediately distributed species groups (11 and 8 species, respectively) but were conspicuously absent from the broadly distributed species group. Of the 14 species of Melanoplinae collected over the 3 yr, 1 fell within the broad species group, 7 fell within the intermediate, and 6 fell within the narrowly distributed species group. Finally, of the 11 species of Gomphocerinae collected, 2, 4, and 5 species fell within the broadly, intermediately and narrowly distributed species groups, respectively.

The differing distribution characteristics among grasshopper species also suggest that they range from patch-indifferent to patch-sensitive species (Kotliar & Wiens 1990). Kotliar & Wiens (1990) define a patch-indifferent organism as one that "does not respond" to patchiness at a particular scale and a patch-sensitive organism is one that "responds to patchiness at a given scale." Thus, it follows that the order of broadly, intermediately, and narrowly distributed species represents increasing patch sensitivity (Hanski 1982, Brown 1984, Kolasa 1989, Kotliar & Wiens 1990). According to Brown (1984), broadly distributed species are, by definition, species that can tolerate a wide range of conditions and secure sufficient resources to attain high densities in optimal habitat. However, such species are able to survive and often reproduce (although at lower densities) in a wide range of less-than-optimal habitats. It is interesting to note that, although patch sensitivity has been generally used to contrast fundamentally different classes of organisms, grasshopper communities of the Gallatin Valley, at the habitat type level, possess species that exhibit low, medium, and high patch sensitivity.

At the valley level, species distribution frequencies were unimodal, and most of the species occurred at <50% of the site-years. Further, there was a positive relationship between the log-transformed mean abundance and the number of site-years collected; similar to that found in studies in the distribution characteristics of other organisms (Hanski 1982, Brown 1984). It is important to note that, although it is useful to construct a species distribution hierarchy consisting of discrete groupings of species (similar to analyses of Kolasa [1989]), what we are actually observing, in terms of species distribution, is a continuum of patch sensitivity as described above (similar to analyses conducted by Hanski [1982], Brown [1984], and Kotliar & Wiens [1990]).

The valley-level species distribution hierarchy found by Kemp (1992a) was also used to test the hypothesis that the proportions of the species represented within the hierarchical groups were equal and were not influenced by habitat type and year. The evaluation of the proportion of species in each of the three distribution groups revealed that, overall, habitat types broadly distributed species made up 18–26% of the species composition, and intermediately and narrowly distributed species made up 58–75 and 6–19% of the species composition, respectively. Thus, it will be important to investigate why intermediately distributed species make up the greatest proportion of the species encountered at the habitat type level and whether similar relationships can be found in the CRB. These results also show that, although there are significant differences within habitat type in the proportion of the respective grasshopper communities made up of narrowly, intermediately, or broadly distributed species, elements of habitat type influence the relative magnitudes of these differences. No significant differences were found among years, habitat types, or for interactions between year by habitat type, for year by species distribution group, or for year by species distribution group by habitat type.

Because census data included subsampling within habitat type for 3 yr, it was possible to examine species distribution characteristics within each habitat type. The species distribution histograms were variable, although some exhibited bimodality (Hanski 1982) not observed at the valley level. In general, as found at the valley level, there was a positive relationship between log mean species abundance and the number of site-years occupied. Therefore, those species that exhibited higher abundances were proportionately more "common" in space and time within each habitat type.

In conclusion, although frequently referred to as a general group with little specific identity, results of this study suggest that rangeland grasshoppers are facultative assemblages of species and that, on average at the habitat type level, they consist of 10–17 species. Because the collection of species at a given site is influenced by habitat type, the generalization of detailed experimental studies beyond the habitat type level must be made with caution. Further, studies at similar scales in other rangeland areas in the western United States and Canada (the CRB would be an excellent region) will be required to assess whether the species distribution hierarchy and related observed patterns from Montana are general phenomena in rangeland grasshopper communities. Finally, it appears that, to understand rangeland grasshopper communities, large-scale observational studies designed to depict pattern must be conducted together with small-scale studies designed to elucidate process (James & McCulloch 1990, Eberhardt & Thomas 1991).

Factors influencing grasshopper species richness and abundance

An analysis of temporal and spatial variation in species richness among rangeland grasshopper communities was conducted in steppe region of Montana during a period of time (1986-1992) that included the extreme drought year of 1988 (Kemp & Cigliano 1994). The main objective of that study was to examine the effects of drastic and geographically extensive environmental variability on species richness. Second, we were interested in whether the species susceptibility to environmental variability showed any kind of phylogenetic constraints. Third, because grasshopper species may differ in their susceptibility to environmental variability (Dempster 1963), we examined whether changes in species richness were related to prevalence (narrowly versus broadly distributed). Last, we re-examined grasshopper intensity data from Kemp (1992b) in an attempt to obtain a more precise estimate of the timing of the observed major shift in general abundance. Again, though additional studies will be necessary to determine whether similar landscape scale processes are important in the CRB, I believe that it is useful to review results of work that we have conducted in Montana as a basis from which to start.

Climatic Conditions. The drought experienced during 1988 was extreme in both the north central and eastern and south central regions of Montana (see Kemp & Cigliano 1994 for regional designations). Since 1895, when records were initiated at many locations, there have been only 5 years in each region where the annual (January-July) drought severity exceeded that recorded during 1988 (north central region - 1961, 1937, 1936, 1931, 1905; eastern and south central region 1961, 1937, 1936, 1935, 1934).

Although both regions suffered extreme drought conditions in 1988, it is important to reference such a year with longer term climatic trends. Examining the drought index trends in both regions during the past 22 years, it was clear that there were differences in the patterns of drought intensity between the two regions. Results of a regression of mean drought index by year (1970-1992) showed that for the north central region the α and β were not significantly different from zero. Thus, although 1988 was an extreme drought year, in the north central region normal conditions returned quickly and the period of the most recent 22 years shows no long term drought trend. However, in the eastern and south central region of Montana, it was obvious that the 1988 drought occurred within a period (1970-1992) of increasing drought intensity. In the eastern and south central region, not only have meteorological conditions not returned to normal since 1988, but there has been a significant long term trend in drought intensity over the past 22 years.

Species Richness. In the north central region, where drought conditions returned quickly to normal and where no evidence of long term drought existed, mean annual species richness was 16.85 and there was no significant difference in mean grasshopper species richness from 1986-1992. In the eastern and south central region, where the 1988 drought occurred during a period (1970-1992) of increasing regional drought, there were significant differences in mean grasshopper species richness over the 1986-1992 interval. Furthermore, means separations showed that the greater than 50% reduction in mean species richness observed in the post drought year of 1989 had not changed through 1992. For univoltine species such as rangeland grasshoppers, eggs produced by the current generation result in populations during the following season. Thus, if drought conditions of 1988 negatively influenced either survival or reproduction of populations (or both) in 1988, we would expect to observe such differences in 1989.

Mean grasshopper species richness (3 years pooled) during 1986-1988 was not significantly different in the two regions, however, during the post-1988 period, the north central region had about 53% more species than the eastern and south central region.

Analysis at the subfamily level revealed that the significant post-drought reduction in species richness occurred in each of the major subfamilies of Acrididae (Oedipodinae, Gomphocerinae, Melanoplinae) in the eastern and south central region of Montana. In the north central region, only the Oedipodinae showed a significant pre- to post-drought reduction.

Neither broadly nor narrowly distributed species (see Kemp & Cigliano 1994 for explanation of species categories) changed significantly over the 1986-1992 interval in the north central region of Montana. In the eastern and south central region, only broadly distributed species showed significant negative trends over the study interval and resulted in reductions of about 50% during post-drought years. Furthermore, although some grasshopper species were missing from post drought collections from both regions, the eastern and south central region suffered the greatest losses.

Abundance. The intensities (density as a function of time, see Kemp & Cigliano [1994]) of grasshopper life stages (small nymphs, large nymphs, and adults) during 1987 and 1988 were computed for the two climatic regions of Montana that we studied. Within each year the intensities of the three life stages are related in that the intensity of small nymphs in a given region and year is the base from which the intensities of large nymphs and adults originate. In general, intensity appears to increase during the year due to the fact that the amount of time spent in a stage increases as the summer progresses (see Kemp & Cigliano 1994). On average, grasshopper nymphs spend about 10 days in each instar;

however, adults may live for more than 90 days (Onsager 1983, Kemp & Dennis 1991). Because we used a time integration method we have a more complete picture of the actual density over time than we could obtain with simple averages.

The most important points to derive from our work (Kemp & Cigliano [1994]) are the relationships between small nymph intensity and subsequent intensities within a given year and between the same life stage in 1987 and 1988. First, it was clear that during 1987 small nymph intensities (grasshopper days/100) of between approximately 11-15 resulted in approximate adult intensities of 38-42. Secondly, even though small nymph intensities were similar in both regions during 1987 and 1988, the expected increases from small nymphs through adults (using 1987 as a model year) failed to materialize during 1988. It was quite evident that overall reductions in abundance observed by Kemp (1992a) during 1988 were disproportionately associated with large nymphs and adults.

Rangeland grasshoppers, which have coevolved within grassland systems, where periodic drought is required (Risser 1988) for maintenance, have behavioral and physiological repertoires which allow them to inhabit such extreme environments (Parker 1930, Uvarov 1977, Capinera 1987, Kemp 1986, Chapman & Joern 1990, Bernays 1990; others). In general the warm, dry weather characterizing the summer period of the Great Plains is considered beneficial to growth, survival, and reproduction of rangeland grasshoppers (Dempster 1963, Capinera 1987, Chappell & Whitman 1990, Joern & Gaines 1990). Given that extreme droughts are characterized more by a lack of moisture rather than an excess of heat, it is unlikely that temperatures experienced during the spring and summer of 1988 were directly limiting to grasshopper development and survival.

Results of previous research suggest that the egg stage is relatively immune to adverse air temperatures, presumably because of the buffering capacity of the soil (Parker 1930, Capinera 1987). Although grasshopper eggs characteristically lose 1/3 - 2/3 of their moisture without dying (Salt 1952, Capinera 1987), the extreme drought conditions during 1988 could have had a detrimental effect on eggs if soil moisture dropped below the critical limit for survival (Mukerji & Gage 1978, Capinera 1987). However, our results of Kemp & Cigliano (1994) showed similar small nymph intensities during 1987 and 1988. Thus, although drought conditions may influence egg survival, there is little evidence to suggest that the heat or lack of precipitation, or both, during the 1988 drought had a direct negative effect on the growth or survival of eggs and small nymphs.

There is, however, abundant evidence to suggest that both grasshopper species distribution and abundance are directly related to quantity, quality, and timeliness of vegetation. Detailed investigations of rangeland grasshopper populations (primarily _Aulocara_ _elliotti_ (Thomas) and _Melanoplus sanguinipes_ (F.)) conducted during 1953 through 1967 on shortgrass prairie in east-central Arizona showed a direct link between precipitation during October-March, springtime vegetation, and observed grasshopper abundance (Nerney 1958, 1960, 1961; Nerney & Hamilton 1969). During periods of adequate and timely rainfall (1953-1954, 1957-1958), Nerney & Hamilton (1969) found that springtime vegetation was abundant and populations of rangeland grasshoppers increased. However, during the dry springs of 1955, 1959, and 1964 the growth of annual plants was sparse and stunted, and initially large hatches of grasshoppers decreased drastically over the summer months. The changes in intensities that we observed throughout Montana during 1988 were similar in general to those observed during dry years in Arizona.

Similar patterns have been observed on grasslands of other western states as well. For example, Fielding & Brusven (1990) found during 1950-1 980, throughout southern Idaho, that precipitation was positively associated with rangeland grasshopper densities (primarily M. sanquinipes and A. elliotti) and they suggested that such precipitation patterns would directly effect springtime vegetation quantity and quality. More recently, detailed investigations in the same region revealed that M. sanquinipes abundance was positively correlated with the aboveground biomass of forbs and annual grasses (Fielding & Brusven 1992). On shortgrass prairie in northeastern Colorado, Capinera & Sechrist (1982) found that Gomphocerinae and Melanoplinae (Acrididae) abundance was related positively to grass and forb biomass. In Montana, Scharff (1954) also demonstrated the importance of annual plants to the growth and development of M. sanquinipes nymphs and postulated that annuals occurring on abandoned fields and rangelands in poor condition, during years of normal springtime precipitation, contributed to the development of grasshopper outbreaks. In sum, observations to date from Montana to Arizona suggest a strong relationship between the winter-spring precipitation, plant production, and subsequent rangeland grasshopper (principally M. sanquinipes) abundance.

The results Kemp & Cigliano (1994), together with those of Tilman & El Haddi (1992), and Haferkamp et al. (1993), show that the drought of 1988 was an extreme meteorological event rarely witnessed even in the grasslands of the Great Plains. That the influence of the 1988 drought on native vegetation was widespread and similar throughout the Great Plains was suggested by the similar results of two widely separated studies. For example, Tilman & El Haddi (1992) found in Minnesota grasslands that overall above-ground biomass decreased 47%, local species richness fell an average of 37% and annual species were reduced some 96%, from pre-drought conditions. Similarly, in Montana, Haferkamp et al. (1993) found that total plant production during 1988 was reduced approximately 51% (dominant perennial grasses down 29%, forbs down 48%, annual grasses down 96%) from pre-drought conditions.

Given the generally accepted arguments concerning the timing of precipitation and abundance of vegetation, particularly annual grasses and forbs, and grasshopper species distribution and abundance, it is likely that the extreme drought of 1988, and the resulting drastic reductions of annuals and forbs (Tilman & El Haddi 1992, Haferkamp et al. 1993), was responsible for the drastic reductions in grasshopper abundance observed throughout Montana (Kemp 1992b) and the dramatic post-drought reductions in grasshopper community species richness that we observed in the eastern and south central region of Montana.

However, although sites in both the north central and eastern and south central regions of Montana lost grasshopper species following the drought year, only those sites within the region of increasing drought severity exhibited significant and severe reductions of the mean grasshopper species richness. In this region, overall species richness of rangeland grasshoppers has not recovered after 4 years.

There is general agreement that rangeland grasshoppers, as a group, tend toward polyphagy, with a few exceptions (Mulkern et al. 1969; Otte & Joern 1977; Joern 1979, 1983, 1985; and others). However, as identified by Joern (1983), it is not uncommon for relatively few plant taxa to comprise a very large portion of the overall diet of individual grasshopper species. Additionally, Joern (1983) found that in the sandhills of Nebraska the Gomphocerinae exhibited the lowest diet breadth and preferred a diet consisting of a high proportion of grasses. Melanoplinae were found to feed primarily on forbs, but exhibited the largest diet breadths observed among the three major subfamilies of Acrididae. The Oedipodinae were intermediate to the Gomphocerinae and Melanoplinae in terms of both diet breadth and preference for forbs versus grasses (Joern 1983).

In the eastern and south central region, there were significant post drought reductions in mean species richness in all three subfamilies. In this region, the Oedipodinae showed the most significant reduction in mean species richness. In the north central region the Oedipodinae was the only group to exhibit significant reductions over time. This suggests that the Oedipodinae as a group may be more sensitive than the Gomphocerinae and Melanoplinae to temporal resource changes in terms of species presence. The Oedipodinae species generally make up a large percentage of the narrowly distributed species at a given region (Kemp 1992a).

All populations experience fluctuations in abundance as a result of variations in environmental resources. When densities become very low and if a species is narrowly distributed in space, even purely chance factors can affect abundance and contribute to local disappearance. In general, the smaller a population becomes and the longer it remains at low density, the more vulnerable it is to extinction (Brown & Gibson 1983). However, this was not the case in the study of Kemp & Cigliano (1994), where no significant losses of narrowly distributed species were detected in either of the two regions, during the post drought period. A reduction of about 50% of broadly distributed species was only observed in the eastern and south central region. Further study will be necessary before we will be able to classify grasshopper communities as recruitment limited as has been suggested for grassland plant communities by Tilman & El Haddi (1992).

The results of Kemp & Cigliano (1994) suggest that resource limitation may be an important aspect of the system in Montana during extreme drought years, however, it is important to note that those data are limited in their spatial extent. For example, although resource limitation may be an important factor in structuring grasshopper communities (species composition and abundance) in the grasslands of northerly latitudes (we are undertaking landscape scale studies to investigate this during FY95 and FY96), including significant portions of the CRB, (Fielding & Brusven 1990, 1992; Kemp et al. 1990a, 1990b; Kemp 1992a, 1992b; Ritchie &

Tilman 1992; Joern & Klucas 1993; others), recent investigations in the tallgrass prairie of Kansas failed to detect interspecific competition over a range of densities and drought/primary production conditions (Evans 1988, 1992). This would suggest that although vegetation influences what species are likely to occupy a site in Nebraska tallgrass prairie (see Evans 1988), factors (for example, predators, parasites, and pathogens) other than resource limitation are important in controlling shifts in temporal abundance.

Additional studies with rangeland grasshopper communities will be necessary before we can determine whether narrowly distributed species (defined by Kemp [1992a]) are more vulnerable to temporal resource fluctuations when compared with broadly distributed species (as suggested by Kolasa [1989]). However, nine narrowly distributed species were collected in < 3 yr during the Kemp (1992a) study. Three species were collected during 2 yr of the study. The species Melanoplus bruneri Scudder was collected only during 1988 and 1990, Stenobothrus brunneus (Thomas) was collected during 1988 and 1989, and, Derotmema haydeni (Thomas) was collected during 1989 and 1990. Finally, six of the narrowly distributed species were collected only during 1 yr of this study: Chloealtis abdominalis (Thomas), Chloealtis conspersa Harris, Spharagemon collare (Scudder), Trimerotropis gracilis (Thomas), Circotettix rabula Rehn & Hebard, and Trimerotropis suffusa Scudder. Because sampling in the Kemp (1992a) study was not designed to determine whether these "winking species" were the result of temporal fluctuations in resource availability or were simply an artifact of sampling intensity, it was not possible to suggest a casual mechanism. However, if the resource-tracking hypothesis is correct for rangeland grasshopper species, it will be important to assess resource availability and quality temporally as well as spatially.

important rangeland grasshopper species of the Columbia River Basin

During FY93 the Grasshopper Common Data Set Project was established as a cooperative effort between the USDA/ARS Rangeland Insect Laboratory, the USDA/APHIS-PPQ Operations Support Staff as well as the Central and Western Regions of APHIS-PPQ. This project involves the 17 western United States and was designed to: 1) Demonstrate that methodologies developed from Geograhpic Information Systems (GIS) could be used to prepare a regional or national grasshopper outlook map; 2) Demonstrate the potential for the development of a distributed rangeland grasshopper database throughout the western United States; and 3) Establish a rangeland grasshopper database that contained information on grasshopper community composition as well as the densities normally collected during the annual adult grasshopper surveys in each state.

The bulk of the CRB consists of areas within the States of Montana, Idaho, Washington, and Oregon (Fig. 1, Vegetation type map). There are more than 550 Grasshopper Common Data Set points within the CRB from those four states (Fig. 2, Point map). Personnel from each of the 17 participating states monitor 10 grasshopper species (selected by the APHIS/PPQ Plant Health Director (PHD) in each state, see Appendix I) occurrence and abundance through annual surveys conducted during the latter portion of the summer season. Because of large differences in the grassland vegetation types throughout the CRB (Fig. 1), it is not surprising that the PHDs in the states of Montana, Idaho, Washington, and Oregon do not monitor the same species in all cases. There is, however, some overlap in the species lists and there are at least 7 rangeland grasshopper species that are likely to be of economic importance to Forest Service Ecosystem Management efforts within the CRB. These are as follows:

Family Acrididae

Subfamily Melanoplinae (Spurthroated grasshoppers)

Melanoplus bivittatus (Say)
Melanoplus femurrubrum (DeGeer)
Melanoplus packardii Scudder
Melanoplus sanguinipes (F.)
Oedaleonotus enigma (Scudder)

Subfamily Gomphocerinae (Slantfaced grasshoppers)

Aulocara elliotti (Thomas)

Subfamily Oedipodinae (Bandwinged grasshoppers)

Camnula pellucida (Scudder)

General biogeographical details for each of the seven species listed above can be found in Appendix II & III below. However, it is important to note that most of the information that has been compiled to date relative to grasshoppers has been for species of significance to agriculture. A conservative estimate of the number of grassshopper species in the CRB would be 75-100, given the observed variation in vegetation throughout this area (Fig. 1) and the fact that current grasshopper surveys focus primarily on rangelands. Three additional activities could improve our estimate of the grasshopper (Orthoptera: Acrididae) species complex of the CRB: 1) Conduct additional surveys in areas not currently monitored on a regular basis (for example, riparian areas, mountain meedows, etc.); 2) Review existing grasshopper collections in Philadelphia, PA and Washington, DC; and 3) expand the identification of APHIS-PPQ annual grasshopper collections, in the four states that make up the bulk of the CRB, to include all species instead of the ten most economically important. Additionally, there is a very high probability that there are a number of grasshopper species that deserve "special concern" at the other end of the spectrum from management directed at reducing their numbers. However, the idea that there may in fact be threatened and endangered grasshopper species is very difficult for many people to accept and no doubt reduces opportunities to test such an hypothesis in the CRB. All of these activities would require additional resources.

From the above discussion on biogeography, it is obvious that grasshoppers as a functional group fluctuate, at the landscape scale, in both the space and time dimensions. Even though data collected during 1993 (Fig.1) represent only a snapshop of recent densities and community compositions, they are useful to review as a basis for initial panel discussions.

Figure 3 shows the 1993 (1994 data are still being shipped to us) grasshopper community density levels observed at each of the Grasshopper Common Data Set sites within the CRB Assessment Area (Fig. 2). Density groupings in the legend of Fig. 3 reflect management thresholds of increasing concern, although in most cases APHIS-PPQ does not actually control grasshoppers on public rangelands until densities are much higher than the 8 + category. With the exception of a few localized "hot spots", grasshopper densities in Idaho were generally low; much of this area is classified by Omernik (revised 1993 Ecoregion Map) as Snake River Basin/High Desert. However, the western portions of the Snake River Basin/High Desert, the Blue Mountains, and the Columbia Plateau ecoregions all show generally higher densities, with densities increasing from south to north.

Figure 4 shows the grasshopper species potential maps for each of the 7 selected species listed above. These maps were developed by intersecting points where a given species was present (a subset of the points in Fig. 2) with the CRB vegetation type map (Fig. 1). This resulted, for each species, in a map of unique conditions where we would expect to encounter it (species potential, Fig. 4). In terms of prevalence within the CRB, M. sanquinipes was the most generally distributed species and O. enigma the most geographically restricted (Table 1, Fig. 4). It is important to note that these 7 species were chosen based on their likely threat to agriculture. No doubt there are a number of other grasshopper species with even more restricted distributions than O. enigma that are not currently recognized in the survey.

Literature Cited

Anderson, N. L. 1964. Some relationships between grasshoppers and **vegetation.** Ann. Entomol. Soc. Am. 57: 736–742.

1973. The vegetation of rangeland sites associated with some grasshopper studies in Montana. Mont. Agric. Exp. Stn. Bull. 668.

Anderson, N. L. & J. C. Wright. 1952. Grasshopper investigations on **Montana** range lands. Mont. Agric. Exp. Stn. Tech. Bull. 486.

Bernays, E. A. 1990. Water regulation. pp. 129-142 *In* Chapman, R.F., and A. Joern (Eds.), Biology of grasshoppers. John Wiley and Sons, Inc, New York.

Brown, J. H. 1984. On the relationship between abundance and distribution of species. Am. Nat. 124: 255-279.

Brown, J. H. & A. C. Gibson. 1983. Biogeography, The C.V. Mosby Co, St. Louis.

Brown, J. H. & M. A. Kurzius. 1987. Composition of desert rodent faunas: combinations of coexisting species. Ann. Zool. Fenn. 24: 227-237.

Capinera, J. L. 1987. Population ecology of rangeland grasshoppers. pp. 162-1 82 *In* Capinera, J.L. (Ed.), Integrated pest management of rangeland: A shortgrass prairie perspective. Westview Press, Boulder.

Capinera, J. L. & T. S. Sechrist. 1982. Grasshoppers (Acrididae) of Colorado: Identification, biology and management. Colorado State University Agriculture Experimental Station Bulletin 584S.

Chapman, R. F. & A. Joern. 1990. Biology of grasshoppers. Wiley, New York.

Chappell, M. A. & D. W. Whitman. 1990. Grasshopper thermoregulation. pp. 143-172 *In* Chapman, R.F & A. Joern (Eds.), Biology of grasshoppers. John Wiley and Sons, Inc, New York.

Clements, F. E. 1916. Plant succession: an analysis of the development of vegetation. Carnegie Inst. Washington Publ. 242.

Daubenmire, R. 1959. A canopy cover method of vegetational analysis. Northwest Sci. 33: 43-64.

Dempster, J. P. 1963. The population dynamics of grasshoppers and locusts. Biol. Rev. 38: 490-529.

Diamond, J. 1986. Evolution of ecological segregation in the New Guinea montane avifauna, pp. 98–125. *In* J. Diamond & T.J. Case [eds.], Community ecology, Harper & Row, New York.

Diamond, J. & T. J. Case [eds.]. 1986. Community ecology. Harper & Row, New York.

Eberhardt, L. L. & J. M. Thomas. 1991. Designing experimental field studies. Ecol. Monogr. 61: 53–73.

Evans, E. W. 1984. Fire as a natural disturbance to grasshopper assemblages of tallgrass prairie. Oikos 43: 9-1 6.

1988. Grasshopper (Insecta: Orthoptera: Acrididae) assemblages of tallgrass prairie: influence of fire frequency, topography, and vegetation. Can. J. Zool. 66: 1495-1 501.

1989. Interspecific interactions among phytophagous insects of a tallgrass prairie: an experimental test. Ecology 70: 435-444.

1992. Absence of interspecific competition among tallgrass prairie grasshoppers during a drought. Ecology 73: 1038-1044.

Evans, E. W., R. A. Rogers & D. J. Opfermann. 1983. Sampling grasshoppers (Orthoptera: Acrididae) on burned and unburned tallgrass prairie: night trapping vs. sweeping. Environ. Entomol. 12: 1449-1 454.

Fielding, D. J. & M. A. Brusven. 1990. Historical analysis of grasshopper (Orthoptera: Acrididae) population responses to climate in southern Idaho, 1950-1980. Env. Entomol. 19: 1786-1791.

1992. Food and habitat preferences of Melanoplus sanguinipes and Aulocara elliotti (Orthoptera: Acrididae) on disturbed rangeland in southern Idaho. J. of Econ. Entomol. 85: 783-788.

Gleason, H. A. 1917. The structure and development of the plant association. Bull. Torrey Bot. Club 44: 463-481.

1926. The individualistic concept of plant association. Bull. Torrey Bot. Club 53: 7-26.

Grant, P. R. 1986. Ecology and evolution of Darwin's finches. Princeton University Press, Princeton, N.J.

Haferkamp, M. R., J. D. Volesky, M. M. Borman, R. K. Heitschmidt & P.O. Currie. 1993. Effects of mechanical treatments and climatic factors on Northern Great Plains rangelands. J. of Range Mgmt. 46: 346-350.

Hanski, I. 1982. Dynamics of regional distribution and the core and satellite species hypothesis. Oikos 38: 21 0-221.

Isely, F. B. 1937. Seasonal succession, soil relations, numbers, and regional distribution of northeastern Texas acridians. Ecol. Monogr. 7: 318-344.

James, F. C. & C. E. McCulloch. 1990. Multivariate analysis in ecology and systematics: panacea or Pandora's box. Annu. Rev. Ecol. Syst. 21: 129-166.

Joern, A. 1979. Resource utilization and community structure in assemblages of arid rangeland grasshoppers (Orthoptera: Acrididae). Trans. Am. Entomol. Soc. 105: 253-300.

1982. Vegetation structure and microhabitat selection in grasshoppers (Orthoptera: Acrididae). Southwest. Nat. 27: 197-209

1983. Host plant utilization by grasshoppers (Orthoptera: Acrididae) from a sandhills grassland. J. Range Manage. 36: 793-797.

1985. Grasshopper dietary (Orthoptera: Acrididae) from a Nebraska sand prairie. Trans. Nebr. Acad. Sci. 13: 21-32.

Joern, A. & S. B. Gaines. 1990. Population dynamics and regulation in grasshoppers. pp. 415-482 *In* Chapman, R.F. & A. Joern (Eds.), Biology of grasshoppers, John Wiley and Sons, Inc, New York.

Joern, A. & G. Klucas. 1993. Intra- and interspecific competition in adults of two abundant grasshoppers (Orthoptera: Acrididae) from a sandhills grassland. Environmental Entomology 22: 352-361.

Joern, A. & L. R. Lawlor. 1980. Arid grassland community structure: comparisons with neutral models. Ecology 61: 591-599.

Kemp, W. P. 1986. Thermoregulation in three rangeland grasshopper species. Can. Entomol. 118: 335-343.

1992a. Rangeland grasshopper (Orthoptera: Acrididae) community structure: A working hypothesis. Env. Entomol. 21: 461-470.

1992b. Temporal variation in rangeland grasshopper (Orthoptera: Acrididae) communities in the steppe region of Montana, USA. Can. Entomol. 124: 437-450.

Kemp, W. P. & M. M. Cigliano. 1994. Drought and rangeland grasshopper species diversity. Can. Entomol. 126: 1075-1 092.

Kemp, W. P. & B. Dennis. 1991. Toward a general model of rangeland grasshopper (Orthoptera: Acrididae) phenology in the steppe region of Montana. Env. Entomol. 20: 1504-1515.

Kemp, W. P. & N. E. Sanchez. 1987. Differences in post diapause thermal requirements for eggs of two rangeland grasshoppers. Can. Entomol. 119: 653-661.

Kemp, W. P., S. J. Harvey & K. M. O'Neill. 1990a. Patterns of vegetation and grasshopper community composition. Oecologia 83: 29–308.

1990b. Habitat and insect biology revisited. Am. Entomol. 36: 44-49.

Kolasa, J. 1989. Ecological systems in hierarchical perspective: breaks in community structure and other consequences. Ecology 70: 36-47.

Kolasa, J. & D. Strayer. 1988. Patterns of abundance of species: a comparison of two hierarchical models. Oikos 53: 235-241.

Kotliar, N. B. & J. A. Wiens. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos 59: 253-260.

Ludwig, J. A. & J. F. Reynolds. 1988. Statistical ecology. Wiley, New York.

MacArthur, R. H. 1972. Geographical ecology. Harper & Row, New York.

Mueggler, W. F. & W. L. Stewart. 1980. Grassland and shrubland habitat types of western Montana. USDA Forest Service GTR INT-66.

Mukerji, M. K. & S. H. Gage. 1978. A model for estimating hatch and mortality of grasshopper egg populations based on soil moisture and heat. Ann. of the Entomol. Soc. of Amer. 71: 183-1 90.

Mulkern, G. B. 1967. Food selection by grasshoppers. Annu. Rev. Entomol. 12: 59–78.

Mulkern, G. B., K. P. Pruess, H. Knutson, A. F. Hagen, J. B. Campbell & J. D. Lambley. 1969. Food habits and preferences of grassland grasshoppers of the north central great plains. N. Dak. Agric. Exp. Stn. Bull. No. 81.

Nerney, N. J. 1958. Grasshopper infestations in relationship to range condition. J.of Range Mgmt. 11: 247.

1960. Grasshopper damage on shortgrass rangeland of the San Carlos Apache Indian Reservation, Arizona. J. of Econ. Entomol. 53: 640-646.

1961. Effects of seasonal rainfall on range condition and grasshopper population, San Carlos Apache Indian Reservation, Arizona. J. of Econ. Entomol. 54: 382-385.

Nerney, N. J. & A. G. Hamilton. 1969. Effects of rainfall on range forage and populations of grasshoppers, San Carlos Apache Indian Reservation, Arizona. J. of Econ. Entomol. 62: 329-333.

Onsager, J. A. 1983. Relationships between survival rate, density, population trends, and forage destruction of instars of grasshoppers (Orthoptera: Acrididae). Env. Entomol. 12: 1099-I 102.

Otte, D. & A. Joern. 1977. On feeding patterns in desert grasshoppers and the evolution of specialized diets. Proc. Acad. Nat. Sci. Phil., 128: 89-126.

Parmenter, R. P., J. A. MacMahon & C. A. B. Gilbert. 1991. Early successional patterns of arthropod recolonization on reclaimed Wyoming strip mines: the grasshoppers (Orthoptera: Acrididae) and allied faunas (Orthoptera: Gryllacrididae, Tettigoniidae). Environ. Entomol. 20: 135-1 42.

Parker, J. R. 1930. Some effects of temperature and moisture upon Melanoplus mexicanus mexicanus Sassure and Camnula pellucida Scudder (Orthoptera), University of Montana, Bozeman, Agriculture Experiment Station Bulletin No. 223.

Quinn, M. A., R. L. Kepner, D. D. Wlagenbach, R. A. Bohls & P. D. Pooler. 1991. Habitat characteristics and grasshopper community dynamics on mixed-grass rangeland. Can. Entomol. 123: 89-105.

Risser, P. G. 1988. Diversity in and among grasslands. pp. 176-180 *In* Wilson, E.O. (Ed.), Biodiversity. National Academy Press, Washington.

Ritchie, M. E. & D. Tilman. 1991. Interspecific competition among grasshoppers and their effect on plant abundance in experimental field environments. Oecologia 89: 524-532.

Salt, R. W. 1952. Some aspects of moisture absorption and loss in eggs of Melanoplus bivittatus Say. Can. J. of Zool. 30: 55-82.

Scharff, D. K. 1954. The role of food plants and weather in the ecology of Melanoplus mexicanus mexicanus (Sauss.). J. of Econ. Entomol. 47: 485-489.

Schluter, D. 1984. A variance test for detecting species associations, with some example applications. Ecology 65: 998-1005.

Strong, D. R., Jr., J. H. Lawton & T. R. E. Southwood. 1984. Insects on plants: community patterns and mechanisms. Blackwell Scientific, Oxford, England.

Tilman, D. & A. El Haddi. 1992. Drought and biodiversity in grasslands. Oecologia 89: 257-264.

Uvarov, B. P. 1966. Grasshoppers and locusts: a handbook of general acridology, vol. 1. Cambridge University Press, London.

1977. Grasshoppers and locusts, vol. 2. Center for Overseas Pest Research, London.

Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. Ecol. Monogr. 22: I-44.

1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecol. Monogr. 30: 279-338.

Wiens, J. A. 1981. Single-sample surveys of communities: are the revealed patterns real? Am. Nat. 117: 90-98.

Table 1. General prevalence of seven important rangeland grasshopper species of concern to CRB managers.

Species	Number of points where present (from Fig. 2)	Number of CRB vegetation types where present (from Figs. 1 and 4)
Melanoplus sanguinipes	288	19
Aulocara elliott	89	16
Melanoplus bivittatus	106	14
Camnula pellucida	43	12
Melanoplus packardii	28	12
Melanoplus femurrubrum	65	12
Oedaleonotus enigma	23	7

Appendix I

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Appendix II

Species Fact Sheets

(excerpted from **Pfadt, R. E. 1988**. Field guide to common western grasshoppers. USDA APHIS - Wyoming Experiment Station, University of Wyoming, Laramie, WY 82071, Bulletin 9 12)

Twostriped Grasshopper
Melanoplus bivittatus (Say)

Distribution and Habitat

The twostripcd grasshopper, *Melanoplus bivittatus* (Say), occurs widely in North America inhabiting tall, lush, hcrbaccous vegetation. Dcnsc populations may reside in tallgrass prairic, wet meadows, roadsides, ditch banks, and crop borders.

Economic Importance

The twostripcd grasshopper is a major crop pest causing much damage to small grains, alfalfa. and corn. During outbreaks, it may completely destroy crops. A population of 10 adults per square yard in a corn field will defoliate the crop. Sorghum plants over six inches tall, howcvcr. arc nearly immune to attack. Experiments indicate that in feeding on spring wheat the twostripcd grasshopper wastes six times as much foliage as it cats. In urban areas the twostripcd grasshopper is a common pest of flowers and vegetables.

Food Habits

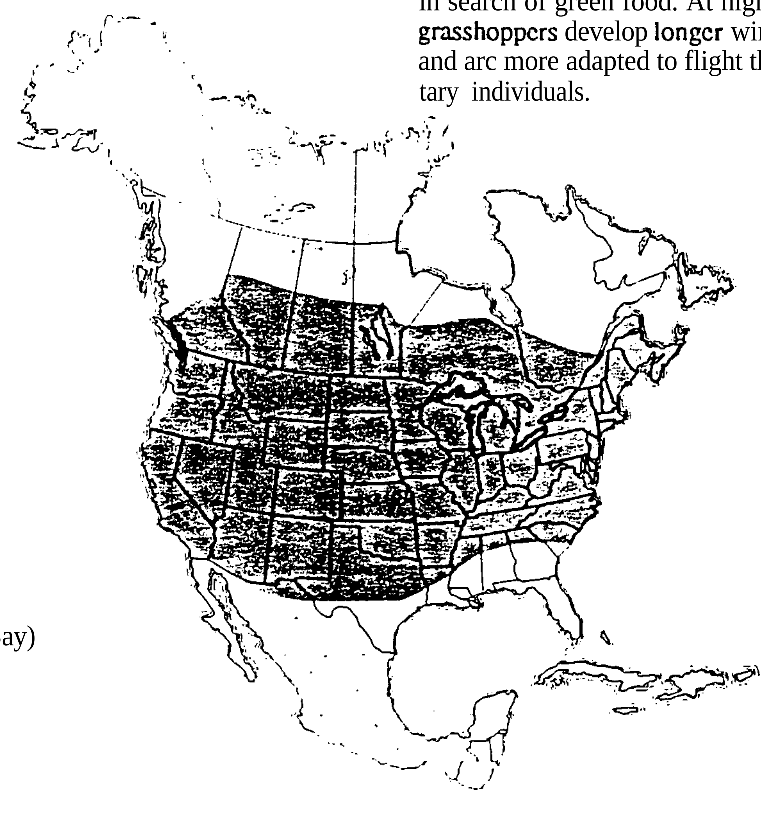
The twostriped grasshopper is a polyphagous insect. It feeds on many kinds of plants. Although grasses and cereals arc eaten and damaged, rearing experiments show that certain forbs furnish the nymphs with diets that promote high survival, fast growth, and heavy weights. Thcsc host plants belong to scvcnl plant families. Included arc mustards (flixwecd tansymustard and prairie pepperweed); a plantain (common plantain): legumes (alfalfa and red clover); and composites (common dandelion, common chicory, wild lettuce, giant ragweed, and butterbur). Microscopic examination of crop contents and field observations indicate that the following species may also bc primary host plants: ball mustard, wcstcm ragweed, prairie sunflower, field sowthistle, fireweed, and leadplant. The twostripcd grasshopper feeds also on dry litter found on the ground.

A meal for the twostripcd grasshopper may be a single species of plant, but usually it consists of two or more species. Laboratory rearings demonstrate that a mixed diet is more nutritious than a single plant diet. The diets of particular populations vary depending on the kinds of plants present in their habitats.

Migratory Habits

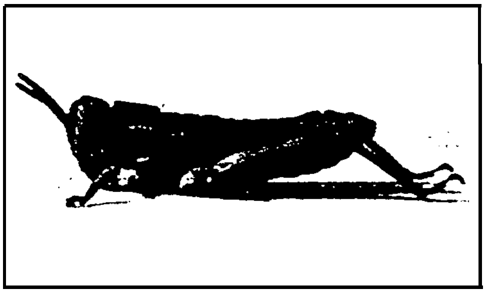
The twostripcd grasshopper exhibits migratory behavior during both nymphal and adult stages. At high dcnsitics, nymphs may move in bands when they reach the third and older instars. Populations invade crops from crop borders and roadsides where eggs are concentrated and nymphs reach densities as great as 500 per square yard. Nymphs start migration around 10 a.m. when skies arc clear and temperature has risen to 75 F. This activity may occur through the day until 6 p.m. Wind has little effect on movement.

Adults begin flying when temperatures reach 86 to 90 F. Flying with the wind at heights of 600 to 1.400 feet above ground level, they may travel long distances. Swarms of adults also move upwind by low, short flights in search of green food. At high densities, twostriped grasshoppers develop longer wings and slimmer bodies and arc more adapted to flight than are low density, solitary individuals.



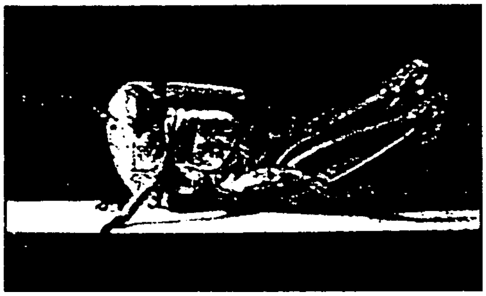
Geographic range of *Melanoplus bivittatus* (Say)

Instar 1



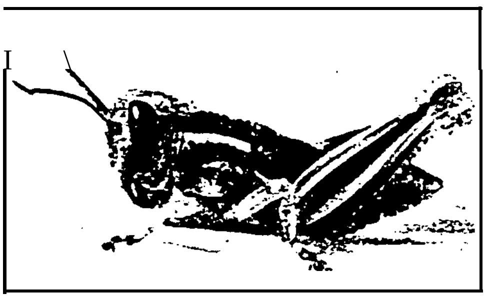
1. BL 5-6.6 mm. FL 2.7-3 mm. AS 12-13.

Instar 2



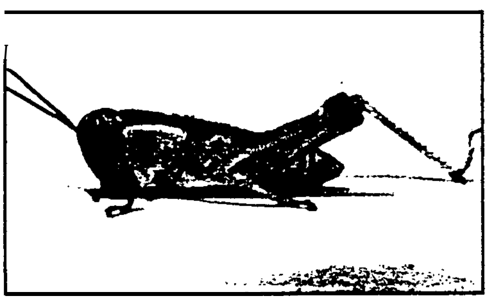
2. BL 7.4-10.4 mm. FL 3.9-4.3 mm. AS 17-18.

Instar 3



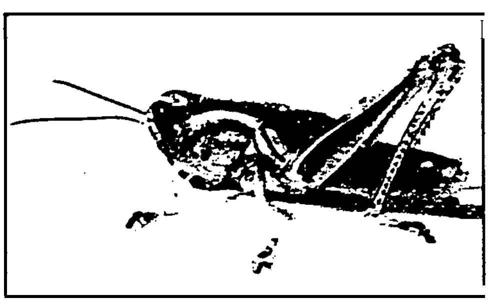
3. BL 9-14 mm. FL 5.7-8.4 mm. AS 19-22.

Instar 4



4. BL 15-21 mm. FL 8.5-12 mm. AS 23-24.

Instar 5



5. BL 20-27 mm. FL 12-14 mm. AS 24-26.

Figures 1-5. Appearance of the five nymphal instars of M. *bivittatus*—their sizes, stuctures, and color patterns. Notice progressive development of the wing pads. BL = body length, FL = hind femur length, AS = antennal segments number.

Identification

The twostriped grasshopper is one of the two largest species in the genus *Melanoplus*. The other is the differential grasshopper, *M. differentialis* (Thomas). Both species are often found together in the same habitat.

The nymphs of the twostriped grasshopper (Fig. 1-5) are identifiable by their spots. stripes, and color patterns:

(1) Compound eye with many uniform light spots and no dark bands.

(2) Front of head tan or green with dark spots; line of dark spots on carinae (ridges) of frontal costa.

(3) Pronotum with light, horizontal stripe at top of lateral lobe: above the stripe a fuscous or brown band at the edge of pronotal disk.

(4) Gena colored tan or green and spotted, without light crescent below compound eye.

(5) Hind femur with black stripe entire, not interrupted by pale band. Stripe fills upper medial area of hind femur except at proximal end and encroaches slightly on the lower medial area.

(6) Hind tibia green or buff with spines or tips of spines black. Front (anterior edge) of tibia fuscous.

(7) General color green or tan.

The adult male (Fig. 6) is easily identified by the shape of the cercus (Fig. 9). Both the male and the female (Fig. 7) have two distinctive light yellow stripes running down the dorsum of the head, pronotum, and tegmina (Fig. 8). The stripes come together posteriorly on the tegmina forming a triangle.

Hatching

The twostriped grasshopper is an early hatching species. It is one of the first species to appear in habitats of roadsides and field borders. Eggs (Fig. 10) begin embryonic growth in the summer of deposition and attain 60 to 80% development before they go into diapause for the winter. When soil temperatures rise in spring, the embryos complete development and hatching begins. Eggs start to hatch eight to ten days ahead of those of the migratory grasshopper, *Melanoplus sanguinipes* (F.) The hatching period lasts from four to six weeks depending mainly on soil temperatures in spring. Hatching may come in two or more bursts following warm temperatures and rain showers.

Figurcs 6-10. Appcarancc of thc adult malc and fcmalc of *M. bivittatus*, two diagnostic: charactcrs, and thc cgg pod and scvcral loosc cggs.

Nymphal Development

Nymphs dcvclop and grow in spring whcn vcgctation is young and grccn. It takcs around 40 days for thcm to rcach thc adult stagc. Dcnsc populations of nymphs do much shifting about and oftcn migratc into crops, particularly barlcy and whcat. Bccausc of an cxtcndcd pcriod of hatching, nymphs may bc prcscnt in thc habitat for as long as 75 days.

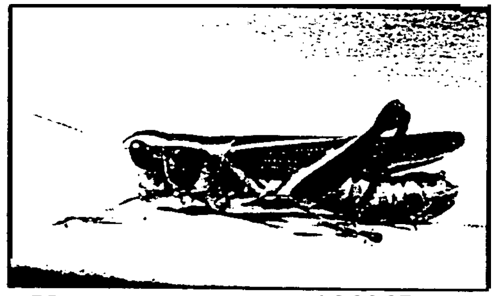
Adults and Reproduction

Although thc cxact datc of adult cmcrgcncc may vary annually by as much as 50 days, this cvcnt usually occurs in thc first part of summcr. Grasshoppcrs that havc movcd into crops return to crop borders and roadsidc habitats for rcproduction. Without signaling a malc will stcalthily approach a fcmalc and makc a copulatory lcap. Aftcr mounting and whilc attaching his gcnitalia, thc malc pcrforms a courtship ritual by shaking his hind fcmora for thrcc or four scconds. Fcmalcs havc a prcoviposition pcriod of onc to two weeks bcforc dcpositing their first clutch of cggs. Favorcd sitcs for oviposition arc ditch banks that hcc south and crop bordcrs with compact drift soil. Thc fcmalcs sclcct crowns of grass or roots of wccds on which to dcposit thcir eggs. Pods may contain from 50 IO 108 cggs. Pods are curvcd, one and onc-cighth to one and onc-half inchcs long and onc-quartcr inch in diamctcr (Fig. IO). Thcy are dclicatc and easily brokcn in sifting thcm from thc soil. Eggs arc olive and 5.1 to 5.3 mm long. Fcd a nutritious dict of radish lcavcs, cagcd grasshoppcrs havc avcragcd 450 cggs pcr fcmalc. The avcragc numhcr of pods and eggs produccd in naturc is unknown.

Most populations of the twostripcd grasshoppcr havc a onc-ycar lifc cyclc but in mountain parks of British Columbia at altitudes abovc 3,000 fcct, populations takc two ycars to complctc a lifc cyclc. A two-ycar lifc cyclc may also occur among populations inhabiting mcadows of thc Rocky Mountains.

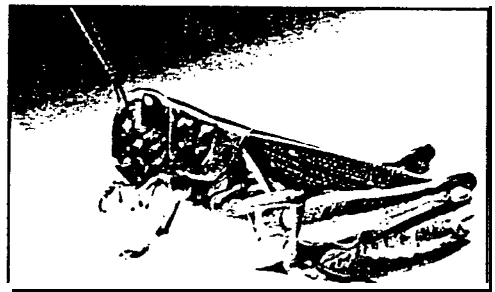
Population Ecology

Thc twostripcd grasshoppcr bccamc a pest whcn agricultural dcvclopmcnt in thc Wcst fostered largc populations of thc insect. Early scttlcrs unwittingly sowcd sccds of various wccds along with thcir crops thus introducing nutritious ncw host plants for this grasshoppcr. The wccds also grcw luxuriantly along crop bordcrs, road sidcs, and ditch banks. This cnvironmcnt providcd cssential habitats, whilc south facing ditch banks and compact drift soil at ficld margins furnishcd idcal cgg laying sitcs.



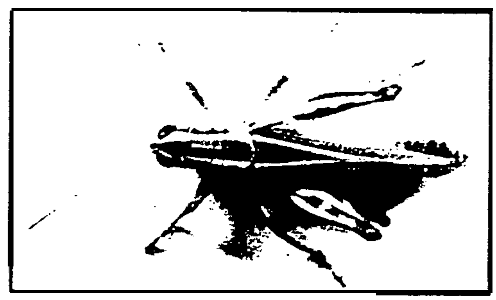
Malc

6. BL 28-30 mm. FL 15-16.5 mm. AS 26-27.



Fcmalc

7. BL 36-41 mm. FL 18.5-20.5 mm. AS 27-28.

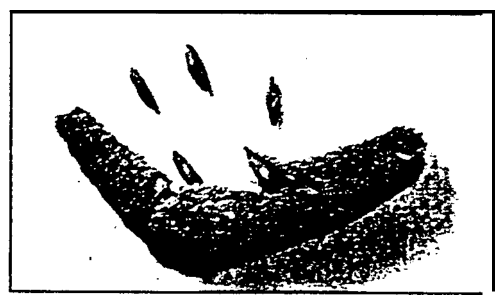


Note Two Stripcs

8. Dorsal view of twostriped grasshopper.

Note Cercus

9. Sidc vicw end of malc abdomcn.



Egg Pod

10. Egg pod and scveral loose eggs.

These factors and favorablc weather over a few consecutive years allowed populations to irrupt. In eastern North and South Dakota such favorable conditions combined to precipitate one of the worst outbreaks of the twostriped grasshopper and differential grasshopper in agricultural history. Populations increased slowly for three years, 1928 to 1930. Both species reached phenomenal numbers in 193 1 and 1932. They devastated fields of alfalfa. small grains, corn. vegetables, and a variety of fruit and shelterbelt trees. In 1933 and 1934 a severe drought not only ruined crops and other vegetation but also terminated the grasshopper outbreak.

Daily Activity

The twostriped grasshopper is a diurnal insect. Its activities occur during the daylight hours when weather is warm and the skies arc clear. The tall vegetation of its habitat influences its behavior. In the evening before sunset as temperatures cool, both nymphs and adults climb the plants and rest, moving from halfway up to nearly the top of the vegetation. In these positions they rest through the night. Shortly after sunrise, the grasshoppers are warmed by the rays of the sun and begin to descend from their overnight perches. On the ground they may continue sunning themselves or begin to feed and then to migrate. Nymphs are usually on the ground from 6 to 11 a.m.

Table 1. Activity of nymphs and adults of the twostriped grasshopper, *Melanoplus bivittatus* (Say) correlated with air and soil temperatures (After Parker and Shotwcll 1932).

Name of activity	Description	Average temperature °F Nymphs Air	Nymphs Soil	Adults Air	Adults Soil
Beginning of activity	Start of descent from plants	65		65	
Beginning of normal activity	Start of feeding	68		68	70
	Start of migration	75		78	
	Start of oviposition			70	
Beginning of escape from heat	Climbing and seeking shade on plants	**90**	**112**	**90**	**112**
	Flying in circles or flying with wind			90	112

Selected Rcfcrcnces

Bailey, C. G. and M. K. Mukcrji. 1976. Feeding habits and food prefcrcnccs of *Melanoplus bivittatus* and *M. femurrubrum* (Orthoptera: Acrididae). Can. Entomol. 108: 1207-1212.

Bird, R. D., W. Allen and D. S. Smith. 1966. The responses of grasshoppers to ecological changes produced by agricultural development in southwestern Manitoba. Can. Entomol. 98: 1191-1205.

Drake, C. J.. G. C. Decker and 0. E. Tauber. 1945. Observations on oviposition and adult survival of some grasshoppers of economic importance. Iowa State College J. Sci. 19: 207-223.

MacFarlane, J. H. and A. J. Thorstcinson. 1980. Development and survival of the twostriped grasshopper, *Melanoplus bivittatus* (Say) (Orthoptera: Acrididae), on various single and multiple plant diets. Acrida 9: 63-76.

Mukcrji, M. K., R. Pickford and R. L. Randell. 1976. A quantitative evaluation of grasshopper (Orthoptera: Acrididae) damage and its effect on spring wheat. Can. Entomol. 108: 255-270.

Moore, H. W. 1948. Variations in fall embryological development in three grasshopper species. Can. Entomol. 80: 83-88.

Parker, J. R. and R. L. Shotwell. 1932. Devastation of a large area by the differential and the two-striped grasshoppers. J. Econ. Entomol. 25: 174-196.

Putnam, L. G. and R. H. Handford. 1958. Two-year and one-year life cycles in *Melanoplus bivittatus* (Say) (Orthoptera: Acrididae) in western Canada. Proc. Tenth Internatl. Congr. Entomol., Montreal 1956, 2: 65 l-656.

Smith, D. S. 1966. Fecundity and oviposition in the grasshoppers *Melanoplus sanguinipes* (F.) and *Melanoplus bivittatus* (Say). Can. Entomol. 98: 617-621.

Smith, D. S. and N. D. Holmes. 1977. Thk distribution and abundance of adult grasshoppers (Acrididae) in crops in Alberta, 1918-1975. Can. Entomol. 109: 575-592.

Redlegged Grasshopper

Melanoplus femurrubrum (DeGeer)

Distribution and Habitat

The redlegged grasshopper, *Melanoplus femurrubrum* (DeGeer), ranges over most of North America except for high mountain altitudes and the frigid north. It is the most widely distributed species of the major crop grasshoppers. Its favorite habitats include tall vegetation of grasslands, mmdows, crop borders, reverted fields, and roadsides. It favors low moist weedy areas where its host plants abound.

Economic Importance

The rcdlcgged grasshopper is a crop pest. During outbreaks of the species, it may severely damage alfalfa, clover. soybeans, and small grains. It has destroyed second crops of clover and has caused losses of 20 to 25 percent to individual fields of oats. In castcm United States and Canada, it is the most abundant species of grasshopper. It becomes a pest not only of legumes and small grains but also corn. tobacco, and vegetables — especially beans, beets, cabbage, and potatoes. Large numbers develop in meadows and damage forage grasses. In laboratory tests the redlegged grasshopper ingested 25 percent of the foliage that it removed from six different host plants and wasted 7.5 percent.

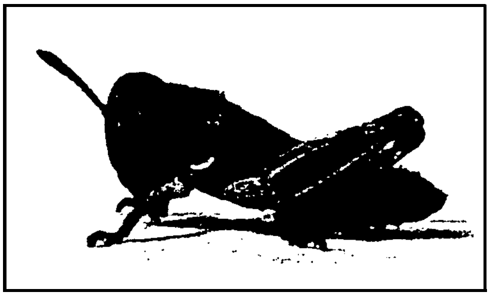
Food Habits

The redlegged grasshopper feeds on a wide variety of forbs and on several kinds of grasses. Depending on availability of host plants in the habitat. it may be either forbivorous or a mixed feeder ingesting significant amounts of both forbs and grasses. Known host plants consist of legumes (birdsfoot trefoil, white and yellow sweetclover. lespedeza, milkvetches, and alfalfa); composites (common dandelion, common chicory, goldenrod, fireweed, and western ragweed); and grasses (Kentucky bluegrass, barley. oats, wheat, smooth brome, Japanese brome, timothy, and reed canarygrass).

Experiments show that host plants vary in their capacity to provide good nutrition. Although alfalfa is readily eaten, a sole diet of this plant causes a high

Ccographic range of *Melanoplus femurrubrum* (DeGeer)

Instar 1

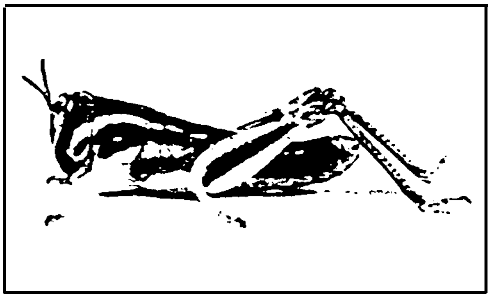


1. BL 4-5.6 mm. FL 1.9-2.4 mm. AS 12-14.

Instar 2

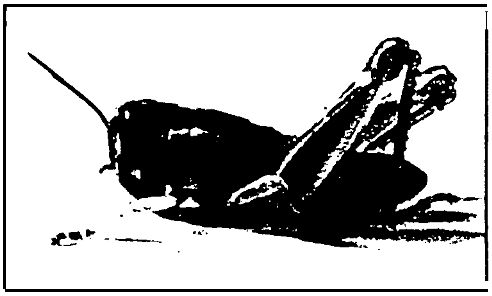
2. BL 6.2-7.2 mm. FL 3.1-3.4 mm. AS 15-16.

Instar 3



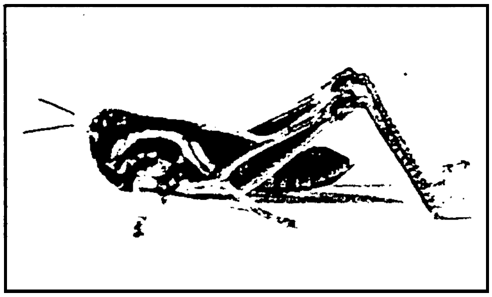
3. BL 7.4-9.7 mm. FL 4.6-5.4 mm. AS 18-19.

Instar 4



4. BL 10-15.5 mm. FL 7.2-9.0 mm. AS 22-24.

Instar 5



5. BL 16.5-225 mm. FL 9.5-l 1.5 mm. AS 24-26.

Figures 1-5. Appearance of the five nymphal instars of *M. femurrubrum*–their sizes, structure, and color patterns. Notice progressive development of the wing pads. BL = body length, FL = hind femur length, AS = antennal segments number.

nymphal mortality of 70 to 90 percent Of three plants, corn, lettuce and radish, tested for growth and performance of nymphs and adults. lettuce yielded the most favorable results — high survival of nymphs, heavy weight of adults, and high egg production. A mixed diet of the three plants provided the best nutrition. This fact is significant because analyses of crop contents show that the majority of individuals collected from natural habitats consume two or more plant species in a single meal.

Migratory Habits

The redlegged grasshopper has strong powers of flight that allow the adults to disperse and find new habitats. In years of drought, the adults develop longer wings, fly more, and make lengthy flights often in company with the migratory grasshopper.

The flight of flushed individuals is swift, even, and three or four feet above the vegetation. The insects generally fly distances of 30 to 40 feet

Identification

Adults of the redlegged grasshopper are medium size and have a bright yellow underside and bright red hind tibia (Fig. 6 and 7). Rarely the hind tibia is colored yellowish-green or blue (Fig. 8). The bulbous subgenital plate and the shape of the cercus (Fig. 9) are diagnostic characters of the male. The nymphs (Fig. l-5) are strikingly marked yellow and black. They are identifiable from their spots and color patterns:

(1) Compound eye brown to burgundy with light yellow or tan spots, more spots on dorsal half than ventral; lacking transverse dark band.

(2) Front of head with dark vertical band in center. light yellow band on each side of the center band; the two yellow bands come together below on the clypeus.

(3) Gena with broad pale yellow crescent continuing on pronotal lobe to first abdominal **segment** and fading along the rest of abdomen.

(4) Dorsum of head to end of abdomen with median pale yellow stripe. Broad black stripe on either side of the median pale yellow stripe. Pronotal lobe with black band or markings below the yellow crescent

Figurcs 6-10. Appcarancc of adult malc and fcmalc, adult fcmalc of uncommon bluc form, thc malc ccrcus, a diagnostic charactcr, and thc cgg pod and scvcnl loosc cggs.

(5) Hind fcmur with black stripe entirc, not interruptcd by pale band. Stripe fills uppcr medial arca of hind fcmur except at proximal cnd. Stripc cncroachcs a third or morc on thc lowcr medial area.

(6) Hind tibia mainly palc ycllow or pale gray, front black: tips of spincs black.

(7) Gcncral color contrasting ycllow and black.

Hatching

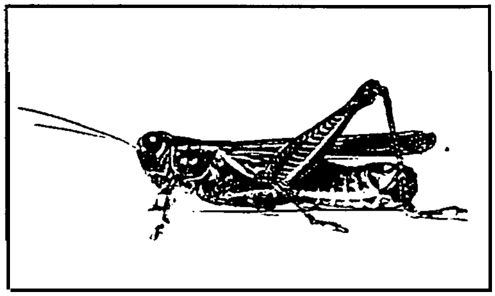
Eggs of thc rcdlcggcd grasshoppcr bcgin to hatch threc wecks after the eggs of the twostripcd grasshoppcr. Thc pcriod of hatching lasts approximatcly 52 days. Bccausc fcmalcs oviposit throughout the habitat in a scattered pattcm, the eggs are subjcctcd to a rangc of soil temperatures and moisture conditions.

Nymphal Development

Nymphal dcvelopmcnt bcgins in late spring and in carly summer when host plants arc usually green and succulent. In approximatcly JO days the nymphs become adult developing at ratcs approximatcly the same as thc twostriped. When rcarcd in cagcs at a constant tempcrature of 85 F, the redleggcd rcquircs a nymphal pcriod of 28 days and the twostriped 29 days. Bccausc of the cxtcndcd pcriod of hatching. somc nymphal grasshoppcrs can bc found nearly all summcr long.

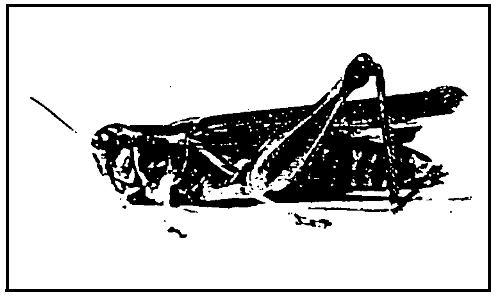
Adults and Reproduction

Adults of the redlcggcd grasshopper are active from carly summer to thc middlc of fall. Although dispersal flights occur, most individuals stay close to where they hatch. There they feed, rcproduce, and face many mortality factors throughout the summcr. Aftcr flcdging, caged fcmalcs require a prcoviposition pcriod of 9 to 15 days at 86 F bcforc bcginning to lay eggs. In naturc thc fcmales havc bccn obscrved ovipositing into sod. Thc pods are slightly curved, three-quartcrs to onc inch long and onc-eighth to thrcc-sixtecnth inch in diamctcr (Fig. 10). Thc top third is dricd froth, the bottom two-thirds contain 20 to 26 cggs. Thc cggs are 4.1 to 4.4 mm long and palc ycllow. Cagcd rcdlcggcd grasshoppcrs fcd a nutritious mixcd dict of grccn lcavcs produced 336 eggs pcr fcmalc. Undcr similar conditions twostripcd grasshoppers produccd 4 12 cggs pcr fcmalc. Thc rcdlegged grasshopper has onc gcncration annually.



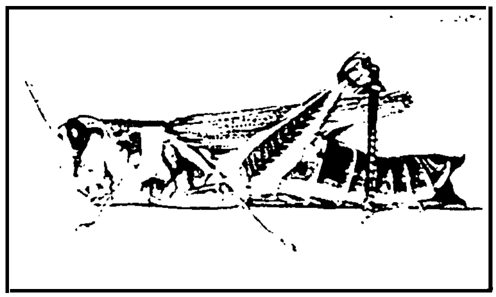
Malc

6. BL 17.5-U mm. FL 10.5-13 mm. AS 25-28.



Female

7. BL 24-28 mm. FL 14-14.5 mm. AS 26-27.



Female

8. Uncommon blue form of redlegged grasshopper.

Note ccrcus

9. Side view end of male abdomcn.

Egg pod

10. Egg pod and scvcral loosc eggs.

Population Ecology

Historical records from the late 1800s till the 1980s indicate that a center of distribution of the redlegged grasshopper is present in a 78,000 square mile area composed of sections of Iowa. Illinois, Minnesota, and Wisconsin. This center is an especially favorable zone where the redlegged grasshopper is abundant and outbreaks are frequent. Populations respond quickly during spring and summer to reduced rainfall and warm temperatures in this distribution zone. Within one to two years small populations may increase to outbreak numbers. Densities in these years reach peaks of 200 to 500 nymphs per square yard. Outbreaks last for two to three years until normal rainfall and cool spring temperatures reduce populations back to low noninjurious numbers. The periods of low densities range from two years to over five years.

In western states densities of the redlegged grasshopper fluctuate widely, apparently in response to annual changes in weather. Large populations develop in irrigated fields of alfalfa and along roadsides, particularly in patches of sweetclover. This species may also add considerably to the density of outbreak assemblages of the migratory, twostriped, and differential grasshoppers.

Daily Activity

The redlegged grasshopper is active during the day. At night adults roost on the tops of grasses and weeds. *Close to* 6:30 a.m. they begin to move from their perches and begin feeding about 7 a.m. Between 4:30 and 5 p.m. they start crawling up vegetation to roost. By 5:30 p.m. the majority are roosting and have settled down for the night. In marshes this grasshopper has been observed at times to feed between 8 p.m. and midnight. Correlations of these activities with temperature have not been made.

Selected References

Bailey, C. G. and M. K. Mukerji. 1976. Consumption and utilization of various host plants by *Melanoplus bivittatus* (Say) and *M. femurrubrum* (DeGeer) (Orthoptera: Acrididae). Can. J. Zool. 54: 1044-1050.

Bailey, C. G. and M. K. Mukerji. 1976. Feeding habits and food preferences of *Melanoplus bivittatus* and *M. femurrubrum* (Orthoptera: Acrididae). Can. Entomol. 108: 1207-1212.

Bellinger, R. G. and R. L. Pienkowski. 1987. Developmental polymorphism in the red-legged grasshopper, *Melanoplus femurrubrum* (DeGeer) (Orthoptera: Acrididae). Envir. Entomol. 16: 120-125.

Cantrall, I. J. 1943. The ecology of the Orthoptera and Dermaptera of the George Reserve, Michigan. Misc. Publ. Mus. Zool. Univ. Michigan, No. 54

Drake, C. J. and G. C. Decker. 1938. Grasshopper outbreaks in Iowa. J. Econ. Entomol. 31: 583-586.

Gangwere, S. K. 1958. Notes on the feeding periodicity of various Orthoptera. Papers Michigan Acad. Sci.. Arts, Letters 43: 119- 132.

Larrimer, W. H. and A. L. Ford. 1922. The daily maximum feeding period *of Melanoplus femurrubrum*. Can. Entomol. 54: 141-143.

Mulkern. G. B.. J. F. Anderson, M. A. Brusven. 1962. Biology and ecology of North Dakota grasshoppers. 1. Food habits and preferences of grasshoppers associated with alfalfa fields. North Dakota Agr. Exp. Stn. Research Report 7.

Shotwell. R. L. 1938. Species and distribution of grasshoppers responsible for recent outbreaks. J. Econ. Entomol. 31: 602-610.

Packard Grasshopper

Melanoplus packardii Scudder

Distribution and Habitat

The Packard grasshopper ranges widely in western North America. It is primarily a rangeland species inhabiting the tallgrass, shortgrass, mixedgrass, bunchgrass, and desert prairies. The species also lives in ruderal habitats and has become recognized as an important cropland grasshopper. It reaches high densities in the northern part of its geographic range and lives in mountain meadows at altitudes as high as 9,000 feet.

Economic Importance

Because of its usual low densities on rangeland and its preference for poor forage plants, such as the scurfpeas, the Packard grasshopper in its natural habitat causes little damage. Nevertheless in the northern region of the mixedgrass prairie, the Packard grasshopper is an important member of the rangeland assemblage, and it is often second in density after the dominant species, *Melanoplus infantilis*.

This grasshopper has adapted well to cropland and ruderal habitats including roadsides, fence rows, edges of cultivated fields, abandoned farm land, and Conservation Reserve Program land. In certain years it develops large populations that cause serious damage to small grains and alfalfa. Grasshopper surveys conducted in cropland areas of Saskatchewan from 1931 to 1966 reveal that the Packard grasshopper often adds substantially to the damage of cereal crops as an important member of an assemblage along with *Melanoplus sanguinipes* and *M. bivittatus*. In certain years the Packard grasshopper is the dominant species, making up 50 percent of the total population. As one moves south the Packard grasshopper becomes less important. It is mentioned as a minor pest in Kansas, although in Oklahoma it has been recorded as damaging cotton, vegetables, small grains, and legumes. The Packard grasshopper is a large species. Dry weight of males and females collected from rangeland and roadsides in eastern Wyoming averaged 141 mg and 208 mg, respectively.

Food Habits

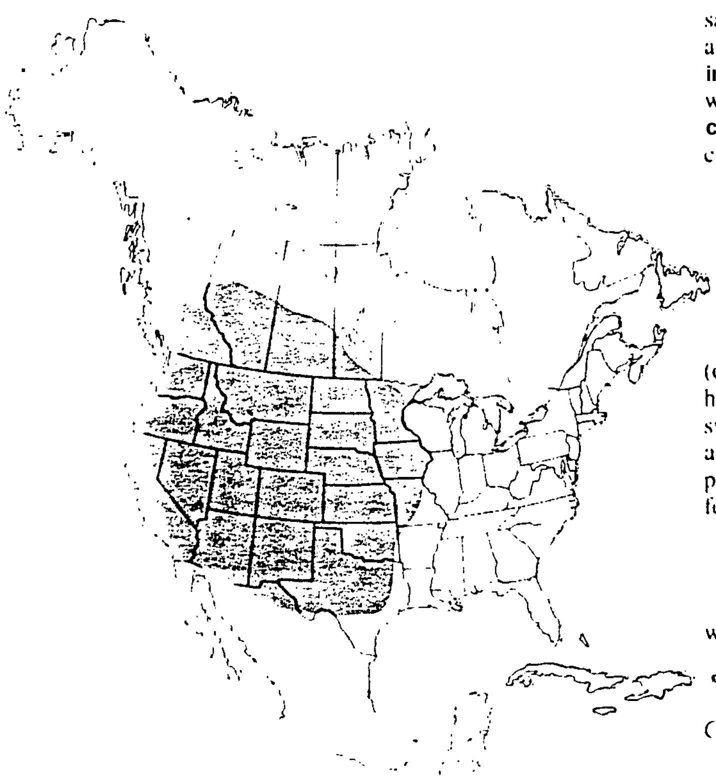
The Packard grasshopper feeds on both forbs and grasses. Examinations of crop contents of grasshoppers collected from the mixedgrass and shortgrass prairies indicate that the scurfpeas, *Psoralea tenuiflora* and *P. esculenta*, are fed upon preferentially. Although the contents of the majority of crops consist of more than one species of plant, a sizeable number consist of only fragments of scurfpea. Several other legumes that grow in the mixedgrass prairie serve as host plants including Missouri milkvetch, woolly milkvetch, and peavine (*Lathyrus polymorphus*). When available in improved grassland, sweetclover and smooth brome serve as preferred host plants.

A total of seven grasses and 26 forbs have been recorded from crops of Packard grasshoppers collected from the shortgrass and mixedgrass prairies. The average consumption of forbs from both mixedgrass and shortgrass prairies equaled 85 percent, while grasses equaled 7 and 13 percent, respectively. Among seven grasses found in crop contents, blue grama, sand dropseed, and needleandthread were present in greatest amounts. The Packard grasshopper also fed on ground litter including dead arthropods. In ruderal habitats a variety of weeds serve as host plants including brome grasses, sweetclover, wild lettuce, western ragweed, and sunflower. In cropland this grasshopper has fed upon winter wheat, barley, fall rye, and alfalfa.

Several direct observations have been made of feeding. On July 11, 1990 at 10 a.m. DST one female was seen crawling on the ground, then stopping to feed a few seconds on plant litter. She then moved to a small peavine plant and reached up her full length to feed on a leaflet. In a roadside habitat, a mule (oriented vertical head up) and a female (oriented vertical head down) were observed feeding on the petals of yellow sweetclover. A female on the ground was observed to feed on a dead darkling beetle. In a study area of the mixedgrass prairie, two females on the ground surface were observed feeding on an unidentified small lichen growing among moss.

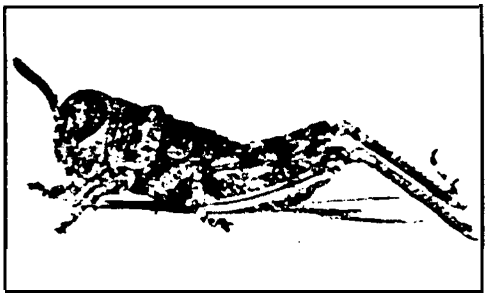
Dispersal and Migration

The Packard grasshopper is a strong flier possessing long wings. In Colorado where the species is regularly resident up



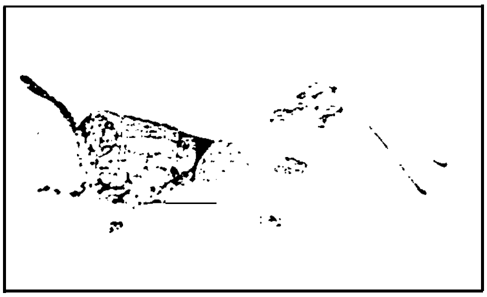
Geographic range of *Melanoplus packardii* Scudder

Instar 1



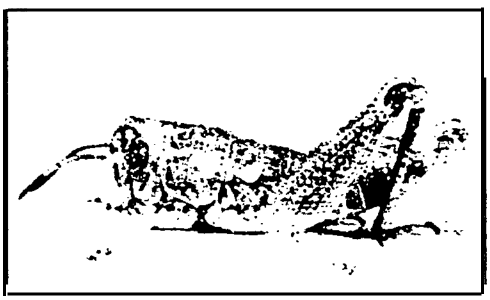
1. BL 4.6-5.6 mm FL 2.7-3.1 mm AS 13.

Instar 2



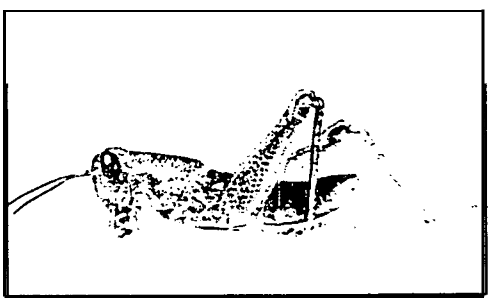
2. BL 5.1-7.3 mm FL 3.4-4.1 mm AS 17-18.

Instar 3



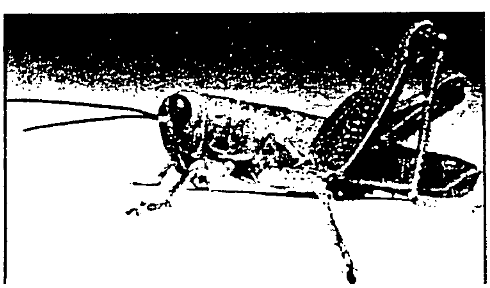
3. BL 7.9-10 mm FL 5.6-6 mm AS 19-21.

Instar 4



4. BL 14-18.7 mm FL 8.2-10.2 mm AS 22-24.

Instar 5



5. BL 19-25.7 mm FL 10.8-13.5 mm AS 24-26.

Figures 1-5. Appearance of five nymphal instars of *Melanoplus packardii* — their sizes, structures, and color patterns. Notice progressive development of the wing pads. BL = body length, FL = hind femur length, AS = antennal segments number.

to 8,500 feet, "accidentals" have been found at altitudes in excess of 11,000 feet, evidently dispersing a minimum of 10 miles in one season. Further evidence for dispersal consists of the discovery of five males and eight females on the ice of Grasshopper Glacier in the Crazy Mountains of Montana. These may have originated in a mountain meadow about one mile below the glacier where a resident population lived at an altitude of approximately 9,000 feet. But it is also possible that they originated from a distant area along with *M. sanguinipes* and *Aulocara elliotti*, which were also present on the glacier.

Identification

Of the three size divisions of grasshoppers, the Packard grasshopper is in the large category. It is, however, smaller than the two largest species of *Melanoplus*, the twostriped grasshopper and the differential grasshopper. The adults have bright color patterns of tan, brown, and yellow (Fig. 6 and 7). Two conspicuous light tan lines run down the occiput of the head and disk of the pronotum (Fig. 8). Wings are long, reaching to at least the end of the abdomen and extending as much as 6 mm beyond. The hind tibiae are red or blue. The male possesses diagnostic characteristics of the species: the cerci are spatulate (Fig. 9) and the lobes of the aedeagus project nearly equally (Fig. 11). This species cannot be separated with certainty from *M. foedus* without exposing the aedeagus, accomplished by lifting and moving the pallium back. The supraanal plate narrows gradually to the pointed end. In a collection of grasshoppers one may identify the females by associating them with the males using size, markings, and color. The nymphs are identifiable by their structures, color patterns, and shape (Fig. 1-5).

1. Head with face nearly vertical; color of head in instars I and II greenish tan, instars III to V green; heads of all instars sparsely spotted brown; compound eye fuscous with many light spots; antennae filiform and fuscous, each segment ringed anteriorly pale yellow.
2. Pronotum with lateral lobes greenish tan in instar I, greenish tan or green in instar II, green in instars III to V; lateral lobes with few to many brown spots in all instars; disk of pronotum somewhat darker than the lobes and spots more dense.
3. Outer medial area of hind femur with three to four rows of spots, first row of spots (below upper carinula) separate, not coalescing into lines. Hind tibia pale gray in instar I, pale green in instar II, green in instars III to V; tibia with fuscous front edge in all instars.
4. General color: instar I greenish tan, instar II green or greenish tan, instars III to V green.

Hatching

The Packard grasshopper is an early hatching species. First instars appear in the mixedgrass prairie at the same time as those of the bigheaded grasshopper, *A. elliotti*. Although eggs of the Packard grasshopper lie deeper in the soil than eggs of the bigheaded grasshopper and receive less heat in spring, they hatch

Figures 6-10. Appearance of the adult male and female of *Melanoplus packardii*, dorsal view of head and pronotum, end of male abdomen, and egg pod and eggs.

at the same time due to their advanced development in fall. In nature, diapause of eggs is broken during winter and only a few days of warm ground temperatures are required for an embryo to reach the final embryonic stage 27, which then must wait for hatching thresholds of temperature and moisture.

In the mixedgrass prairie of eastern Montana and Wyoming, eggs of the Packard grasshopper hatch from May to early June depending on seasonal weather. In different years first instars may appear as early as May 1 or as late as May 30.

Nymphal Development

Nymphs develop at nearly the same rate as the bigheaded grasshopper. Based on dates of first appearance of nymphs and adults in the mixedgrass prairie, the nymphal period of the Packard grasshopper ranges from 47 to 63 days. Both males and females develop through five instars to become adults. Rearing nymphs in the laboratory at constant temperatures has shown that the Packard grasshopper completes the nymphal period in 47 days at 77°F and in 70 days at 70°F.

Adults and Reproduction

Although emigration of some adults may occur, the majority remain in the same habitat in which the nymphs develop. In the mixedgrass prairie of Colorado, Wyoming, and Montana, both male and female adults begin to appear in early July. Only a few observations have been made of maturation and reproduction of this species. In a study site of the mixedgrass prairie in eastern Wyoming the first adults of both sexes were seen 11 July 1990. Courting by a male was observed on 30 July 1990, approximately 20 days after adults began to emerge. The first observation of oviposition was made 16 August 1990, 36 days after adults began to emerge; however, examination of ovaries indicates a maturation period of 21 days.

Longevity of adults is relatively long, as decline of densities in summer are almost imperceptible. An average adult longevity of 50 days has been estimated from sampling populations in the mixedgrass prairie. A large part of the adult population of the Packard grasshopper lives through the months of August and September.

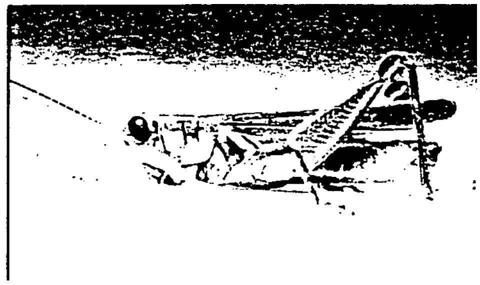
Females oviposit in bare ground and lay a clutch of 16 to 29 eggs. Laboratory rearing of adult Packard grasshoppers resulted in an average fecundity of 153 eggs per female at 33°C and 94 eggs at 27°C; the average numbers of pods was 7.7 and 4.8 per female, respectively.

The pod is slightly curved and 1 1/8 inches long and 3/16 inch in diameter (Fig. 10). The eggs lie in the bottom 3/4 inch; froth occupies the top part of the pod. Eggs are tan and 4.7 to 5.1 mm long.

Population Ecology

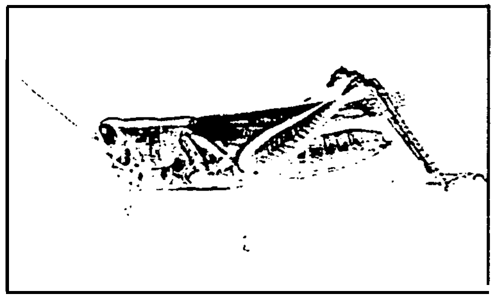
Small numbers of the Packard grasshopper commonly inhabit grasslands of the West. Densities usually range from less than 0.1 to 0.4 per square yard. Sampling in the mixedgrass prairie of eastern Wyoming indicates that although the species is one of the least abundant members of the rangeland grasshopper assemblage, it persists from year to year at low densities and does

Male



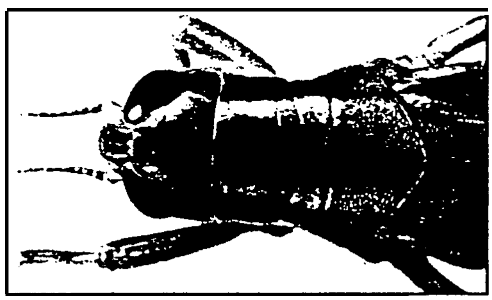
6. BL 27-32 mm FL 13.8-15.5 mm AS 25-27.

Female



7. BL 32-35.5 mm FL 15.5-18 mm AS 25-27.

Dorsum



8. Dorsal view of head and pronotum of a female.

Cercus

9. End of male abdomen showing cercus and supraanal and subgenital plates.

Egg Pod

10. Egg pod and exposed eggs in bottom of broken pod.

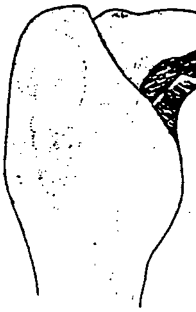


Figure 11. Shape of male aedeagus, view of left side. Drawing by Arthur R. Brooks.

not track the fluctuations of the dominant species or that of the assemblage (Table 1). However, the Packard grasshopper's abundance in Alberta and Saskatchewan and its residency in meadows of the Rocky Mountains at relatively high altitudes indicate a center of distribution for the species in the colder regions of its geographic range. A summary of relative densities from 1928-44 in a mixedgrass prairie of southeastern Alberta show that populations fluctuate and that in certain years the species may occur in outbreak numbers, but no absolute densities are available for these populations.

A Montana study ascertained that the Packard grasshopper occupied nine of 3X sites in the mixedgrass prairie and in one site, consisting of 19 species wilh 3 density of IO grasshoppers per square yard, it was second in abundance io *M. infantilis*. The same study found the Packard grasshopper occupied eight of I I abandoned fields. In one of the sites the Packard grasshopper was the dominant species at approximately live per square yard.

In ruderal habitats and cropland the Packard grasshopper may be a serious pest. The ecological changes brought about hy crop agriculture have created ideal habitats for no less than six species of grasshoppers including the Packard grasshopper. Crop damaging outbreaks in Alberta and Saskatchewan have often consisted of three species: the Packard grasshopper, the migratory grasshopper *M. sanguinipes*, and the twostriped grasshopper *M. bivittatus*. In certain localities the Packard grasshopper becomes the dominant species, hut more often the migratory grasshopper is dominant, the twostriped is second, and the Packard is third. Factors that appear io have made ruderal tracts more favorable for these species include the formation of better egg-laying sites of drift soil and south-facing slopes, and the introduction of succulent weeds and cereal crops that serve as reliable, abundant, and nutritious sources of food. Estimates based on relative densities indicate that the Packard grasshopper may increase to six adults per square yard in weedy roadsides.

Daily Activity

In its natural habitat in the mixedgrass pmiric, the Packard grasshopper spends most of its time on the ground. Nights are passed resting horizontally on the ground surface on bare soil or litter. Early in the morning before the sun has risen, late instar nymphs and adults may sil under canopies of grasses or close io vegetation. A few individuals rest vertically, head up, on stems ofslimtlowcr scurfpea and silver sagebrush at heights of 8 to 12 inches.

As soon as the rays of the sun strike their resting places, the grasshoppers orient a side perpendicular io the rays and may tilt in the direction of the sun and lower a hind leg io expose more of the abdomen. Individuals that have spent the night on vegetation turn their back or a side io the sun. After basking for two to three hours (soil surface temperatures usually have risen io XO'F and air temperatures io 70°F), the grasshoppers become active. A few adults may become active sooner in courting and mating activities.

When temperatures become too hot, soil above 120°F and air above 00°F, grasshoppers cease activities and take evasive actions. They climb vegetation and rest vertically, head up, 2-10 inches high. They may spread their flexed hind legs and hold onto a grass stem or leaves with their fore and mid legs. There has been one observation of basking in the evening at 4:55 p.m. DST in which an adult male and female resting on the ground turned their sides perpendicular io the rays of the sun.

Table I. Population fluctuations of grasshoppers in a mixedgrass pmiric site of eastern Wyoming (Platte County). P = present but not found in 200 t-square foot samples.

	Number per square yard						
	1968	1969	1970	1971	1972	1973	1974
Melanoplus packardii	0.1	0.1	0.1	0.1	0.3	P	0.2
Ageneotettix deorum	3.4	2.2	0.8	1.2	0.8	1.3	3.3
Assemblage of 19 species	12.8	6.1	2.9	5.6	4.0	3.3	10.5

Selected References

Anderson, N. L., 1973. The vegetation of rangeland sites associated with some grasshopper studies in Montana. Montana Agr. Exp. Stn. Bull. 668.

Hardman, J. M. and S. Smoliak. 1980. Potential economic impact of rangeland grasshoppers (Acrididae) in southeastern Alberta. Can. Entomol. 112: 177-1x-l.

Hewitt, G. B. 1985. Review of factors affecting fecundity, oviposition, and egg survival of grasshoppers in North America. USDA ARS-36.

Lockwood, J. A., J. C. Burne, L. D. DeBrey, K. A. Nunamaker and R. E. Pfadt. 1990. The preserved fauna cd grasshopper glacier (Crazy Mountains, Montana): Unique insights to Acridid biology. Boletin de Sanidad Vegetal 20: 223-236.

Riegert, P. W. 1968. A history of grasshopper abundance surveys and forecasts in Saskatchewan. Memoirs Entomol. Soc. Can. No. 52.

Salt, R. W. 1949. A key to the embryological development of *Melanoplus bivittatus* (Say), *M. mexicanus mexicanus* (Sauss.), and *M. packardii* Scudder. Can. J. Res. (D) 27: 233-235.

Shotwell, R. L. 1941. Life histories and habits of some grasshoppers of economic importance on the Great Plains. USDA Tech. Bull. 774.

Migratory Grasshopper

Melanoplus sanguinipes (Fabricius)

Distribution and Habitat

The migratory grasshopper, *Melanoplus sanguinipes* (Fabricius) is widely distributed in North America arid lives in a multitude of habitats. It is a common inhabitant of grasslands, meadows, and fields of small grains and alfalfa. Host plants include many kinds of forbs and grasses. Depending on availability of plant species, it may be either a mixed herbivorous or a forbivorous feeder.

Food Habits

Examinations of gut contents show that the migratory grasshopper is usually feeding on several species of plants in its habitat. This behavior is important in its ecology because laboratory studies have demonstrated that a mixed diet affords individual grasshoppers better nutrition. Although polyphagous the migratory grasshopper selects host plants from its habitat. Preferred foods include dandelion, tumbling hedgemustard, charlock mustard. pepperweed, western ragweed, cheatgrass brome, Kentucky bluegrass, barley, and wheat. Nymphs and adults ingest dry materials lying on the ground surface including plant litter, cattle manure, and bran flakes.

Capacity for Increase

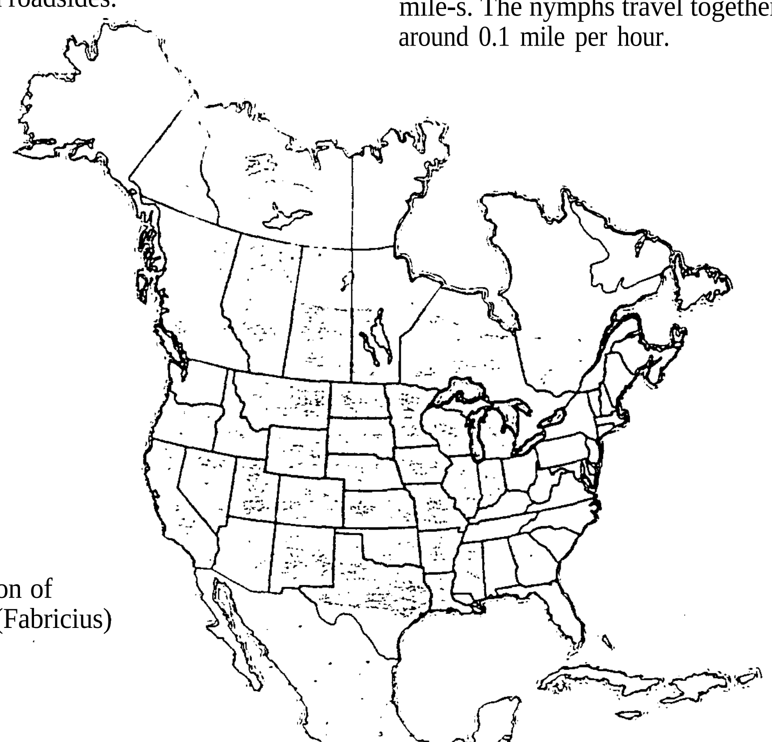
The migratory grasshopper has a great capacity for increase. Large populations develop in disturbed or cultivated land, e.g., overgrazed rangeland, crops of small grains, reverted fields and roadsides.

In a favorable year, a noneconomic population of three adults per square yard can reproduce so that in the next year the population may reach an outbreak density of 30 adults per square yard. Over a period of several favorable years, densities may reach enormous numbers. In 1938 in northeastern South Dakota, densities of the migratory grasshopper reached as high as 1,500 to 8,000 nymphs per square yard in cropland. idle land, and depleted rangeland. Restraints of weather and enemies (predators, parasites, and diseases) usually keep populations from increasing to such a high degree. Densities arc normally between 0 and 9 nymphs or 0 and 3 adults per square yard.

Migration

The migratory grasshopper, as the common name implies, is a migratory species. Many accounts of adult swarming have been published, although there are few records of nymphal migration and still fewer accounts of adult migration in the absence of mass swarming. Recent research has revealed that migratory behavior is inherent and regularly displayed. Much variability occurs, however, among different populations. The greatest degree of migration has been found in populations inhabiting areas where resources are patchy and unpredictable, as in Arizona and New Mexico. The least degree of migratory behavior was detected in a population inhabiting a relatively lush and stable environment in Colorado.

The older nymphs, third to sixth instars, may migrate as far as 10 miles but usually the distance is less than five mile-s. The nymphs travel together in a band at rates of around 0.1 mile per hour.



Know? general distribution of *Melanoplus sanguinipes* (Fabricius) in North America.

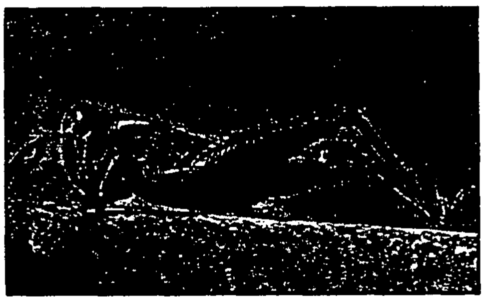
Instar 1

1. Body length 4-6 mm. Antennal segments 12-13.

Instar 2

2. Body length 6-8 mm. Antennal segments 16-17.

Instar 3

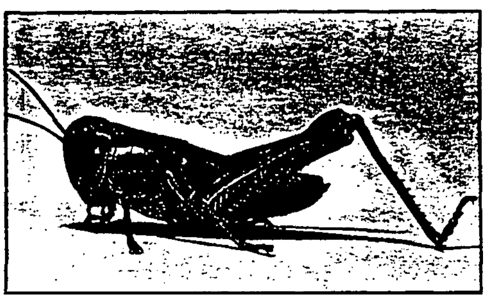


3. Body length 8-11 mm. Antennal segments 18-20.

Instar 4

4. Body length 11-16 mm. Antennal segments 21-22.

Instar 5



5. Body length 14-23 mm. Antennal segments 22-24.

Figures 1-5. Appearance of the five nymphal instars of *M. sanguinipes*—their sizes, structures, and color patterns. Notice progressive development of the wing pads and the black spot at the base of metathoracic wing pad, especially evident in picture of second instar.

Adults are highly migratory in their prereproductive stage. Swarming occurs on clear days when temperatures approach 80 F and winds are gentle and intermittent. Migrants take off into the wind and then turn around and fly with the wind at speeds of 10 to 12 miles per hour. They usually begin flight in late morning. fly during the middle of the day, and alight in the afternoon to feed and rest. With favorable conditions the following morning they continue their migration. From trials of marked adults, individuals are known to travel 30 miles in a day and probably fly much farther. In 1938 one record of migration indicates a swarm averaged 66 miles per day for four days, flying from Highmore, South Dakota to Beach. North Dakota, a distance of 265 miles. The longest migrations recorded in 1938 were made by swarms that travelled from northeastern South Dakota to the southwestern comer of Saskatchewan, a distance of 575 miles.

Flights of the migratory grasshopper have been classified as low flights which are 25 feet or less above the ground or high flights, more than 25 feet above ground. The high flights occur at various elevations. Pilots of observation aircraft in the grasshopper control program often encounter swarms flying 1.000 feet above ground and pilots of ferrying aircraft encounter swarms 2,000-3,000 feet above ground. Pilots of commercial aircraft have reported encountering swarms at all elevations up to 13,000 feet above sea level.

Swarms in the sky can be observed by cupping a hand over the eye and looking toward the sun. The flying grasshoppers reflect the sun's rays and this shimmer of light can be seen at great distances.

Identification

The migratory grasshopper, *Melanoplus sanguinipes* (Fabricius), is a medium sized representative of this large genus.

The nymphs (Fig. 1-5) are identifiable by their spots and color patterns:

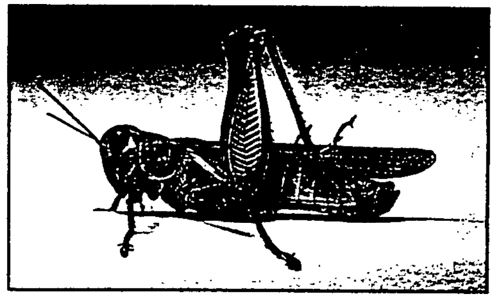
(1) Compound eye with many light spots, narrow brown bar across middle.

(2) Narrow pale yellow crescent on gena below eye and continuing on pronotal lobe to principal' sulcus.

(3) Metathoracic wing pad with black spot near base.

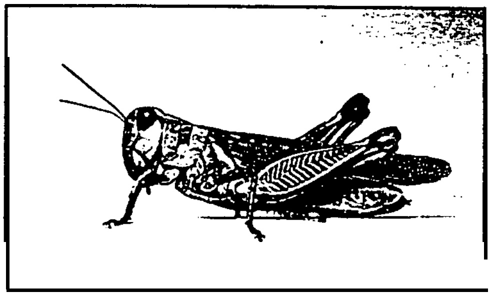
Figures 6-9. Appearance of the adult male and female of *M. sanguinipes* and two diagnostic characters of the male—the shape of cercus (Fig. 8) and the notch in the apex of the subgenital plate (Fig. 9). Notice the two different color forms of hind tibia-red and pale blue.

Male



6. Body length 16-26 mm.

Female

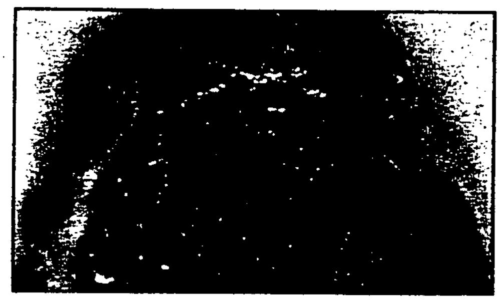


7. Body length 20-29 mm.

Note Cercus

8. Side view end of male abdomen.

Note Notch



9. End view of male abdomen.

(4) Hind femur with dorsal black stripe cut in middle by light bar: light bar on each end.

(5) Hind tibia of first instar fuscous with pale basal ring; hind tibia of other instars pale blue green or reddish without pale ring.

(6) General color of majority tan or gray, few light green.

Adult males (Fig. 6) are easily identified by the shape of the cercus (Fig. 8) and the notch of the subgenital plate (Fig. 9). The females (Fig. 7) are slightly larger than the males and can be associated with them and distinguished by their similar color patterns. Hind tibia blue green or red.

Hatching

The migratory grasshopper is an early hatching species appearing on rangeland about one week after the bighcaded grasshopper begins to hatch. Several environmental factors, especially soil temperature and moisture, affect the exact timing and duration of this event. Hatching starts first along open south slopes, in fields and rangeland with little vegetative cover, and in sandy soils. Hatching is retarded by heavy clay loam soils and by tall vegetation that shades the ground. In any one year, a mosaic of these conditions in an area as well as below normal temperatures may extend the hatching period to six weeks. The duration of hatching is shortened by uniform soil and vegetation and high temperatures and may be completed in three weeks. For complete embryonic development the eggs require 527 day-degrees above a threshold of 50 F soil temperature. Under favorable conditions 80% of development occurs during the summer that the eggs are laid and 20% the following spring.

Nymphal Development

Nymphs develop and grow during late spring when weather is usually warm and food plants are green and abundant. Under these favorable conditions the young grasshoppers pass through the nymphal stage in 35 days. Cool weather, however, may lengthen the nymphal stage to 55 days. Nymphal instars range from five to six. The females usually require the larger number.

Adults and Reproduction

Emergence of adults begins the first part of summer and may continue for three or four weeks. The first adults to emerge have the best chance for reproductive success. At this time there is more likely to be an abundance of grccn food plants to providc thc nourishmcnt ncccssary for rapid cgg production. In addition thc first cggs laid will usually cxpericncc morc favorablc soil moisturc and havc a longcr timc to rcach an advanccd dcvelopmcntal stagc bcforc cntcring diapausc.

Thc fcmalcs havc a prcovipsition pcriod of two to thrcc wccks. During this timc thcy incrcasc in wcight and maturc thcir first group of 18 to 24 cggs. Thc malc is ablc to rccognizc a maturc, virgin fcmalc and pcrforms a short courtship in which hc wavcs his antcnnac and vibratcs his hind fcmora bcforc hc makcs a suddcn copulatory lcap onto thc fcmale. A mated fcmalc oviposits around six days latcr and takcs nearly an hour to pcrform this act. Hcalthy adults copulatc many timcs during thc rcproductivc pcriod.

The fcmalcs dcposit thcir cggs on rangeland among thc roots of blue grama grass. In cropland they oftcn dcposit thcm around thc base of whcat stubblc or alfalfa. Pods are slightly curved, onc inch long and one-eighth inch in diameter. They are positioned somcwhat vertically in the soil. The top half of the pod is dricd froth, the bouom half contains thc cggs. Thc midpoint of thc clutch is thrcc-fourths inch bclow thc soil surface. Eggs havc a banana-like shape, arc 4.5 mm long, and palc ycllow or cream colorcd. A long-lived fcmalc may produce as many as 20 pods and a total of 400 cggs. Thc avcragc fccundity in naturc is unknown, but may not bc morc than 20 cggs.

Daily Activity

The migratory grasshoppcr, a diurnal insect, is ordinarily active during the day and inactive at night. Thc activitics of both nymphs and adults are largely controllcd by tcmpcrature. Most fccding occurs bctwccn 8 and 11 a.m.; most mating bctwccn 8:30 a.m. and 12 noon; and oviposition through thc day. When tcmpcratures drop in the evening the grasshoppcrs form aggregations on the ground and may even scck protection from the cold. They remain inactive at night and only start activity the next morning whcn temperatures rise. J. R. Parker categorized their activities and corrclatcd thcse with air and soil tcmpcraturcs (Table 1).

Table 1. Activity of nymphs and adults of the migratory grasshopper, *Melanoplus sanguinipes* (Fabricius) corrclatcd with air and soil temperatures (After Parker 1930).

Name of activity	Description	Average temperature °F Nymphs Air	Nymphs Soil	Adults Air	Adults Soil
Beginning of activity	Basking, exposure to sun	61	75	62	79
Beginning of normal activity	Feeding	64	92	66	94
	Starting migration	71	94	84	112
	Starting oviposition			71	100
Beginning of climbing to escape heat	Climbing vegetation			81	113
Bcginning of clustering	Aggregating on ground	69	87	71	88
Ending of activity	Ceasing to move or hiding	66	77	69	79

Selected References

Kcmp, W. P. and N. E. Sanchcz. 1987. Diffcrcnccs in post-diapausc thcrmal rcquircmcnts for cggs of two rangcland grasshoppers. Can. Entomol. 119: 653-661.

MC Anclly, M. L. and M. A. Rankin. 1986. Migration in thc grasshoppcr *Melanoplus sanguinipes* (Fab.). Biol. Bull. 170: 368-392.

Parker, J. R., R. C. Newton, and R. L. Shotwcll. 1955. Obscrvations on mass flights and othcr activities of thc migratory grasshoppcr. USDA Tcch. Bull. 1109.

Pfadt, R. E., J. A. Lockwood, and T. M. Foppe. 1988. Dicts of three common grasshoppcrs (Orthoptera: Acrididae) inhabiting dcscrt grassland. Can. Entomol. 120: 415-424.

Pfadt, R. E. and D. S. Smith. 1972. Nct rcproductivc ratc and capacity for incrcase of thc migratory grasshopper, *Melanoplus sanguinipcs sanguinipes* (F.). Acrida 1: 149-165.

Pickford, R. and C. Gillott. Courtship behavior of the migratory grasshoppcr, *Melanoplus sanguinipes* (Orthoptera: Acrididac). Can. Entomol. 104: 715-722.

Shotwcll. R. L. 1930. A study of the lcsscr migratory grasshoppcr. USDA Tech. Bull. 190.

Valley Grasshopper

Oedaleonotus enigma (Scudder)

Distribution and Habitat

The valley grasshopper is a Great Basin rangeland species, inhabiting the sagebrush-grass associations of this western region. Native host plants include springparsley. balsamroot. big sagebrush. and rabbitbrush. The valley grasshopper has found several introduced weeds to its liking: redstem filaree. tansymustard, and cheatgrass brome. The increase in number of favorable food plants appears io be an important factor in outbreaks of the species due to better nutrition. Abandoned farmland and Conservation Reserve Program (CRP) land are especially favorable sites for development of large populations.

Economic Importance

High densities of the valley gmsshopper on rangeland cause severe injury to forage plants. These grasshoppers are particularly damaging to young grasses and legumes in newly reseeded rangeland. The species has a high reproductive capacity. Density of adults may reach 20 per square yard and higher. Nymphs and adults in outbreak populations often migrate into alfalfa. gnins. spearmint. and vegetable seed crops, causing serious damage. The valley grasshopper may be beneficial at low densities as it prefers weeds for food. thereby thinning and reducing these strong competitors of valuable forage plants. No quantitative study. however, of damage or benefits of this grasshopper has been made.

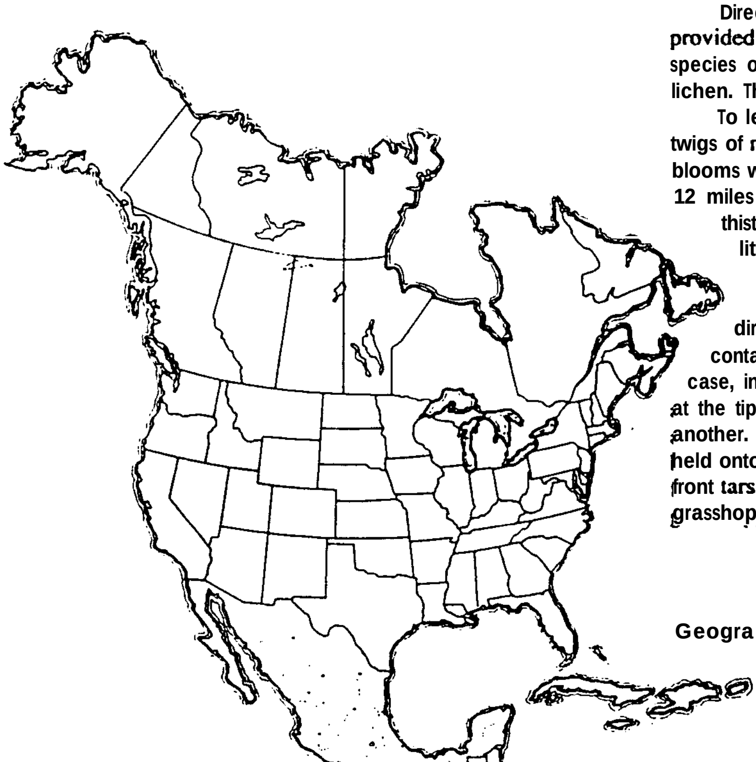
The sizes attained by adults from one population to another are highly variable and are probably due to variations in environmental factors among habitats. such as temperature and quality and supply of food. Weights of adults collected in a drought-stricken habitat 12 miles south of Mountain Home. Idaho, and then caged and fed cheatgrass brome for I I days averaged 365 mg for live males and 530 mg for live females (dry weight: males I 10 mg, females 165 mg).

Food Habits

The valley grasshopper is primarily a forb and shrub feeder, but it also feeds to some extent on grasses. It has been observed to feed heavily on introduced weeds that often grow abundantly in its habitat. These include redstem filaree, tumbkmustard. draba mustard. pepperweed, and cheatgrass brome. It likewise feeds heavily on lichen. In summer. when annual weeds have matured and dried, big sagebrush becomes an important host plant. In abandoned fields and CRP fields where big sagebrush no longer occurs. Russianthistle is often the only green plant available to the valley grasshopper in mid-summer. It does not feed upon this plant. but it does use it for roosting. Adult grasshoppers have been observed nibbling on the leaves of Russianthistle but never found to ingest any substantial amount of the plant. This may indicate that other members of the goosefoot family. including the sugarbeet, are essentially immune to attack. Under drought conditions the grasshoppers resort to feeding on ground litter and dead or dying grasshoppers, and they will skirmish over an appk core thrown on the ground.

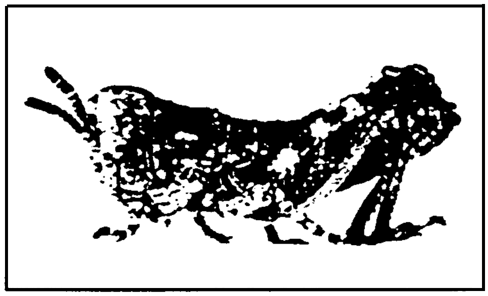
Direct observations and examination of crop contents have provided records of the valley grasshopper feeding on seven species of forbs. four shrubs, two grasses. one sedge, and one lichen. This list of food plants is undoubtedly incomplete.

To learn how the valley grasshopper attacks food plants. twigs of miniature rose (variety Meiponal) bearing leaves and blooms were transplanted 2 August I99 I in an abandoned field 12 miles south of Mountain Home. Idaho. Except for Russianthistle. the field contained only dry vegetation and ground litter. Shortly after king transplanted in the morning, the rose began to attract the adult grasshoppers. Some grasshoppers jumped onto the stem before making direct contact. while others kept crawling until making contact and then began to feed on lower leaves. In either case, individuals fed on the leaf edge beginning at the base or at the tip and often consumed the entire leaf before attacking another. A feeding grasshopper either stood on the ground or held onto the plant with the midlegs and hindlegs and used the front tarsi to hold the leaf and direct it to the mouthparts. Some grasshoppers cut through the petiole of leaves. which fell to the



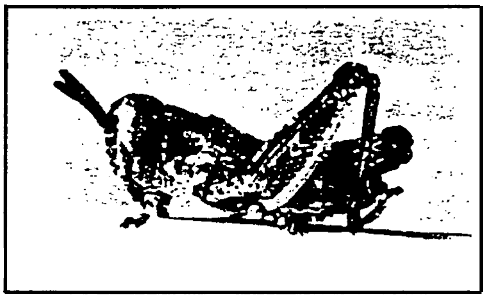
Geographic range of *Oedaleonotus enigma* (Scudder)

Instar 1



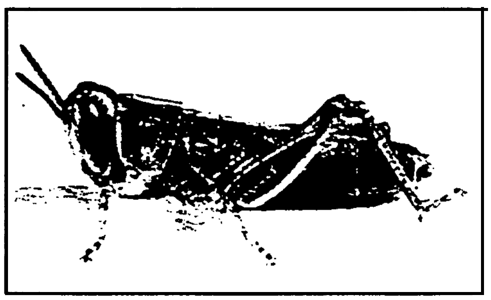
1. BL 4-4.8 mm. FL 2.4-2.7 mm. AS 13.

Instar 2



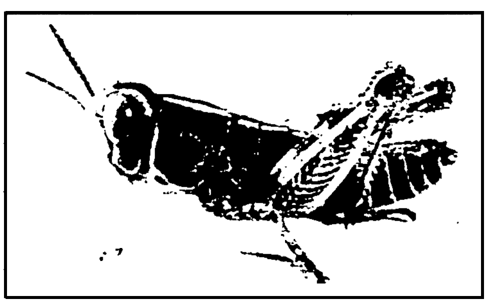
2. BL 4.9 mm. FL 3.2-3.3 mm. AS 17.

Instar 3



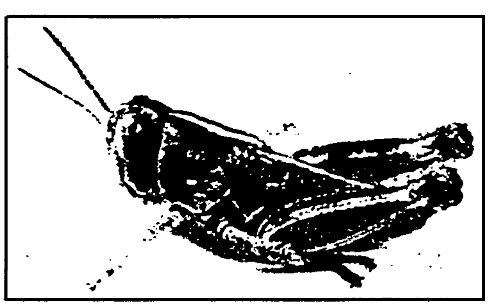
3. BL 7.7-8.9 mm. FL 4.4-4.9 mm. AS 18-19.

Instar 4



4. BL 8.3-10.5 mm. FL 6.1-6.5 mm. AS 20.

Instar 5



5. BL 12-15.5 mm. FL 8.6-9.3 mm. AS 22-24.

Figures 1-6. Appearance of the six nymphal instars of *Oedaleonotus enigma* – their sizes, structures, and color pat terns. Notice progressive development of the wing pads. B body length, FL = hind femur length, AS = antennal segmer number.

ground. Fallen leaves were eaten by grasshoppers still crawling on the ground. The grasshoppers also fed on the bracts and petals of flowers.

Valley grasshoppers were also offered transplanted spearmint. They fed on this plant in essentially the same way as on rose. They were observed to walk to the mint and then began to feed on the edge of the leaf down to mid rib and beyond. They also climbed the plant and then began to feed. Grasshoppers on the rose and mint assumed various orientations suited to their feeding on the edges of leaves. At times they fed on the centers of leaves by folding them.

Dispersal and Migration

Slow dispersal of older nymphs and adults occurs almost daily. During an outbreak nymphs tend to migrate in concentrated bands of 20 to 30 per square yard. The grasshoppers may move in one direction while following or entering a draw with greener vegetation or they may spread out in all directions. Populations are known to move from abandoned fields and rangeland into irrigated crops.

Long-winged adults may disperse by flight. They are able to fly from deteriorating habitats into more favorable areas. Evidence for such flights comes from a drought-stricken habitat 12 miles south of Mountain Home, Idaho. On 24 June 1991 a dense population of young adults consisted of 54 percent macropterous and 46 percent brachypterous individuals. Sixteen days later the population had significantly decreased in density and consisted of only 18 percent macropterous and 82 percent brachypterous, indicating emigration out of the area by a majority of the long-winged adults.

Evasive flights of adults are straight, silent, and range from 4 to 8 feet in distance and 4 to 10 inches in height. On landing they face directly or diagonally away from the intruder. Brachypterous adults evade an intruder by jumping distances of 2 to 8 feet. The larger, stronger individuals jump farther than the smaller grasshoppers.

In spite of its importance to integrated pest management of destructive populations, no special study of the dispersal and migration of the valley grasshopper has been made. We do not know the length nor height of flights, nor whether macropterous adults leave their original habitat individually, in groups, or en masse.

Identification

The adult valley grasshopper is a medium-sized, colorful, spurthroated grasshopper (Fig. 7 and 8). The tegmina range from short to long. Short tegmina are as long or longer than the pronotum. Seven other species of the genus *Oedaleonotus* can be distinguished by their possession of tegmina shorter than the pronotum, and the tegmina are usually narrow and widely separated. These seven species are distributed mainly in California.

Valley grasshoppers with long tegmina also have long hindwings that are functional organs of flight. Adults with short tegmina have even shorter, nonfunctional hindwings.

Figures 7-10. Appearance of the adult male and female, the male cercus, and the egg pod and eggs.

The anterior edge of the pronotum has a narrow, conspicuously white to cream-colored band, giving this grasshopper the appearance of wearing a clergyman's collar.

The medial area of the hind femur is marked with fuscous chevrons separated by light tan lines. The proximal end of the inner medial area and the lower marginal area are colored orange. The hind tibiae are blue. The cercus of the male is broad basally with apex abruptly narrowed and fingerlike (Fig. 9).

Nymphs are identifiable by their color patterns, structures, and shape (Fig. 1-6).

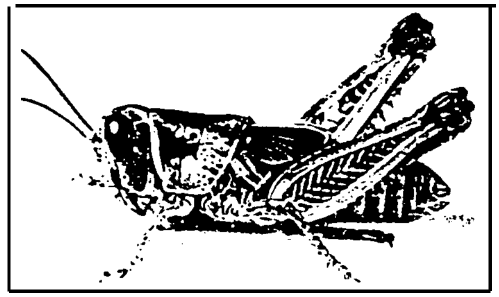
1. Head. Face slightly slanting, vertex and occiput with fuscous band down middle divided by narrow cream-colored line. Antennae filiform, first two segments pale tan or yellow with several darker spots, remainder of segments fuscous, each with narrow light ring on anterior edge. Compound eye with many cream-colored spots in brown reticulum, relatively large dark spot near center.
2. Thorax. Disk of pronotum dark brown with longitudinal cream-colored, narrow, fusiform band down middle. The entire dorsal light band begins on head and extends onto abdomen becoming faint posteriorly.
3. Hindleg. Medial area of hind femur with fuscous chevrons that are broken in middle at proximal half; hind tibia light gray with fuscous maculations.
4. General color light tan with fuscous spots and maculations. Shape is robust, pronotum widens posteriorly, matching wide meso- and metathorax.

Hatching

Overwintering as eggs in an advanced embryonic stage, valley grasshoppers hatch early in spring. Hatching may start in early April in Nevada and Idaho and continue for a month or longer. Hatching usually occurs in the morning when air temperatures are between 45° and 90°F and soil temperatures are between 76° and 98°F.

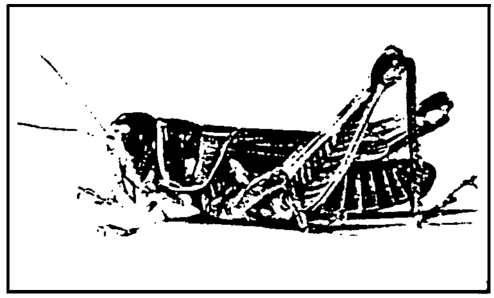
Nymphal Development

Upon hatching in early spring the nymphs usually have a plentiful supply of food, but because of cool weather during this time of year they develop slowly, becoming adults in about 42 to 50 days. Compared with later-hatching species, the valley grasshopper has a long nymphal period, due to both the cooler temperatures and to the greater number of nymphal instars, six instead of the usual five. The proportion of males to females is nearly 1 : 1. In different years, the proportion of short-winged adults to long-winged adults ranges from all short-winged to over 50 percent long-winged. Laboratory tests indicate that temperature may be one factor that influences this proportion. Cooler developmental temperatures (constant 80°F) result in greater proportions of long-winged adults, while warmer temperatures (constant 100°F) result in more short-winged adults.



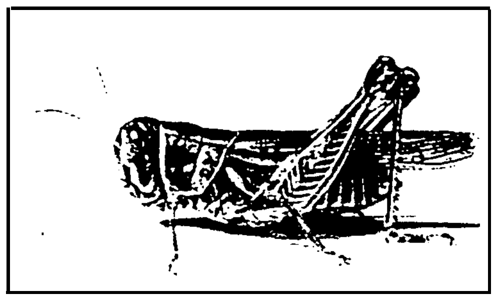
Instar 6

6. BL 15-21.5 mm. FL 9.5-11.7 mm. AS 23-25.



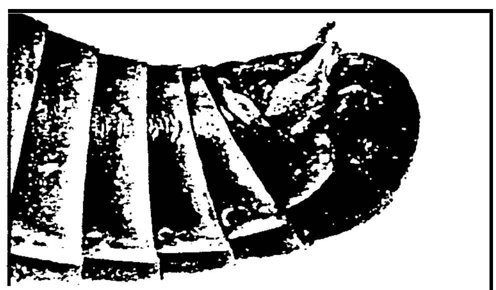
Male

7. BL 17.5-21.5 mm. FL 11-13.5 mm. AS 24-26.



Female

8. BL 19-24 mm. FL 11-15 mm. AS 24-26.



Cercus

9. Side view end of male abdomen showing shape of cercus.

Egg pod

10. Egg pod and eggs.

Adults and Reproduction

Although many adult valley grasshoppers disperse from their nymphal habitats. variable numbers remain and reproduce. even in a deteriorating habitat. In a north-central Nevada site in 1954 when average temperatures were slightly above normal. the first adults appeared on 22 May, mating pairs were noted 20 days later. and egg deposition began two weeks after mating. Eggs bcpin development uponbeing laid in summer: by fall they reach an advanced developmental stage (after blastokinesis. stage 23). and then go into diapause. During winter the diapause is broken and warming weather in spring enables the eggs to complete embryonic development.

Females oviposit in bare ground near the base of big sagebrush or in the open. The pods. placed horizontally one-eighth to one-quarter inch below the soil surface. contain 16 to 22 eggs each. Anterior ends of the eggs face diagonally toward the soil surface. On hatching. the nymphs emerge from the side of the pod rather than through the end as is usually the case with other species of grasshoppers. The pods are slightly curved. short. and wide -one-half to five-eighths inch long and one-eighth to three-sixteenths inch diameter. Eggs are olive tan and 4.8 to 5.2 mm long (Fig. 10).

Population Ecology ,

The valley grasshopper has the capacity to increase to high numbers on rangeland and cause serious outbreaks. Densities may rise to over 20 adults per square yard. Outbreaks may be terminated by drought. At these times vegetation turns brown and desiccates. causing nutritional problems for the grasshoppers. Older instars and adults may disperse to survive in other areas with green host plants. Predation may also effectively end an outbreak. During June of 1954 three species of digger wasps (*Tachysphex*). which provision their offspring with nymphs of the valley grasshopper. reduced a population in south central Idaho from 25 per square yard to 3 per square yard. Large numbers of wasps emerged in June 1955 but they had virtually no grasshoppers on which to prey. Field studies indicate that the principal dipterous parasite is the tangleveined fly. *Neorhynchocephalus sackenii* (Williston); rate of parasitism during four years of study was variable. ranging from 0 to 24 percent.

Regrettably. no population has been studied for more than three years. a period too brief to gain useful information and insights into the population ecology of this grasshopper.

Important questions for integrated management remain unanswered – how long outbreaks last. how long populations remain at low densities. and how many years are required for populations to grow from low to high numbers.

Daily Activity

The behavior of adults inhabiting a drought-stricken abandoned field I2 miles south of Mountain Home, Idaho was observed for three days in August 199 I. Early food plants. tumblemustard and cheatgrass brome. had matured and dried and only Russianthistle remained green. Valley grasshoppers refused to eat this plant but regularly used it for roosting.

The majority of valley gmsshoppers spent the night roosting head-up on the main or secondary stems of Russianthistle plants, but a small number rested on the ground exposed or under a canopy of Russianthistle. At daybreak, before the sun had risen. the adults were quietly resting in different orientations. At this time (6 a.m. DST). surface soil temperatures ranged from 52" to 64°F and air temperatures I inch from the ground ranged from 52" to 62°F. An hour later the vertically roosting grasshoppers assumed a basking orientation by adjusting their position so that the sun's rays shone perpendicularly on their sides. They remained quietly basking on the Russianthistle plants for an hour, then began to climb down to the ground. head first. where they again basked by turning a side perpendicularly to the sun's rays and lowering the exposed hindleg to the ground. A few spread this hindleg to the side, exposing even more of the abdomen.

Regular activities of pottering. feeding, and mating began at 8:30 a.m. when surface soil temperatures had risen to 82°F and air temperature I inch above ground level to 67°F. The grasshoppers fed on ground litter and on dead or dying bigheaded grasshoppers, *Aulocara elliotti*. By 10:45 a.m. ground temperatures mse to 110°F. inducing grasshoppers to elevate their bodies off the soil surface by stilting (raising up on their legs). By noon the soil surface temperature was 130°F. and the majority of the grasshoppers had climbed or jumped into Russianthistle. resting at heights of 4 to 7 inches. A few crawled into the shade of Russianthistle and remained on the ground. When temperatures moderated in late afternoon the grasshoppers again became active pottering. feeding. and mating. By 8 p.m.. an hour before sunset. the majority of grasshoppers were roosting on Russianthistle and remained in these positions for the night.

Selected References

Brusven. M. A. 1972. Differentiation and ecology of common Catantopinae and Cyrtacanthacridinae nymphs (Orthoptera: Acrididae) of Idaho and adjacent areas. Melanderia 9: I-31.

Brusven. M. A. and J. D. Lamley. 197 I. The food habits and ecology of grasshoppers from southern Idaho rangeland. Univ. Idaho in cooperation with USDA. Project Completion Report I 967- 197 I.

Hostetter. D. L.. S. L. Breeding. J. A. Onsager. D. K. Brocmcling. and S. L. Zugoni. 1990. Impact of insect parasites and predators on grasshopper populations. I (Idaho). 1990 Annual Report Cooperative Grasshopper Integrated Pest Management Project. pp. 265-273.

Newton. R. C. 1956. Digger wasps, *Tachysphex* spp., as predators of a range grasshopper in Idaho. J. Econ. Entomol. 49: 615-619.

Seaton. Lee. 1955. Life history and habits of *Oedaleonotus enigma*. USDA ARS Special Report Z-33.

Sheldon. J. K. and L. E. Rogers. 1978. Gmsshopper food habits within a shrub-steppe community. Oecologia 32: 85-92.

Xiangchu. Y. and R. L. Smith. IYXY. Three new grasshopper species from the Western United States (Orthoptera: Acrididae). Pan-Pacific Entomologist 65:166- I7 I.

Bigheaded Grasshopper
Aulocara elliotti (Thomas)

Distribution and Habitat

Thc bighcaded grasshopper, *Aulocara clliotti* (Thomas), distributed widely in wcstcrn North Amcrica, inhabits a varicty of grasslands from southcrn Canada to ccntral Mexico. Large populations develop in thc mixcdgrass, shortgrass, and bunchgrass prairics and in dcscrt grassland.

Economic Importance

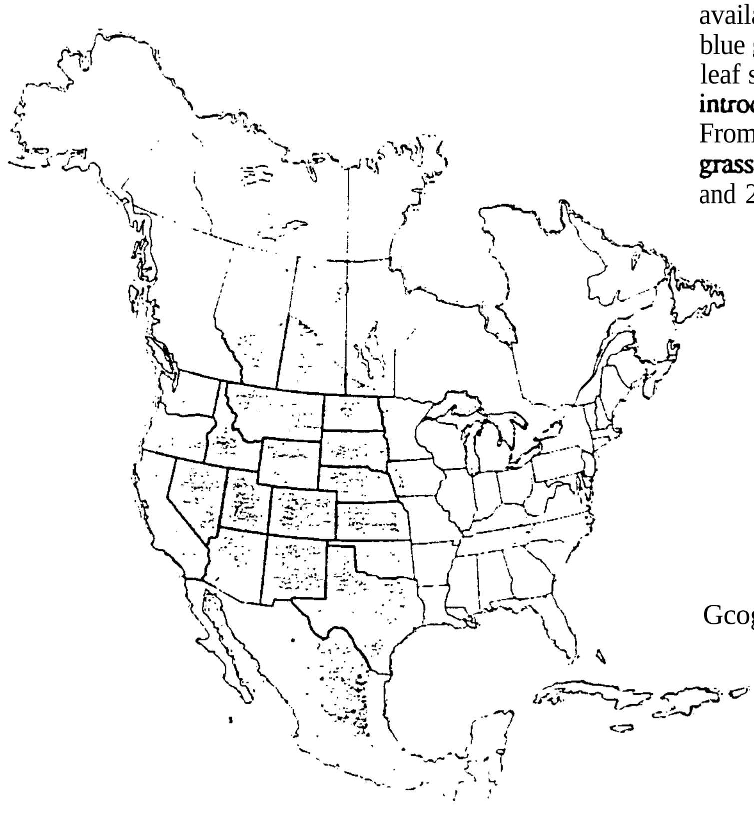
The bigheaded grasshoppcr is a scrious pcst of grasses. It is oftcn thc dominant species in outbrcaks on rangcland. Survey records reveal that it may rcach dcnsities of 20 per squarc yard in the mixedgrass prairic and 40 per square yard in desert grassland. Such high dcnsitics destroy the value of rangcland for grazing of livestock and may even lay the land barc, opening it to wind and watcr crosion. More oftcn, thc bighcadcd grasshopper is destructivc at lcsser densities as a dominant member of an assemblage of species. Although mcdium sized for a grasshopper, it is onc of the largest of the graminivorous species. Live weights of females inhabiting thc mixcd-grass prairie range from 285 to 663 mg (average 476 mg) and of males 13 1 to 230 mg (average 189 mg). In the desert grasslands of Arizona thc bighcaded grasshoppcr grows evcn larger.

This grasshopper not only rcduccs grass forage by consuming it but also by cutting it down. Thc cut grass may bccomc litter but it may also bc uscd for food by grasshoppers including thc bighcadcd grasshoppcr and by other insects that fccd on thc ground Ficld cage tcsts run in Montana and in Wyoming have dcmonstratcd that the feeding activity of one bigheaded grasshopper per square yard rcduces grass foragc equal to 20 pounds per acrc.

Food Habits

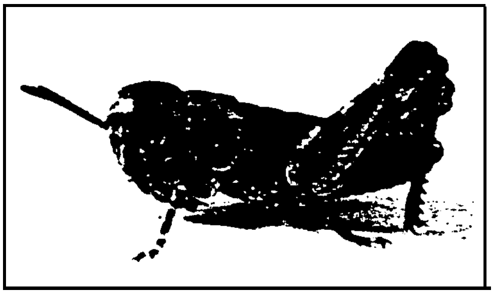
Thc bighcadcd grasshopper feeds mainly on the grccn lcavcs of grasses and sedges. It often attacks a plant by climbing a bladc, turning around head down, and chewing into the lcaf at various distances from the tip. The grasshopper frqucntly cuts the lcaf which drops to the ground. Thc insect may then continue to feed on the attach& section of the leaf. The bigheaded grasshopper also feeds on ground litter – cut grass leaves (green or dry). seeds, bran, and even dead grasshoppers. It searches these out crawling about on bare ground.

Microscopic examinations of crop contents of older nymphs and adults show that the majority of crops contain fragments of more than one plant species (average 2.2). These determinations indicate that thc bigheaded grasshopper is obtaining a mixed diet, although one species of plant is most abundant in a crop. Depending on availability, the bigheaded grasshopper grazes heavily on blue grama, wcstcrn wheatgrass, nccdlcandthread, thrcadleaf sedge, and nccdlclcaf scdge. Crested whcatgrass, an introducced forage plant, is a prcfcrrcd and nutritious host. From direct observations and crop cxaminations, this grasshoppcr is known to feed on two spccics of sedges and 22 spccics of grasses.



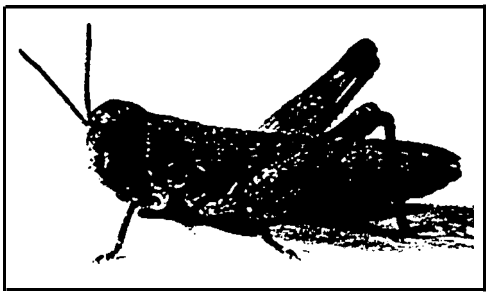
Gcognphic rangc of *Aulocara clliotti*(Thomas)

Instar 1



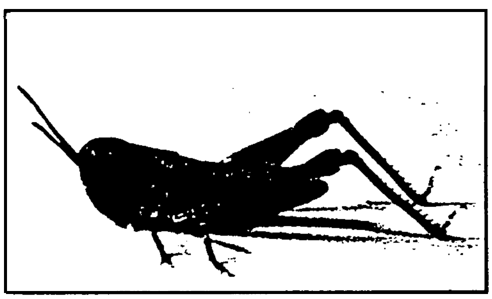
1. BL 5-6.3 mm FL 3.3-3.6 mm AS 14.

Instar 2



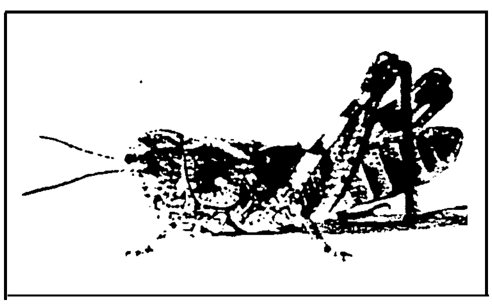
2. BL 6.6-9.8 mm FL 4.5-5.3 mm AS 18-19.

Instar 3



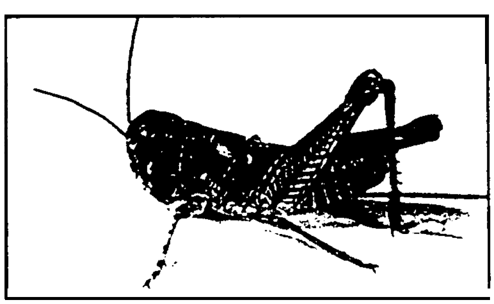
3. BL 9.8-12.2 mm FL 6.3-7.2 mm AS 20-21.

Instar 4



4. BL 12.5-16 mm FL 8.3-9 mm AS 22-23.

Instar 5



5. BL 14.5-19.5 mm FL 9.5-11.1 mm AS 22-25.

Figures 1-5. Appearance of the five nymphal instars of A. *elliotti* – their sizes, structures, and Color patterns. Note the progressive development of the wing pads. BL = body length, FL = hind femur length, AS = antennal segments number.

Migration and Dispersal

With wings fully developed, adults of the bigheaded grasshopper are able to fly evasively, to disperse, and to migrate. Flushed by an intruder, the adults fly straight. silently, low (4 to 12 inches), and short distances (2 to 7 feet). Evasive flights may be with the wind, into the wind, or across the wind.

Although no specific investigations of dispersal and migration of the bigheaded grasshopper have been made, evidence of long distance movements has been found incidental to other studies. At two locations, one in Arizona and one in Wyoming, sites that were found with no or few bigheaded grasshoppers at one sampling date had high densities of adults a few days later. Migrants in Arizona have been recorded as traveling distances of one to seven miles. Evidence of mass migration by the bigheaded grasshopper is provided by the recent discovery of large numbers of adults preserved on the ice of Grasshopper Glacier in the Crazy Mountains of Montana. Presumably swarms of the bigheaded grasshopper arose from areas of the mixedgrass prairie lying northeast of the mountains at lower altitudes, where outbreaks occur repeatedly.

Identification

Adults of the bigheaded grasshopper are of medium size and usually colored gray with fuscous markings. They possess relatively large heads with slightly slanted faces and have spotted forewings that extend slightly beyond the abdomen. The disk of the pronotum is distinctively marked by light lines that give the appearance of an "X"; several other patterns, however, exist in every population (Fig. 8). The hind femur has two black bars on the upper part of medial area; bars continue on upper marginal area, and around onto inner medial area; the knee is black. The hind tibia is medium blue. The male (Fig. 6) is smaller than the female (Fig. 7).

The nymphs (Fig. 1-5) are identifiable by their color patterns, structures, and shape:

(1) Head with lateral foveolae triangular and visible in dorsal view; antennae filiform but flattened: face moderately slanted.

(2) Pronotum with disk patterns like the adults, chiefly with light lines in form of an "X".

(3) Hind femur with two dark bars on upper part of medial area and four to seven dark spots on

Figurcs 6-10. Appcarance of the adult male and female of *A. elliotti*, diagnostic characters, and the egg pod and several eggs shown in situs in the opened pod.

lower carinula. Hind tibia blue with three dark annuli.

(4) Color drab gny and tan with fuscous markings.

Females of ***A. elliotti*** and ***A. fcmoratum*** arc distinguishable by the shape of the posterior margin of the eighth abdominal stcmum. In ***A. elliotti*** the posterior margin is without deep clefts (Fig. 9); in ***A. femoratum*** the posterior margin has two deep clefts.

Hatching

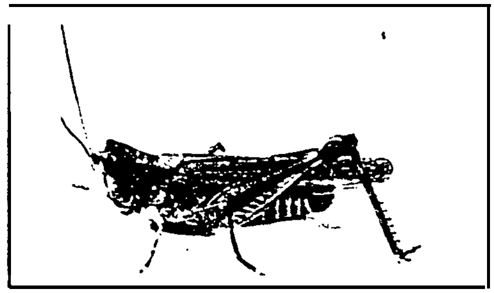
The bighcadcd grasshopper is an early hatching species. Eggs begin embryonic growth in the summer of deposition and continue until they attain 60 percent of development (stage 19 embryo). Because the eggs arc laid in early summer and at a shallow depth (average depth three-eighths inch), they arc exposed to warm temperatures and most reach the advanced stage before they diapausc. Eggs arc able to survive desiccation during drought periods of summer and fall. but predators – birds, rodents, beetles, bee flies, and others – tic a large toll. Density of eggs decreases 54 percent bctwccn fall and spring.

Exposed to low soil tempcraturcs, eggs break diapause during winter. In the laboratory eggs held at 37 to 4 1 F break diapause in 80 days. With warming spring temperatures, the soil temperature rising to 50 F and above, the eggs resume embryonic dcvclopmcnt. They complete the process after exposure to 450 day-dcyccs (base 50 F) of heat and arc ready to hatch. Emergence of the first instars occurs in mid-spring mainly during morning hours, and especially when the temperature is rising rapidly and the soil is moist. Eggs of a particular pod hatch in succession within seconds of each other. On the surface of the soil the young grasshopper squirms to free itself from the embryonic membrane. It usually takes six to eight minutes to complete this process and crawl away. During this time the young grasshopper is vulnerable to predation by ants:

Nymphal Development

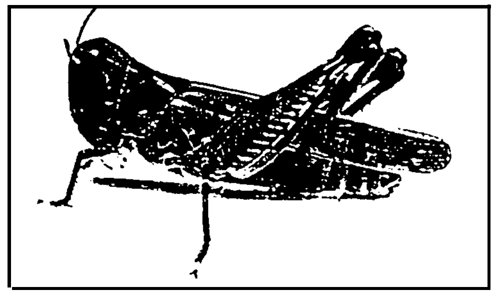
Nymphs cmcrgc in mid-spring over a period of three to four weeks. They feed and dcvclop in the same area as they hatch. Nurtured by warm spring weather and. nutritious green grass, they complete nymphal development in 36 to 42 days. The males, usually with only four instars, dcvclop faster than the females with five instars.

Male



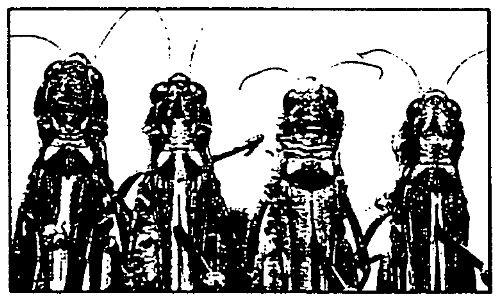
6. BL 17-20 mm FL 9.5-l 1.3 mm AS 23-24.

Female



7. BL 20.5-25 mm FL 12.3-14.3 mm AS 24-25.

Patterns

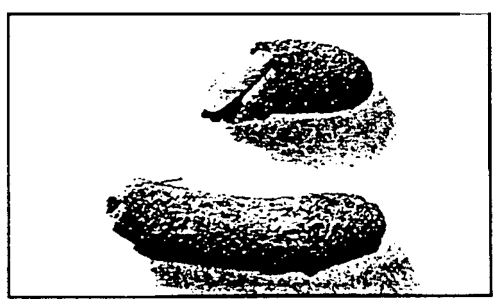


8. Dorsal view. pattern variations of pronotal disk.

Sternum

Y. Ventral view, shape of eighth abdominal sternum.

Egg Pods



10. Two egg pods. one opened to show eggs.

Adults and Reproduction

Adults of the bighcadcd grasshopper may dispersc to new habitats, but most often they remain in the same area where the nymphs hatched and devclopcd. There they fecd, maturc, reproduce, and eventually are eaten by a predator or die from other causes.

Female adults become receptive to mating when they arc six to eight days old. Pair formation and courtship consists primarily of visual cues. Normally the male makes a quick approach to the female and silently displays himself by tipping the hind femora and waving the antennae. Once the male mounts and succeeds in making genital contact, copulation lasts 40 to 70 minutes.

Females deposit their first group of eggs when they arc 12 to 20 days old (average 15 days). When ready to lay eggs a female will select one of the many bare areas in her habitat and work her ovipositor into the soil. She then deposits in the top one-half inch of soil seven to nine eggs which become enclosed in a tough pod. Immediately after ovipositing a female spends a minute actively sweeping soil particles over the hole left by extraction of her ovipositor. She performs this final act of maternal care with her hind legs using the tarsi as brushes.

Fecundity of the bigheaded grasshopper is less than that of the migratory grasshopper. When pairs were reared individually in field cages and fed leaves of western wheatgrass, females lived an average of 72 days and produced 76 eggs per female. When they were fed wheat leaves, females lived an average of 87 days and produced 116 eggs. The greatest rate of reproduction -- 161 eggs -- was by a female fed wheat leaves. Unprotected from predators in their natural habitat, individuals have a shorter life and lower fecundity. Research suggests an average adult longevity of approximately 20 days and a fecundity of 15 eggs per female under natural conditions. There is one generation annually.

The pod is slightly curved, one-half to five-eighths inch long and three-sixteenths inch in diameter (Fig. 10). The pod cap has a short nipple in the ccntcr. Eggs are pale yellow and 5.2 to 5.5 mm long.

Population Ecology

Populations of the bigheaded grasshopper irrupt frequently in the mixcdgrass prairie and in desert grasslands. Populations may increase gradually, doubling their numbers each year for a period of three or four years. Then in one year they may increase their densities by three or four fold precipitating an outbreak. Several hypotheses have been proposed to explain these outbreaks -- increase in physiological vigor of the grasshopper, changes in nutritive composition of the vegetation, and environmental release (favorable weather and fewer enemies). Scientists doing research on population ecology have yet to gather enough data to make firm conclusions on the causes of outbreaks of the bigheaded grasshopper.

Once the bigheaded grasshopper has reached an outbreak condition, the population may continue at high densities for five or more years. For generally unknown reasons. populations eventually decline or crash. In a few cases, however, causes are apparent. Naturally occurring diseases such as Noscma may decimate populations, and insecticidal control can reduce densities much below the economic level.

Daily Activity

The bigheaded grasshopper is a ground-loving insect whose activities are influenced greatly by temperature and light Individuals rest on the ground at night. One to two hours after sunrise they begin basking by resting perpendicular to the rays of the sun (side exposed to sun) and hugging the ground surface. They bask for about an hour, then around 70 F air and 95 F soil surface temperatures, the adults begin their normal activities of pottering (intermittent wandering with frequent changes in direction), feeding, mating, and egg laying. Activity slows when air temperatures rise to 90 F and soil tcmpcraturcs to 120 F. Usually they seek the shade of small shrubs and rest on the ground or litter. They may also raise up on their legs to hold their bodies off the hot surface. As temperatures decline in the afternoon. they again take up normal activities. Two to three hours before sunset they begin basking once more on the ground surface. After sunset they remain on the ground without cover through the night.

Selected References

Hewitt, C. B. 1978. Reduction of western wheatgrass by the feeding of two rangeland grasshoppers, *Aulocara elliotti* and *Melanoplus infantilis*. J. Econ. Entomol. 71: 419421.

Hussain, N. and R. E. Pfadt. 1976. The utilization of food by bigheaded grasshopper. *Aulocara elliotti* (Thomas). Pakistan J. Forestry 26: 171-176.

Kemp, W. P. and N. E. Sanchez. 1987. Differences in post-diapausc thermal requirements for eggs of two rangeland grasshoppers. Can. Entomol. 119: 653-661.

Onsager, J. A. and G. B. Hewitt. 1982. Rangeland grasshoppers: average longevity and daily rate of mortality among six species in nature. Environ. Entomol. 11: 127-133.

Pfadt. R. E. 1949. Food-plants. distribution, and abundance of the big-headed grasshopper. *Aulocara elliotti* (Thos.). J. Kansas Entomol. Soc. 22: 69-74.

Van Horn. S. N. 1966. Studies on the cmbtyogenesis of *Aulocara elliotti* (Thomas) (Orthoptera, Acrididae). I. External morphogenesis. J. Morph. 120: 83-l 14.

Clearwinged Grasshopper

Camnula pellucida (Scudder)

Distribution and Habitat

The clearwinged grasshopper, *Camnula pellucida* (Scudder), is distributed widely in North America. It inhabits a variety of grasslands including the northern mixedgrass prairie, the palouse prairie, and mountain meadows. A resident population lives in a mountain meadow at 10,800 ft in Colorado, just below timberline.

Economic Importance

The clearwinged grasshopper is a severe pest of small grains and grasses. It is most destructive early in the season when it often completely destroys spring wheat. Outbreaks on rangelands may devastate grass forage in areas as large as 2,000 sq miles. A population with a density of 20 adults per sq yd will consume the entire available yield of forage grasses on rangelands of British Columbia. Cage plot tests on native grassland of interior British Columbia showed that the feeding of this grasshopper during its nymphal life reduced the yield of Kentucky bluegrass by 5.1 pounds per acre for each grasshopper per square yard. An infestation of one young adult per square yard reduced yield one pound per day over one acre. Swarms may invade vegetable crops and feed preferentially on onions, lettuce, cabbage, and peas.

Food Habits

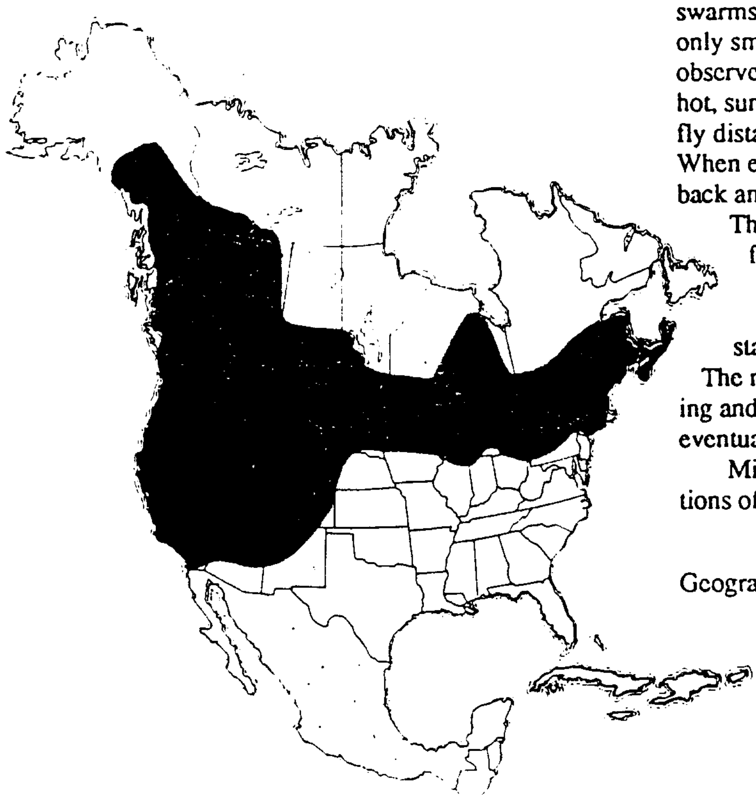
The clearwinged grasshopper feeds mainly on grasses. It prefers succulent plants of western wheatgrass, reed canarygrass, barley, and wheat. Field observations at several locations show that it feeds heavily on many species of grasses, including fescues (Idaho fescue and red fescue), bluegrasses (Sandberg bluegrass and Kentucky bluegrass), wheatgrasses (western wheatgrass and crested wheatgrass), bromes (cheatgrass brome, smooth brome, and soft brome), and slender hairgrass. These grasses are not equally nutritious. The most favorable single species diets consist of red fescue, three species of bluegrass, wheat, crested wheatgrass, and intermediate wheatgrass. In its natural habitat, the clearwinged grasshopper consumes small amounts of forbs such as fireweed and several species of legumes.

Migration and Dispersal

Myriads of the clearwinged grasshopper hatch in egg beds that may contain as many as 3,000 to 100,000 eggs per sq ft. Pressure of high densities and depletion of food result in movement of the young nymphs away from egg beds to the nearest green vegetation. Immature grasshoppers continue to disperse through all of the nymphal stage. The older instars march in cohesive bands.

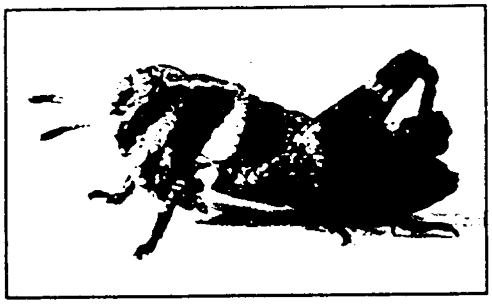
Adults may migrate long distances in huge flying swarms at either low or high altitudes, but in recent years only small swarms in flights of short duration have been observed. These flights may occur in the afternoons of hot, sunny days. Masses take off into a gentle wind and fly distances of one hundred to several hundred yards. When egg laying begins, migration ceases but females fly back and forth between feeding grounds and egg beds. They move to the egg beds during the heat of the day for oviposition. After a particular female deposits a clutch of eggs, she flies back to the feeding grounds in the evening or the next morning and stays there until another batch of eggs is mature. The males appear to remain on the egg beds outnumbering and attending the females as they oviposit. Males eventually die on the egg beds.

Migratory behavior is not characteristic of all populations of the clearwinged grasshopper. Individuals infest-



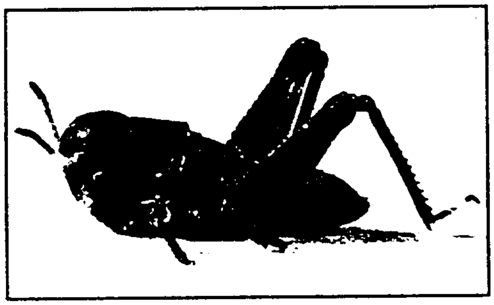
Geographic range of *Camnula pellucida* (Scudder)

Instar 1



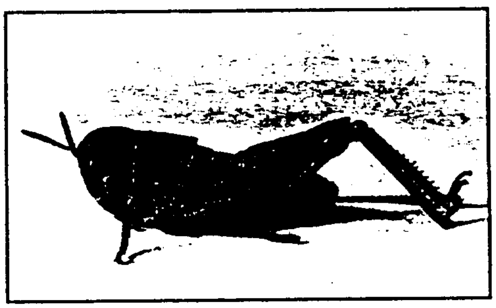
1. BL 4.2-5.5 mm. FL 2.4-2.7 mm. AS 11-13.

Instar 2



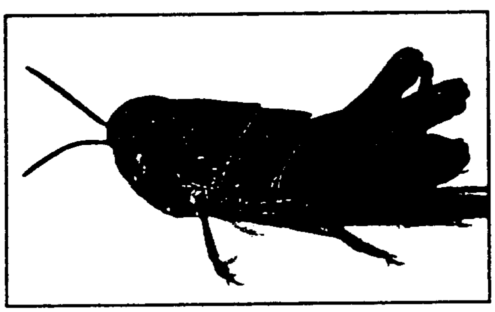
2. BL 5-7.1 mm. FL 3.4-3.8 mm. AS 14-16.

Instar 3



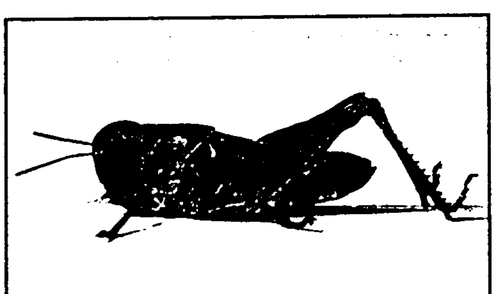
3. BL 7.3-8.9 mm. FL 4.7-5.2 mm. AS 18.

Instar 4



4. BL 10-14.5 mm. FL 6-7.2 mm. AS 20-22.

Instar 5



5. BL 14-20 mm. FL 8.4-9.9 mm. AS 22-25.

Figures 1-5. Appearance of the five nymphal instars of *C. pellucida*–their sizes, structures, and color patterns. Notice progressive development of the wing pads. BL = body length, FL = hind femur length, AS = antennal segments number.

ing sodded pasture near Harney, Minnesota, exhibited little movement. Nymphs developed to maturity close to where they had hatched and the adults showed little tendency to migrate, flying only short distances. Mating and egg laying occurred in the same area where eggs had been deposited the previous year.

Identification

Adults of the clearwinged grasshopper are of medium size, yellow to brown, and possess mottled forewings and transparent hindwings (Fig. 8). The forewings have along their angles light stripes that in the resting grasshopper with closed wings converge near the middle. The male (Fig. 6) is noticeably smaller than the female (Fig. 7). First instar nymphs are strikingly colored cream, tan, and black (Fig. 1).

The nymphs (Fig. 1-5) are identifiable by their color patterns and external structures:

(1) Head with lateral foveolae triangular (Fig. 9). Usually a dark bar crosses transversely across front of head under antennal sockets, across lower part of compound eyes, and onto sides of head.

(2) Pronotum with median carina low but uniformly elevated; median carina entire (without notch) in early instars, notched once in front of middle in the older instars (Fig. 9). Pronotum with lateral carinae clearly defined (Fig. 9).

(3) Hind tibia fuscous in first to third instar, fuscous or tan in fourth and fifth instars.

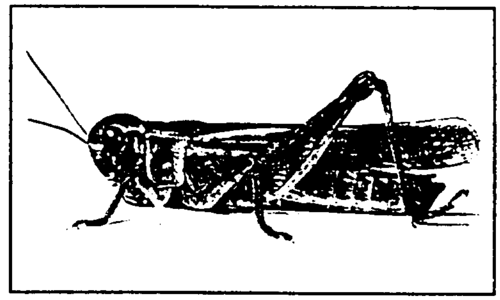
Hatching

The clearwinged grasshopper is an early hatching species. Eggs begin embryonic growth in the summer of deposition and continue until they attain 30 to 50 percent of development. To reach the advanced stage, they require 400 day-degrees of heat at which point diapause stops further summer development. Lack of soil moisture may retard this initial development.

Diapause in eggs is broken during winter. At 41 F eggs require a minimum of 70 days of chilling. The rise of soil temperatures above a threshold of 55 F the following spring starts the final stages of embryonic development. After experiencing 150 day-degrees of heat, the eggs are ready to hatch. Emergence begins when soil temperature reaches 80 F and air temperature 65 F. Hatching of all eggs in an individual pod may be completed on the same day but this process generally lasts two

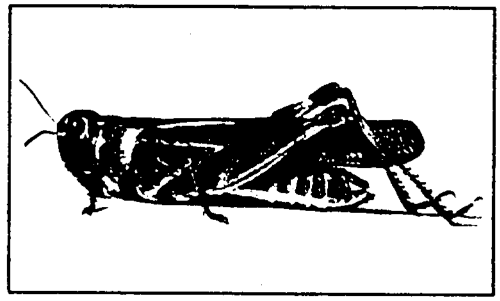
Figures 6-10. Appearance of the adult male and female of *C. pellucida*, diagnostic characters, and the egg pod and several loose eggs.

Male



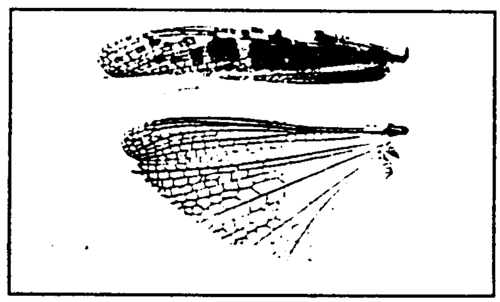
6. BL 19.5-21.5 mm. FL 10.5-11.8 mm. AS 25-29.

Female



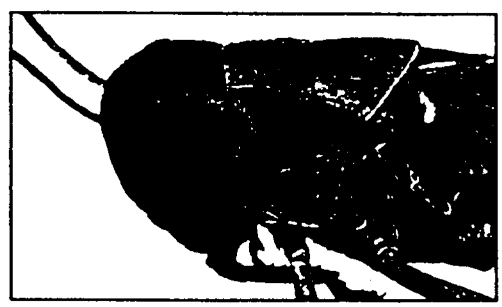
7. BL 22-25 mm. FL 12.2-13.6 mm. AS 24-26.

Wings



8. Forewing (tegmen) and hindwing.

Head and Pronotum



9. Note lateral foveola on head and carinae on pronotum.

Egg pod

10. Egg pod and four loose eggs.

to four days. A warm spring and favorable soil moisture shorten the hatching period of all the eggs in a bed. Because the hatching period may be completed in 12 days, the nymphs seem to appear en masse on bed grounds. Cool, dry weather, however, may delay the start of hatching by a month and may extend the hatching period for a month or longer. Hatchlings emerge in the morning when temperatures are rising rapidly, especially after a shower the previous evening. Hatching begins around 9 a.m. and reaches a maximum between 11 a.m. and 12 noon.

Nymphal Development

The nymphs disperse quickly in search of food when large numbers of hatchlings are present on egg beds of native sod. Movement may be in any direction and often continues through the entire nymphal stage. Invasion of young fields of wheat at this time results in extensive crop damage. Nymphs exposed to warm temperatures and nutritious food plants complete development in 26 days. Less favorable conditions may extend this period to 40 days or longer.

Adults and Reproduction

Because nymphs of the clearwinged grasshopper develop faster than those of the twostriped, adults of the clearwinged may appear first. The young adults are dark brownish gray, but as they mature, they turn lighter. When they become sexually active on the breeding grounds, they turn bright yellow. In laboratory cages under conditions simulating the natural environment, males become reproductively mature in five to seven days after fledging and females in seven to ten days.

Courtship by the male involves holding the antennae upright in a V-shape and moving the hind femora rapidly up and down and against the tegmina (ordinary stridulation). The male climbs onto the back of a receptive female and quickly lowers his abdomen down to make genital contact. Perched precariously and to one side, the male often becomes dislodged and comes to rest on the ground at the side of the female or is pulled along behind her.

After a copulatory period averaging 55 minutes, the female seeks a suitable oviposition site by probing in sod. She digs her abdomen down among grass roots by opening and closing the ovipositor valves and quickly lays (average time 22 minutes) a clutch of 28 eggs (range 10-38) in the top inch of soil. She then covers the hole with a back and sideways motion of the hind legs. The females, in seeking favorable sites for oviposition, often aggregate on egg beds that may range from a few square yards to 20 acres or more depending on size of the grasshopper population.

Pods are short and stout, 5/8 inch long and 3/16 inch in diameter, and are slightly curved (Fig. 10). Eggs are light brown and 4.7 mm long. Confined in field cages on winter wheat and Kentucky bluegrass at Saskatoon, Saskatchewan, females averaged 60 days adult life and produced 8 pods or 180 eggs each. The clearwinged grasshopper has one generation annually.

Population Ecology

Populations of the clearwinged grasshopper exhibit extremes of abundance and range. The species can remain virtually unseen for five to ten years, then increase gradually over three to four years and reach peaks the following two to three years. During the period of increase, a population may spread from a few acres of rangeland to more than 2,000 square miles. These outbreaks consist almost entirely of the clearwinged grasshopper. The cause of outbreaks appears to be a combination of favorable weather, nutritious host plants, and reduced rates of predation, parasitism, and disease. Weather that supports population growth consists of above normal temperatures in spring and summer and sufficient rain to keep host plants green and succulent, particularly fescue, bluegrass, and wheat. Crashes of dense populations are caused by epizootics of the fungus, *Entomophaga grylli* (Fresenius) pathotype I; by drought resulting in starvation of nymphs or adults; by below normal spring and summer temperatures that retard development of nymphs and reproduction of adults; or by low soil temperatures in winter that may cause up to 100 percent mortality of eggs.

Daily Activity

The clearwinged grasshopper, a diurnal insect, is active during the day and inactive at night. During the night it rests in sheltered places protected from the cold. As the morning sun warms the habitat, the grasshoppers slowly crawl from their hiding places and seek sunny positions aggregating on bare soil, earth clods, and dried cattle dung. As temperatures rise further, the grasshoppers start moving about and feeding. They are active during the greater part of the day. If the ground becomes too hot, they crawl up stems of plants a distance of 2 inches. Just before sundown, they seek stones and other objects that have retained heat and orient their sides to the sun. As the habitat continues to cool, they crawl to sheltered places and become hidden. Several weather elements, particularly temperature and radiation of the sun, modify behavior (Table 1).

Table 1. Activity of nymphs and adults of the clearwinged grasshopper, *Camnula pellucida* (Scudder) correlated with air and soil temperatures (After Parker 1930).

		Average temperature °F			
		Nymphs		Adults	
Name of activity	Description	Air	Soil	Air	Soil
Beginning of activity	Basking, exposure to sun	60	76	62	78
Beginning of normal activity	Feeding	65	94	67	95
	Starting migration	67	93	75	102
	Molting	70			
	Mating			68	
	Starting oviposition			72	101
Beginning of climbing to escape heat	Climbing vegetation			80	107
Beginning of clustering in evening	Basking, exposure to sun	68	87	70	90
Ending of activity	Moving to shelter	65	77	67	80

Selected References

Gage, S. H. and M. K. Mukerji. 1977. A perspective of grasshopper population distribution in Saskatchewan and interrelationship with weather. Environ. Entomol. 6: 469-479.

Misra, S. D. and L. G. Putnam. 1966. The damage potential of the grasshopper, *Camnula pellucida* (Scudd.) (Orthoptera: Acrididae) on pastures and ranges in Canada. Indian J. Entomol. 28: 224-233.

Parker, J. R. 1924. Observations on the clear-winged grasshopper (*Camnula pellucida* Scudder). Minnesota Agr. Exp. Stn. Bull. 214.

Pickford, R. 1963. Wheat crops and native prairie in relation to the nutritional ecology of *Camnula pellucida* (Scudder) (Orthoptera: Acrididae) in Saskatchewan. Can. Entomol. 95: 764-770.

Pickford, R. 1974. Reproductive behaviour of the clear-winged grasshopper, *Camnula pellucida* (Orthoptera: Acrididae). Can. Entomol. 106: 403-408.

Riegert, P. W. 1967. Some observations on the biology and behaviour of *Camnula pellucida* (Orthoptera: Acrididae). Can. Entomol. 99: 952-971.