LIVESTOCK
Grazing
& Grasshoppers:
An Interregional Perspective

Introduction

Considerable research has been directed toward the assessment of livestock forage losses to grasshoppers (Hewitt 1977, Onsager 1984, Davis et al. 1992). By contrast, the effects of livestock grazing on grasshoppers has been given relatively little attention. Recently, much public debate has centered on issues of livestock production on public rangelands in the western United States (USDI-BLM and USDA-FS 1994). The sustainable use of western rangelands requires detailed knowledge of ecosystem responses to livestock grazing. Such knowledge may also provide insights into basic ecological processes (Mack 1989, Painter and Belsky 1993). Because of the importance of grasshoppers in grassland ecosystems (Bailey and Riegert 1973, Mitchell and Pfadt 1974, Lockwood 1993), as well as in ranching-based economic systems (Davis et al. 1992), consideration of grasshopper/grazing relationships is important. This article presents a framework to help examine complex interactions that may occur between livestock, plants, grasshoppers, and other biotic and abiotic components of rangeland ecosystems. This article also provides a summary of historical information about grasshoppers and livestock grazing in western North America. Throughout this article, we emphasize the effects of grazing on grasshoppers, as opposed to the effects of grasshoppers on livestock production.

Environment influences the expression of insect life history parameters, such as survival, fecundity, and dispersal. Livestock grazing can alter the environment of rangeland grasshoppers by affecting their food resources, physical environment, and the temporal and spatial heterogeneity of their habitat. The first part of this paper discusses possible direct and indirect links between grazing and grasshoppers, and identifies information gaps that prevent a more complete understanding of the effects of grazing on grasshoppers. The second part examines the literature that specifically addresses grasshopper population responses to grazing by large herbivores among different ecoregions of the western United States.

Ecological hierarchies

Hierarchy theory provides a way to interpret complex ecological systems by dividing the phenomenon into its constituent subsystems (Allen and Starr 1982,

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O'Neill et al. 1986). In a hierarchical system, the structure of a system is determined by interactions among subsystems of the next lower-level, while higher-level systems constrain, or set the context for, interactions among lower-level systems (O'Neill et al. 1986). Lower-level processes and interactions of lower-level subsystems occur at faster rates and on smaller spatial scales than do the dynamics of higher levels.

Pickett et al. (1989) considered a disturbance to be an external force that destroys or alters the structure of a system and some of its physical components. Types of disturbances and their effects differ between hierarchical levels (Pickett et al. 1989). In this paper, we conceptualize grazing as a potential disturbance that may alter or disrupt ongoing grasshopper/plant interactions.

We recognize at least three levels of organization that are relevant to the consideration of grasshopper responses to grazing. At the lowest level, the short-term, immediate effects of consumption and trampling of plants by ungulates can greatly influence the environment experienced by grasshoppers within a single season within a single grazed patch. This may occur on a spatial scale of tens to hundreds of meters. Such effects may last only a few weeks or until the next growing season. Grasshopper population responses, such as increased mortality or fecundity, are evident within a single season or in the following season.

At the next higher level, grazing regime determines the spatial and temporal patterns of grazed patches on a landscape (Coughenour 1991). At this landscape level, spatial scales probably are on the order of tens of kilometers. The frequency of grazing over an interval of decades determine the temporal patterns. Grazing regime also can affect the long-term dynamics of plant communities, effects of which may be evident after a few seasons or only after several decades. At this scale, grazing effects would be reflected in community-level measures (e.g., species diversity), the types of grasshopper species present (e.g., grass-feeders vs. forb-feeders) and characteristics of their population dynamics (e.g., frequency of outbreaks).

At the highest level, climate constrains the range of variability in annual primary production as well as the seasonal pattern of biological activities, including the type of grazing regime that can be implemented. The temporal and spatial scales of climatic regimes are large, on the order of decades or centuries (Davis 1986) and hundreds of kilometers (Bailey 1978).

O'Neill et al. (1986) discussed the pitfalls associated with ignoring hierarchical structure when analysing ecosystem processes. Most studies of grasshoppers in relation to grazing have ignored the distinctions between the immediate effects of a single grazing event and the long-term effects of grazing regime, thereby confounding effects operating at two different hierarchi-cal levels. There is a possibility that observed differences between grazed and ungrazed patches could be erroneously attributed to the short-term immediate effects of grazing, when the different plant communities and their constituent grasshopper assemblages may have different dynamics over several years. This could lead to unreliable prescriptions regarding grazing for grasshopper management.

Mechanisms of grazing effects on grasshopper biology may also vary with scale. For example, in the short-term, grazing may alter microclimates available to grasshoppers, which may influence survival of nymphs or oviposition by adults. In the long-term ecosystem scale, grazing may affect the composition of plant communties in the region, and thereby affect the availability of food plants and the species composition of grasshopper assemblages in the region. Thus, it is important to maintain a clear distinction between levels in the hierarchical structure of a grasshopper's environment to arrive at a more reliable and specific understanding of how grasshopper populations respond to livestock grazing.

Short-term, immediate effects of grazing

Short-term effects include altered host plant availability, plant chemical and physical constituents (Detling 1987), plant structure (e.g., height), and microclimate. Such effects may disappear within weeks or months after cessation of grazing. At this fine scale, grazing affects a grasshopper's ability to find appropriate microclimates (e.g., shade vs. direct sun) and food items (including different tissues of a single plant).

Food quantity

The most obvious short-term effect of grazing is the removal of plant biomass. The degree of overlap between the food preferences of livestock and grasshoppers is a major factor in determining the damage potential of various species of grasshoppers (Mulkern et al. 1969, Hewitt 1977). Conversely, dietary overlap may determine which species of grasshoppers are most likely to suffer from competition with livestock. Whether or not the response of a particular species of grasshopper to livestock grazing is related to the species' food preferences has never been investigated. Also, the intensity of competition for food plants depends on whether the grasshopper populations in question are food limited. Belovsky and Slade (1994) and Chase and Belovsky (1994) reported evidence that populations of grasshoppers in Montana are limited by food under certain circumstances. The complex of factors that limit and/or regulate grasshopper populations are not well understood and probably are contigent on weather, grassland type, grasshopper species, and other factors (Joern and Gaines 1990). Nevertheless, it seems likely that these factors all interact to

determine the net effect of grazing on quantity of food available to grasshoppers.

Food quality

In recent reviews, Joern (1987) and Joern and Gaines (1990) described the nutritional characteristics of plants that are important factors influencing grasshopper population dynamics. These characteristics include digestibility, protein content and composition, and plant growth hormones. Livestock grazing can affect these attributes of plants in complex ways (Detling 1987). Plant responses to grazing may vary inter- and intra-specifically (Caldwell et al. 1981, Jaramillo and Detling 1988, Painter el al. 1989).

Plant responses to grazing also depend on the intensity and timing of grazing and weather (Detling 1987). For instance, younger plant tissue is generally more digestible and has higher protein content than older tissue. In situations where plants regrow following defoliation, the regrowth may provide higher quality forage for grasshoppers. In seasons and climates without adequate soil moisture to allow for regrowth, defoliation results in lesser quantities and probably lower quality food. For these reasons, it may be inferred that grazing effects on host plant quality vary by location and season. In England, population variables, e.g., fertility and survival, of *Chorthippus brunneus* (Thunberg) differed inside and outside of a fenced area that excluded rabbits, probably by affecting host plant quality (Grayson and Hassall 1985). The dominant grass, *Festuca ovina*, had higher nitrogen content in the early summer where it was protected from grazing by rabbits and was believed to have contributed to the greater survival, growth rate, adult size, and fecundity of grasshoppers within the exclosure.

Habitat structure

Livestock grazing also affects the structural attributes of vegetation and microclimate. Reduced plant height, increased bare ground, and higher temperatures and lower relative humidity within selected microclimates are generally associated with grazed habitats (Johnston et al. 1971). Anderson et al. (1979) showed that microhabitat selection by two species of grasshoppers was consistent with their physiological temperature and humidity requirements.

The cryptic coloration of many grasshopper species implies that predation is an important selection pressure. Grazing may increase or decrease the amount of escape space available to grasshoppers, depending on whether they are cryptic against bare soil (e.g., many *Oedipodinae*) or cryptic against vegetation, especially upright grass stems (e.g., *Amphitornus coloradus*, *Parapomala wyomingensis*). Grasshopper predators may also respond positively or negatively to grazing-induced habitat changes (Reynolds and Trost 1980, Hanley and Page 1982) However, actual predation rates may not be as important as the grasshoppers' behavioral responses to vegetative structure. Behavior that evolved in response to predation remains in effect even in the absence of significant predation. Accordingly, grasshoppers that are cryptic against vegetation may prefer habitats that provide an abundance of refuges, i. e., ungrazed habitats.

Grazing may affect the availability of oviposition sites. Some grasshoppers prefer to oviposit in bare soil, others in soil beneath vegetation, and others within the base of bunchgrasses. *Aulocara elliotti* prefers to oviposit in bare ground whereas *M. sanguinipes* prefers to oviposit under plants (Nerney and Hamilton 1969, Kemp and Sanchez 1987, Fisher 1992). The oviposition sites favored by a particular species of grasshopper is probably influenced by the thermal characteristics of the soil microclimate. Grazed sites typically have more bare ground and the soils may be warmer in the spring than ungrazed sites that are more shaded or have more litter on the ground (Johnston et al. 1971). Given the sensitivity of grasshopper egg development to temperature (Kemp and Sanchez 1987), changes in soil temperatures could affect grasshopper population levels positively or negatively, depending on the species and the season.

Within-patch environmental heterogeneity

Studies show that within-patch heterogeneity can affect foraging efficiency (Roese et al. 1991). Grazing may increase or decrease the heterogeneity of certain habitat characteristics, depending on the intensity of grazing. For instance, considering plant height, with high stocking rates, such as under short-duration, high-intensity grazing systems, a greater proportion of the plants are grazed (Senft 1989), and heterogeneity may be reduced (a mowing effect). At intermediate grazing levels, some plants may be heavily utilized while others may be untouched, so that the heterogeneity of plant height increases.
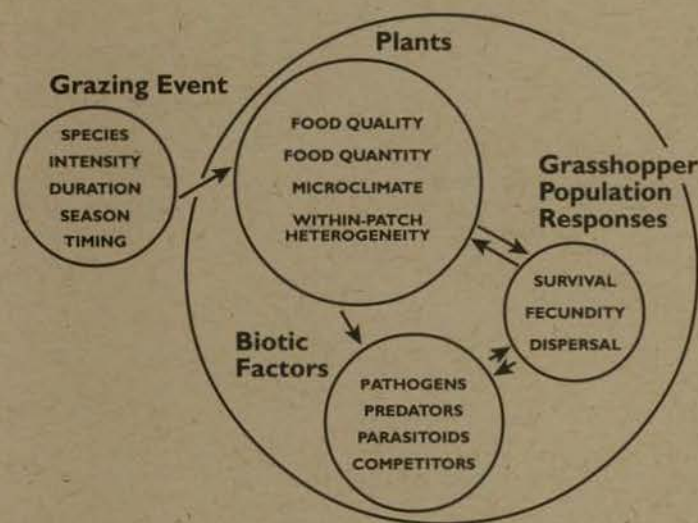
At intermediate intensities, grazing effects on grasshoppers may not be related to the within-patch average level of grazing (Coughenour 1991). A threshold-type of response by grasshoppers to grazing is likely. Up to a certain level of grazing, food and suitable microclimate may be readily accessible to grasshoppers. As grazing intensity increases, suitable microhabitat or food may become increasingly more difficult to locate, until at some level, grasshoppers will either emigrate or die. A reverse relationship could exist for species of grasshopper that favor grazed habitats.

Few studies of grasshoppers have examined effects of grazing on within-patch heterogeneity. Miller and Onsager (1991)

provide a detailed account of the temporal heterogeneity of ground cover and food resources of grasshoppers in crested wheatgrass pastures under different grazing regimes. It appeared that a short-duration, high-intensity grazing regime produced the greatest temporal variability in several habitat variables, such as percent ground cover by crested wheatgrass, percentage water and protein content of the grass, compared to low-intensity, season-long grazing. The increased habitat variability over the season did not appear to affect the normal seasonal development of the resident grasshopper populations.

With (1994) examined small-scale (5x5 m) patterns of movement by grasshoppers in relation to heterogeneity of the plant community and grazing treatments. Results indicated that different species of grasshoppers responded differently to microlandscape heterogeneity, although grazing treatment had little, if any, effect on the patterns of movement by grasshoppers (With 1994).
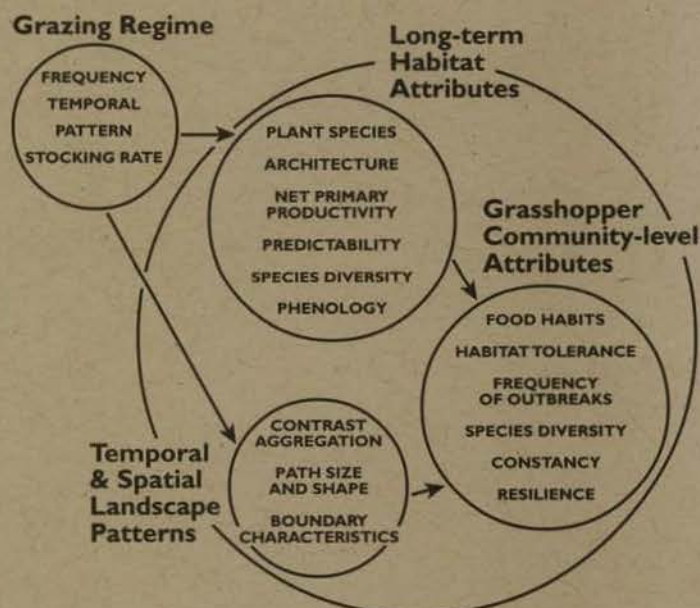
Long-term effects of grazing regime

On an ecosystem scale (fig. 1), the focus is on the cumulative effects of grazing regime, not a single grazing event. A disturbance to the system at this higher-level would consist of a change in grazing regime from evolutionary historical patterns (Milchunas et al. 1988, Hobbs and Huenneke 1992). Long-term changes in habitat resulting from changes in grazing regime may include alterations of the dominant plant species and soil attributes. These changes result from the culmulative effects of the frequency, timing, and intensity of grazing integrated over many years. Such changes may be evident for many years after the cessation of grazing, especially in drier climates (Robertson 1971, McClean and Tisdale 1972, Anderson et al. 1982, Anderson and Holte 1981, West et al. 1984, Roundy and Jordan 1988).

Another effect of grazing regime involves the spatial pattern of grazed and ungrazed patches on a landscape (fig. 2). Depending on the grazing system, the spatial heterogeneity of grazing across a landscape could influence habitat selection by adults of more mobile species.

Fig. 1 A cause-effect flow model showing short-term effects of a single grazing event on habitat attributes, biotic factors and grasshopper population responses. For instance, grasshopper populations are directly affected by the abundance of predators and parasitoids, by microclimate and food quality, and by the direct effects of weather. Grazing in turn may effect many characteristics of the habitat. Weather may affect all of these interactions by, for example, affecting choices of grazing duration and season of use, by affecting plants' response to grazing, by affecting the abundance of predators, and by direct effects on grasshoppers.

Fig. 2 A cause-effect flow model showing long-term effects of repeated grazing on higher level habitat attributes, landscape patterns, and resultant grasshopper community characteristics. At this level, the composition of the plant community, the types of plants (e.g., shrubs or grasses, annuals or perennials), site productivity may all reflect the culmulative effects of grazing. On a landscape scale, grazing regime will determine patterns such as, spatial patterns of grazed and ungrazed patches, temporal patterns (frequency of grazing), and size and shape of grazed patches. These broad-scale, long-term effects of grazing may influence the type of grasshopper species present (their food habits, niche breadth, frequency of outbreaks), as well as their competitors and predators.

Plant community alteration

Plant community responses to long-term grazing differ regionally (Ellison 1960, Holechek 1980, Willms et al. 1985, Milchunas et al. 1989), although any plant community can be degraded by repeated, severe over-grazing. Some regions, such as the short-grass prairie of the Central Great Plains, are more tolerant of relatively heavy grazing (Milchunas et al. 1989), whereas other regions, such as the sagebrush steppe of the Intermountain region, are very susceptible to habitat degradation due to overgrazing.

Different evolutionary histories of these regions may account partly for their differing responses to grazing (Stebbins 1981, Mack and Thompson 1982, Milchunas et al. 1988, Hobbs and Huenneke 1992). For example, on the Great Plains, east of the Rocky Mountains, enormous herds of bison grazed in the recent past. Mack and Thompson (1982) hypothesized that the short-grass prairie grasses, such *Bouteloua gracilis* are adapted to frequent grazing. In contrast, there is strong evidence that great concentrations of ungulates did not occur in the Intermountain region (Mack 1981), where the native bunchgrasses are easily damaged by grazing (Hanson and Stoddard 1940, Blaisdell and Pechanec 1949, Caldwell et al. 1981, Eckert and Spencer 1987, Ganskopp 1988).

Many regions of the western United States have experienced long-term habitat degradation from over-grazing (Mack and Thompson 1982, Hobbs and Huenneke 1992). Grasshopper community composition in these areas nearly always differs from the undisturbed situation. Coyner (1938) and Smith (1940) reported higher grasshopper populations in overgrazed pastures than in moderately grazed pastures in Kansas and Oklahoma during the Dust Bowl era. Quinn and Walgenbach (1990) reported that grazing of a mixed-grass prairie in South Dakota shifted the plant community composition towards short-grass species, mainly *B. gracilis*, while ungrazed areas had a much higher proportion of mid-tall grasses, such as *Agropyron smithii* (western wheatgrass) and *Stipa viridula* (needle and thread grass). A concomitant shift in grasshopper species composition was reported.

Heavy grazing of grasses can lead to an increase in less palatable shrubs in rangeland communities. Rangeland in the southwestern United States has experienced livestock grazing since the 1600's. Grazing, along with changes in climate, has been implicated in the change from perennial grasslands to shrub-dominated desert communities in many areas of the southwest (Neilson 1986, Hobbs and Huenneke 1992). We are not aware of any studies comparing grasshopper species composition between desert shrubland and perennial grasslands in the southwest.

In the Intermountain West, uncontrolled grazing during the active growing season, may deplete and eventually kill the native bunchgrasses and allow sagebrush to form dense stands (Tisdale and Hironaka 1981). Pierson and Wight (1991) demonstrated that soil near-surface temperature regimes under sagebrush differed considerably from that of interstices, and suggested that the magnitude of these differences could be enough to strongly influence insect developmental rates. Anderson (1964) and Fielding and Brusven (1993) reported lower grasshopper densities and different species composition on sites with abundant sagebrush cover compared to sites without shrub cover.

Severe, repeated disturbance often results in dominance by annual grasses and forbs. In the sandhills prairie of Nebraska, Joern (1982) described how heavily-disturbed areas around water sources (piospheres) were dominated by weedy annual plants and supported higher grasshopper densities with a greater proportion of grasshoppers in the subfamily Melanoplinae compared with relatively undisturbed native grassland. Where wildfires have removed the shrub cover, depleted range sites in many areas of the Intermountain West are very susceptible to invasion and dominance by annual grasses, especially cheatgrass, *Bromus tectorum*, and medusahead, *Taeniantherum asperum* (Hironaka et al. 1983). Fielding and Brusven (1993a,b, 1994) reported higher grasshopper densities, especially *M. sanguinipes*, a primary pest species prone to outbreaks, in these annual grasslands compared to perennial-dominated plant communities. The annual grasslands in southern Idaho exhibited low grasshopper species diversity and were dominated by generalist species found in a broad range of habitats. Similar observations were reported by Pfadt (1982) in Arizona. Heavily disturbed sites dominated by annual grasses had lower diversity of grasshopper species and greater numbers of *M. sanguinipes*, compared to less-disturbed sites with more perennial grass cover (Pfadt 1982). However, total grasshopper density was greater on the perennial grassland. California annual grasslands have probably sustained the greatest degree of alteration in the West, but we are not aware of any studies of grasshopper-grazing relationships in this region.

In areas where grazing has been a strong selective force in the evolution of plant communities, it may be expected that the local grasshopper species have also adapted to grazing-induced habitat changes. Bird (1961) suggested that heavy grazing by bison promoted outbreaks of grasshoppers in the Plains areas, although no evidence for this has been reported.

Jaramillo and Detling (1988) suggested that grazing by prairie dogs exerted enough selection pressure to account for morphological and physiological differences between popula-

tions of blue grama grass, *Bouteloua gracilis* (H.B.K.) Griffiths from sites with different grazing histories. Painter el al. (1989) also found genetic differences between populations of *Agropyron smithii* Rybd. from sites with different grazing histories. Given the rapid evolutionary rate of insects in general and the plasticity of some grasshopper species (such as *M. sanguinipes*), it would not be surprising to find differences between populations of grasshoppers from areas with different grazing histories, although the greater mobility of grasshoppers suggests that intraspecific differences would be observed between widely separated regions.

Soil properties

Livestock can have long-term effects on properties of soil (Daddy et al. 1988) that may indirectly effect grasshoppers. In semi-arid and arid ecosystems, microbiotic soil crusts (composed of lichens, bryophytes, cyanobacteria) may be important in nitrogen fixation (Snyder and Wullstein 1973), seedling establishment (St. Clair et al. 1984), and soil moisture balance (Brotherson and Rushforth 1983). Trampling by livestock can destroy the fragile microbiotic crust which then requires a lengthy period for recovery (Anderson et al. 1982, Johansen and St. Clair 1986, Marble and Harper 1989). Many species of grasshoppers occasionally feed, and certain species may feed extensively, on mosses and lichens (Sheldon and Rogers 1978, Pfadt and Lavigne 1982). Also, the presence or absence of microbiotic crust could influence oviposition and subsequent development of eggs. In addition, given the pervasive influence of soil properties on host plant quality, destruction of microbiotic crusts could indirectly affect grasshopper population dynamics by reducing the nutritional quality of the host plants (Johansen 1993, Belnap and Harper 1995). Similarly, soil compaction and erosion due to overgrazing could affect grasshoppers by influencing plant community composition and host plant quality.

Landscape spatial patterns

Grazing may alter many characteristics that contribute to the overall quality of the habitat, such as plant physiognomy, microclimate, and nutrient availability. Thus, the spatial and temporal heterogeneity of habitat quality for grasshoppers may be greatly influenced by the particular grazing system in place. No studies to date have examined the consequences of grazing-induced landscape heterogeneity on grasshopper population and community dynamics. Nevertheless, we believe that concepts of landscape ecology can provide insights into grasshopper-grazing relationships and guide future investigations.

Without consideration of landscape-scale patterns produced

by grazing, the aggregate effect of grazing can only be estimated as a function of the average level of grazing across a landscape. A central tenet of landscape ecology is that the whole is not always equal to the sum of the parts, i.e., that the spatial and temporal arrangement of landscape units can influence ecological processes occurring within a landscape (Turner 1989, Dunning et al. 1992). Consequently, averaging heterogeneity across a landscape may not fully account for the population or community dynamics that emerge from patterns caused by livestock grazing.

Landscape ecologists have identified several attributes of landscape structure that could affect population and community dynamics (Dunning et al. 1991, Danielson 1991), such as the shape of patches and the amount of edge between patches, boundary characteristics (Wiens et al. 1985), contrast between patches (Kotliar and Wiens 1990), relative amount of source and sink habitat (Pulliam 1988), diversity of habitat patches, and distance and degree of connectivity between patches (Turner 1990).

The landscape patterns produced by grazing largely depend on the type of grazing system. Coughenour (1991) reviewed the spatial and temporal characteristics of a variety of pastoral, ranching, and natural grazing systems. Intensively managed grazing systems, with fencing and water developments, tend to more fully exploit the available landscape, compared to grazing patterns of native ungulates. Pastoral systems may graze the same areas at the same time each year (yearly migrations between seasonal ranges, such as are in place for grazing sheep in many areas of the West), or may follow random variation in precipitation (Coughenour 1991). Rotational grazing systems create a dynamic mosaic of grazed and ungrazed pastures that changes every year and tend to increase the temporal and spatial heterogeneity of the landscape (fig. 2). Patch grazing occurs when an area is preferentially grazed year after year, resulting in a more static pattern of grazed patches on the landscape. Patch grazing can lead to the development of grazing lawns with nutritional and structural characteristics different from ungrazed patches (McNaughton 1984, Hobbs and Swift 1988). Severe long-term patch grazing can lead to environmental degradation and long-term changes in plant community (Fuls 1992, Bakker et al. 1983).

Grazing systems where grazed patches differ from year-to-year (rotational grazing) may favor species with life histories adapted to frequent disturbances (Southwood 1988), i.e., highly vagile species and/or species with high reproductive potential able to exploit short-duration habitats. High-intensity/short-duration grazing systems designed to fully utilize preferred and less-preferred plants result in a more uniformly grazed patch.

For a less mobile grasshopper confined to a single grazed patch, this will result in a less predictable habitat from year-to-year. For more mobile grasshoppers, intensive grazing will increase landscape heterogeneity and create greater contrast between grazed and ungrazed habitats. If suitable habitat is locally available, a mobile species may be able, in effect, to reduce the temporal heterogeneity of its environment by migrating to more favorable patches of habitat.

Contrast between grazed and ungrazed sites is also relative to the species of grasshopper. Grasshoppers that are very sensitive to grazing-induced habitat changes will perceive greater contrast between grazed and ungrazed patches than will those that are indifferent to such changes.

The temporal and spatial heterogeneity of the landscape may affect competitive interactions and predator-prey, host-parasitoid relationships. Theoretical and empirical studies suggest that environmental heterogeneity may lessen the effects of predation on prey populations by providing refugia for prey (Huffaker 1958, Hassell 1982, Kareiva 1986). Similarly, it has been hypothesized that environmental heterogeneity can disrupt competitive interactions, allowing for the coexistence of competing species (Hanski 1983, Ives 1988, Danielson 1991). The way in which grazing-mediated environmental patchiness affects interspecific interactions is probably highly situation-specific, depending on the life-history characteristics of the organisms involved as well as the composition of habitat types within the landscape.

The degree to which landscape structure influences populations depends in part on the relative scales of habitat patches and dispersal ranges of the organisms (Turner 1989, Danielson 1991). Fahrig and Paloheimo (1988) suggested that if a species disperses long distances in random directions, then landscape structure has little influence on its population dynamics. There is tremendous variation in dispersal range among, and within (McAnelly and Rankin 1986), grasshopper species. Nymphs and brachypterous species may have a home range measured in 10s of meters (Riegert et al. 1954), while macropterous adults may be capable of dispersing over many kilometers (Uvarov 1977, Farrow 1990). Thus, the relevant scale of spatial heterogeneity due to grazing depends partly on the life stage and species of grasshopper involved.

Grasshoppers and grazing: case studies

The objectives and methods of the studies of grasshoppers and grazing varied, making direct comparisons difficult. The various studies also often measured different elements of grazing/grasshopper interactions. Most grazing/grasshopper studies have involved comparisons between grazed and ungrazed patches (pastures). Few studies have described within-patch heterogeneity or the spatial or temporal landscape heterogeneity of grazed and ungrazed patches. Most studies did not discriminate between short-term or long-term effects.

Early surveys (Coyner 1939, Weese 1939, Smith 1940) from the Dust-Bowl era documented greater abundance of grasshoppers on overgrazed areas within the tall-grass prairie region of central Oklahoma. These overgrazed pastures had experienced severe soil erosion. Long-term habitat degradation was evident from the decline of the formerly dominant tall-grass species (*Andropogon scoparius*) and the increase in formerly subdominant grasses and forbs, such as *Buchloe dactyloides* (Weese 1939, Smith 1940). Grazing occurred at the time of sampling, thus it was not possible to determine whether the greater abundance of grasshoppers on the grazed plots was because of the different plant species present or because of the immediate effects of grazing.

More recently, Campbell et al. (1974) reported similar observations in eastern Kansas. Absolute densities of grasshoppers were not measured, but more grasshoppers were captured in sweep samples on pastures that were heavily grazed than on lightly grazed pastures. Heavy grazing had resulted in a considerable decline in range condition (measured as percentage of climax or original perennial grass species) (Herbel and Anderson 1959), a long-term change in habitat. Most species of grasshoppers were more numerous on heavily grazed pastures (as well as on pastures that were burned in early spring), except for *Phoetaliotes nebrascensis*, which was more abundant on lightly grazed pastures. Because short-term effects of grazing and long-term effects of habitat changes were not factored out, it is impossible to determine how much of the differences in abundance of grasshoppers was due to long-term changes in plant species and how much was due to immediate effects of grazing. Results of this study agreed with earlier studies from the tall-grass prairie region (Coyner 1939, Weese 1939, Smith 1940). The authors reasoned that the warmer microclimates associated with burning and grazing were responsible for the increased abundance of grasshoppers, but offered no direct evidence for this hypothesis.

Holmes et al. (1979), in a *Festuca scabrella* Torr. grassland study in Alberta, did not find large differences in grasshopper abundance and species composition over seven years on four fields grazed at different intensities. Johnston et al. (1971) and Willms et al. (1985) described short-term (microclimate and plant biomass) and long-term (plant species composition) differences between grazing treatments, which had been in place for approximately 20 years. The grazing treatments provided high contrasts: at the end of the grazing season, the

most lightly grazed pasture averaged 167 g/m2 aboveground plant biomass, compared to only 8 g/m2 for the most heavily grazed pasture. The heavily grazed pastures experienced a greater range in soil temperatures (at 20 cm depth), being colder in winter and warmer in summer than in the lightly grazed pastures. Soil moisture during the growing season was lower on the heavily grazed pastures than the lightly grazed pasture (Johnston et al. 1971). Long-term degradation of the plant communities in these same pastures was reported by Willms et al. (1985). Rough fescue (*Festuca scabrella* Torr.) disappeared from the more heavily grazed pastures, largely replaced by Parry oatgrass (*Danthonia parryi* Scribn.) at intermediate levels of grazing, and by mixed grasses and forbs at the heaviest levels of grazing. Grasshopper abundance was measured by sweepnet sampling. Absolute densities were not measured. The greatest numbers of grasshoppers were collected from the most heavily grazed pasture, but no tests of statistical significance were reported. Proportions of two of the dominant species, *Melanoplus dawsoni* (Scudder) and *Chorthippus longicornus*, increased and decreased, respectively, with increasing grazing intensity. Other species did not show consistent trends. Although this was one of longest running experiments, the lack of statistical rigor makes it difficult to draw conclusions from this study.

Capinera and Sechrist (1982) and Welch et al. (1991) conducted studies on the shortgrass prairie of northeastern Colorado. Both were relatively small-scale studies (130 ha pastures), comparing grasshopper densities between pastures grazed at different intensities since 1939. Neither study attempted to differentiate between short-term and long-term effects. Klipple and Costello (1960) documented some vegetative changes on the same pastures due to grazing treatment, but Capinera and Sechrist (1982) did not report any significant differences in biomass of particular plant species between grazing treatments. However, total aboveground plant biomass, after grazing, averaged 38 and 149 g/m2 on the heavier and lighter grazed pastures, respectively. Capinera and Sechrist (1982) found greater densities of grasshoppers on the lightly grazed pastures, but members of the subfamily *Oedipodinae* were more abundant on the heavily grazed pastures. Again, it was not possible to differentiate between long-term and short-term effects in this study.

In pastures that were part of the same long-term experimental grazing treatments studied by Capinera and Sechrist (1982), Welch et al. (1991) compared grasshopper densities in 1989 to densities reported by Van Horne et al. (1970) 19 years earlier in the same pastures. In 1970, no significant differences were detected. In 1989, season-long average grasshopper density was greater in the lightly grazed pasture than in the heavily grazed pasture. Total density of grasshoppers averaged less than 2 /m2 in both years. These studies contributed little to our understanding of grazing effects on grasshoppers because no analysis of plant or grasshopper species composition was reported (Welch et al. (1991) did report that the more heavily grazed pasture had 38 percent more bare ground and cactus than the lightly grazed pasture), and both studies were conducted over only one season.

In a mixed-grass prairie study in South Dakota, Quinn and Walgenbach (1990) compared grasshopper species composition among three locations, one of which had not been grazed by domestic livestock for 60 years. The two grazed locations had been heavily grazed, relative to the ungrazed area, until recently, when stocking rates were lowered. This was a large-scale study, with the ungrazed area encompassing 98,000 ha. Grazing in the region apparently contributed to long-term habitat alteration. The ungrazed locations were dominated by *Agropyron smithii*, *Bromus* spp., *Poa* spp., and *Stipa viridula*, whereas the grazed locations were essentially converted to a short-grass prairie, with *Bouteloua gracilis*, *Buchloe dactyloides*, and *Agropyron smithii* as the dominant plant species. Absolute densities were not measured. The greatest variation in total numbers of grasshoppers collected in sweepnet samples was due to site differences within grazing treatment. Grazing treatment effects were confounded with other location specific differences such as soils and plants. Location explained relatively little of the variation, indicating little effect of grazing on total numbers of grasshoppers. However, habitat alteration due to grazing apparently did affect species composition. The dominant species on the grazed and ungrazed locations were Opeia obscura and M. sanguinipes, respectively.

Miller and Onsager (1991) monitored grasshopper populations in crested wheatgrass pastures in Montana grazed under two systems: short-duration, high intensity and season-long low intensity. This study depicted, in detail, short-term changes in host plant quality (protein, water content, and phenolics) in response to grazing and normal phenological development. Bare ground and litter increased, and cover of crested wheatgrass decreased following grazing events. Some regrowth of grasses was observed in the summer after grazing. Protein and water content decreased after grazing in the high-intensity pastures, but increased when regrowth occurred. Fluctuations of protein and water were not as great in the season-long, low intensity pastures. After rain in August, all pastures showed substantial increases in protein and water content. No clear patterns emerged regarding concentrations of phenolics. The authors concluded that grazing had little effect on the normal seasonal

development of populations of the dominant species of grass-hoppers (*M. sanguinipes, Aulocara elliotti,* and *M. infantilis*). However, no ungrazed control pastures were monitored, so one cannot determine whether survival rates would have been different in the absence of grazing.

Fielding and Brusven (1995) measured grasshopper density on fifteen pairs of grazed and ungrazed plots in southcentral Idaho. The ungrazed plots were tracts of rangeland that had not been grazed for at least 10 years and the matching grazed plots were grazed under various systems, mostly rest-rotation systems, where season-of-use is rotated yearly among pastures and one pasture is rested (not grazed) each year. Most rangeland in this area below 1500 m elevation has been heavily impacted by grazing, wildfires, and invasion of exotic annual grasses. The permanently ungrazed plots showed little evidence of recovery from the various disturbances. This is not unexpected, given slow rates of secondary succession in semi-arid climates. However, percentage bare ground was greater and cover of perennial grasses and total vegetative cover was less on the grazed plots. Density of *M. sanguinipes* and total grasshoppers was highest on the ungrazed plots on two of three sampling dates. Because there was little difference in plant species composition between the grazed and ungrazed plots, it seems likely that the grasshoppers were responding primarily to short-term habitat changes. There were no differences in densities between grazing treatments where grazed plots had not been grazed during the growing season prior to sampling (as part of the rest-rotation system). Where grazing had already occurred prior to sampling, differences in densities were more pro-nounced and total grasshopper density was greater on the ungrazed plots on all three sampling dates. No interaction was detected between effects of vegetation type and grazing. These data were taken during years of below-normal precipitation and low density of grasshoppers. More recent observations (Fielding and Brusven, unpublished data) indicated that during a year of above-normal precipitation and below-normal temperatures, *M. sanguinipes* showed a slight preference for grazed habitats. These results suggest that the short-term effects of grazing on quality of habitat are highly dependent on weather conditions.

The dynamic nature of grasshopper populations was empha-sized by Jepson-Innes and Bock (1989). On desert grasslands of southern Arizona, they reported lower grasshopper densities on grazed plots during July and August. In September, density of melanoplines apparently increased greatly, especially on the grazed plots. The authors did not explain the sudden increase in melanoplines or indicate whether plant species dominance changed during late summer, nor did they indicate whether grazing continued during or after September. Climatic patterns probably influenced the results, because this area typically has a rainy season during late summer. However, no data were presented regarding weather and vegetation patterns and no conclusions can be made regarding the shift in grasshoppers species composition in late summer and the differing response to grazing then.

Constraints of climate

Large-scale climatic patterns represent the highest level of the hierarchy described in this paper. As a higher level, it sets constraints on the dynamics operating at lower levels. The seasonal distribution and amount of precipitation, rates of evapotranspiration, and temperatures influence the types of plant community, species of grasshopper, and types of grazing regimes that are viable alternatives within a geographic region. Therefore, it seems likely that grasshopper-grazing dynamics vary geo-graphically. One trend seems evident regarding geographical variation in grasshopper responses to grazing. Results from the studies discussed previously indicate an apparent trend towards a more negative response to grazing with decreasing productivity of arid regions. However, too few observations have been made to test this relationship statistically.

Summary

The question "Does livestock grazing promote or prevent grasshopper outbreaks"? is overly simplistic. The answer varies according to species of grasshopper, geographic region, plant community, grazing system, and yearly variation in weather. Long-term effects of grazing may differ from short-term effects. Therefore, generalizations are impossible. Most studies have noted species-specific responses to grazing. The responses in some studies varied by season (Jepson-Innes and Bock), or by year (Welch et al. 1991, Fielding and Brusven, unpublished data).

Before it is possible to make reliable, situation-specific predictions of grasshopper responses to grazing, we need much more knowledge of the specific mechanisms underlying the observed patterns. Unfortunately, scientists know little more now than they did in 1924 when Treherne and Buckell in British Columbia observed grazed grasses "continually throwing up small green shoots … [that] afforded ideal food for the develop-ing grasshoppers. … at the first severe heat wave of July, the range moisture gave out entirely, … [and] the grasshoppers, deprived of their succulent feed, … finally descended upon the plants in the fenced [ungrazed] area…" (Treherne and Buckell 1924, quoted in Weese 1938). Most, if not all, studies of the effects of livestock grazing on grasshopper populations have not been very useful because they were only single-sample 'snap-

shots,' or did not report species composition, were not replicated, or data were gathered only at very low densities. Most studies have lacked adequate experimental control to determine the specific mechanisms underlying the observed patterns.

One fairly consistent trend seems to be that where long-term habitat degradation has promoted a plant community consisting of weedy annuals, a relatively greater abundance of grasshopper species with broad niche breadths occurs (Nerney 1958, Pfadt 1982, Joern 1982, Fielding and Brusven 1995). These species of grasshoppers tend to be some of the most pestiferous. Short-term effects vary widely depending on weather, climate, soils, and among plant community. However, it seems that the immediate effect of grazing is more likely to be detrimental for grasshoppers in drier, less productive regions.

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