

Sustainable Management of Insect Herbivores in Grassland Ecosystems: New Perspectives in Grasshopper Control

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Grasshoppers are insect herbivores common to grassland ecosystems worldwide. They comprise important components of biodiversity, contribute significantly to grassland function, and periodically exhibit both local and large-scale outbreaks. Because of grasshoppers' potential economic importance as competitors with ungulate grazers for rangeland forage, periodic grasshopper outbreaks in western US rangeland often elicit intervention over large areas in the form of chemical control. Available information combined with alternative underlying conceptual frameworks suggests that new approaches for sustainable management of grasshopper outbreaks in US rangeland should be pursued. There are many reasons to believe that approaches to grasshopper management that aim to reduce or prevent outbreaks are possible. These habitat manipulation tactics maintain existing ecological feedbacks responsible for sustaining populations at economically nonthreatening levels. Sustainable strategies to minimize the likelihood and extent of grasshopper outbreaks while limiting the need for chemical intervention are a rational and attainable goal for managing grasslands as renewable resources.

Keywords: insect population dynamics, grassland ecology, sustainable pest management, habitat manipulation, prevention of grasshopper outbreaks

Grassland ecosystems cover 30% to 40% of the earth's terrestrial surface, provide critical habitat for large numbers of species, and support extensive grazing economies on every continent except Antarctica (Coupland 1979, Samson and Knopf 1996). In the United States alone, there are approximately 312 million hectares of rangeland (NRC 1994). Fire, grazing, and climate combine to act as the primary ecosystem drivers in grasslands. In combination with local species interactions, these processes set the stage for the unique local structure and function of the system (Coupland 1979). Grasslands that are used to support grazing activities are renewable natural systems, requiring management practices that capitalize on appropriate natural feedbacks and constraints (Fuhlendorf and Engle 2001). This need contrasts significantly with high-input, intensely managed row-crop agriculture, in which many of the natural feedbacks found in grazing systems have been irrevocably altered. Against this backdrop of grasslands as a renewable system, we address the underlying assumptions and strategies for managing grasshopper populations—models of economically significant insect pests in rangeland—to assess and highlight the importance of natural feedbacks in developing appropriate ecologically based strategies.

Insect grazers such as grasshoppers, locusts, and Mormon crickets are common native components of grasslands worldwide. Major plagues of these insects periodically affect the livelihoods of people on six continents and have been reported throughout recorded history (figure 1). Because they feed on plants, their presence in large numbers often puts them in direct competition with livestock and other grazing herbivores.

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Figure 1. This horse-powered grasshopper-catching machine, in use near St. Ignatius, Montana, in 1917, illustrates an early nonchemical technique for grasshopper control. In 2 hours and 15 minutes, approximately 363 kilograms of grasshoppers were caught with this machine, bagged, and dried for use as winter poultry food. Numerous designs for grasshopper-catching machines, or “hopper dozers,” were developed beginning in the 1870s. Although their effectiveness as a control technique was debated, grasshopper-catching machines were advocated as a means of reducing grasshopper populations in infested fields and providing poultry feed, while avoiding risks to livestock from the use of highly poisonous, arsenic-based baits. Photograph: US Department of Agriculture photo archive.

Hewitt and Onsager (1983), for example, estimated economic losses to grasshopper herbivory based on 16 years of data on grasshopper densities, compiled from across the western United States over a period that included both outbreak and nonoutbreak periods. By their calculations, grasshoppers regularly cause the loss of roughly \$1.25 billion per year (converted to 2005 dollars) in forage that could potentially be fed on by livestock.

Despite the negative impacts associated with their voracious appetites, grasshoppers can also make positive contributions to ecosystem-level processes necessary for sustained grassland health (Lockwood 1993, Belovsky 2000, Belovsky et al. 2000a, Lockwood and Latchininsky 2000). For example, grasshoppers can play a major role in nutrient cycling when they are abundant, sometimes increasing primary production (Belovsky 2000) and also serving as a critical food supply for other organisms, especially grassland birds (McEwen and DeWeese 1987). Despite their potential ecological and economic importance, surprisingly little is known about the mechanisms and interactive effects that underlie grasshopper population dynamics and outbreaks (Joern and Gaines 1990, Lockwood 1997, Joern 2000). The situation is complex: Many grass-

hopper species interact with each other, as well as with domesticated and unmanaged grazing animals, in highly variable environments across hundreds of millions of hectares in multiple ecosystem types. Unfortunately, broadly applicable understanding of the processes regulating grasshopper populations is lacking.

The scope, conflicts, and potential pitfalls involved in managing insect pests in renewable resource ecosystems are exemplified by grasshopper control programs in the grasslands of western North America. Although this is a highly complex and often subtle problem, it can largely be distilled into two conflicting issues. Grasshopper outbreaks often elicit responses in the form of large-scale chemical control measures to mitigate potential economic losses. However, the management response itself may do more harm than good, particularly in the long term, thereby jeopardizing the sustainability of grasslands as a renewable resource system (Joern 2000, Lockwood and Latchininsky 2000). We recognize that chemical control is one of only a few options currently available for controlling grasshoppers. Recent advances in environmentally benign application methods and available control agents are having a positive impact (e.g., Lockwood

and Schell 1997) and application methodologies finely tuned to most needs already exist (Cunningham and Sampson 2000). However, the need for control programs of any type to deal with outbreaks after the fact suggests that natural population limits have been breached.

Although economic and political pressures largely drive current approaches to grasshopper management, it is time to develop and institute ecologically based management strategies that minimize the likelihood that damaging grasshopper outbreaks will occur, rather than merely reacting to them when they occur. Situations exist in which short-term grasshopper outbreaks can actually rejuvenate rangeland (Belovsky et al. 2000a), much as fire can be utilized to increase forage quality in many sustainable grasslands. This suggests that chemical control of grasshopper outbreaks should not be the default response under all circumstances (Belovsky 2000). Furthermore, management strategies that reduce the likelihood of grasshopper outbreaks have the potential to be compatible with other sustainable rangeland management practices that aim to improve overall grassland health (Samson and Knopf 1996, WallisDeVries et al. 1998). Our main thesis is that the seemingly utopian goal of preventive management, although challenging, can be achieved by synthesizing available ecological principles with existing methodologies and targeted empirical work.

The grasshopper problem and chemical control in North American rangeland

Grasshoppers and Mormon crickets in western North America often reach outbreak densities that have significant economic impacts on the grazing industry, especially during drought periods when forage is already scarce (Hewitt and Onsager 1983). Collectively, grasshoppers are often the dominant herbivore at a given site and can rival large mammalian grazers in terms of ecosystem impact when at high densities (Mitchell and Pfadt 1974, Belovsky 2000). For example, annual vegetation consumption by grasshoppers averaged 1.25 to 2.5 times more than that of mammalian herbivores in Palouse prairie (Belovsky 2000). In tallgrass prairie (Konza Prairie, Kansas), grasshopper biomass in 2002 was 0.6 to 1.2 grams (g) per square meter (m^2), comparable to bison biomass of 1.3 g per m^2 . Grasshopper outbreaks can also serve as a source of mass movement from large expanses of public rangeland to adjacent private cropland, where significant crop damage can occur (Onsager and Olfert 2000). Extensive grasshopper outbreaks tend to occur somewhat cyclically in western North America, while severe but localized infestations typically occur somewhere in western North America every year (figure 2; Belovsky 2000). Once observed, high densities of grasshoppers and Mormon crickets often trigger human intervention in the form of insecticides to limit future

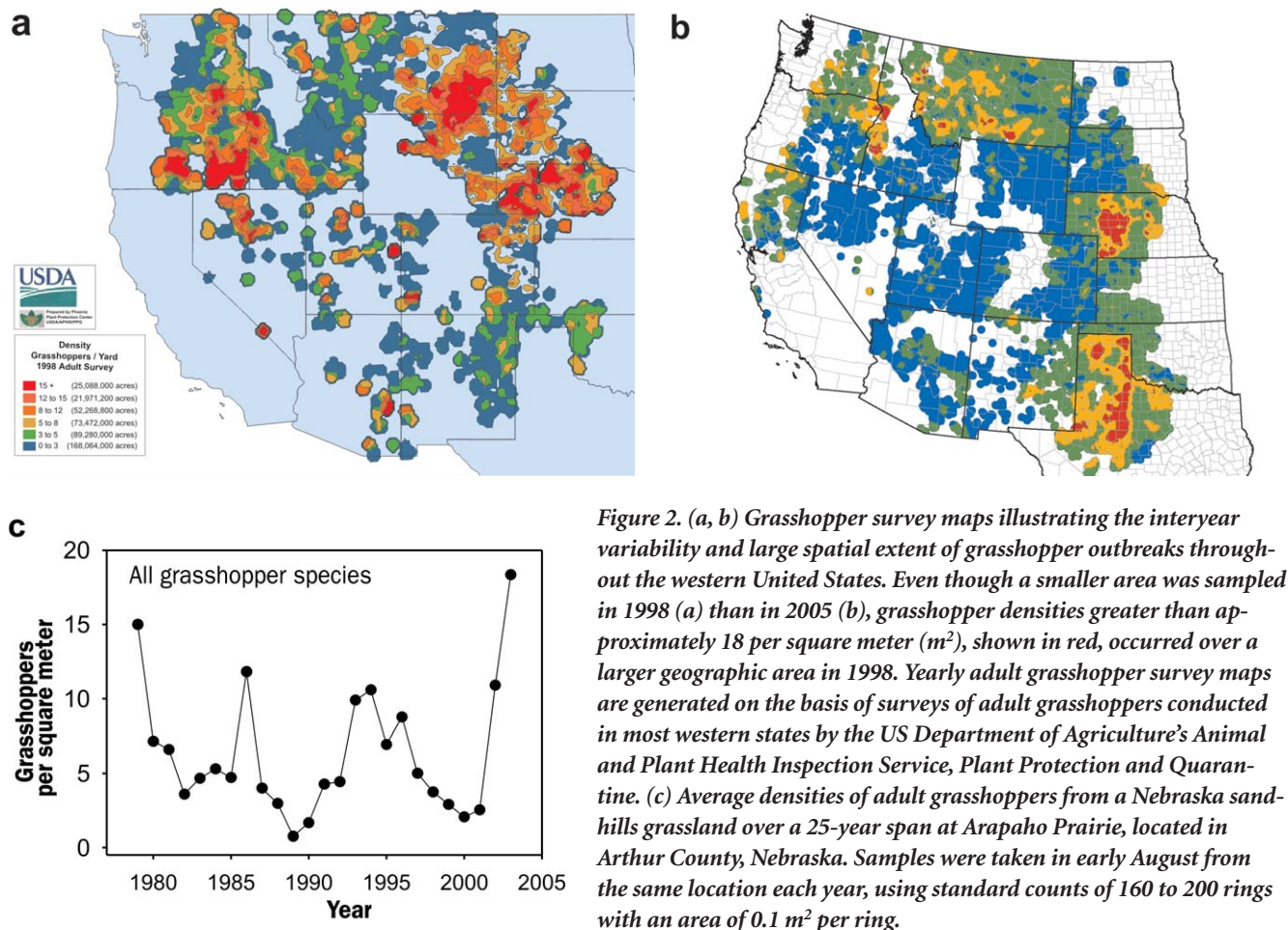


Figure 2. (a, b) Grasshopper survey maps illustrating the interyear variability and large spatial extent of grasshopper outbreaks throughout the western United States. Even though a smaller area was sampled in 1998 (a) than in 2005 (b), grasshopper densities greater than approximately 18 per square meter (m^2), shown in red, occurred over a larger geographic area in 1998. Yearly adult grasshopper survey maps are generated on the basis of surveys of adult grasshoppers conducted in most western states by the US Department of Agriculture's Animal and Plant Health Inspection Service, Plant Protection and Quarantine. (c) Average densities of adult grasshoppers from a Nebraska sandhills grassland over a 25-year span at Arapaho Prairie, located in Arthur County, Nebraska. Samples were taken in early August from the same location each year, using standard counts of 160 to 200 rings with an area of $0.1 m^2$ per ring.

movement or damage to rangeland (figure 3). Control efforts during major grasshopper outbreaks often include the aerial application of broad-spectrum insecticides, such as malathion and carbaryl, to millions of hectares of US grasslands, typically with minimum treatment blocks of about 4000 hectares each (Quinn et al. 2000).

Population dynamics

A fundamental problem in the current approach to managing grasshoppers is the reliance on an inappropriate conceptual model as a basis for understanding grasshopper population dynamics. Historically, the climate release hypothesis (Andrewartha and Birch 1954) has dominated decisionmaking in grasshopper management. This model assumes that the potential for unconstrained, exponential population growth is coupled to unpredictable weather that fluctuates between suitable and unsuitable states. In accordance with this model, the main goal in traditional grasshopper control has been to use invasive methods to reduce rangeland grasshopper populations during outbreaks. A critical disadvantage of relying on climate release as a primary conceptual

framework, however, is that these measures are largely alien and even contrary to the many underlying nonweather-determined ecological feedbacks (e.g., competition and natural enemies) inherent in renewable ecosystems.

It is time to incorporate significant advances in researchers' understanding of insect population dynamics into grasshopper control. A variety of nonlinear population responses that are important for understanding grasshopper population dynamics, including feedbacks and thresholds, have been discovered in population models. These complex population responses arise from dynamic density-dependent and frequency-dependent food web interactions (Schmitz 1998, Danner and Joern 2004) and predict a range of indirect feedback relationships that can greatly modify direct responses. Density dependence results from limited resource (e.g., food) availability within a trophic level, or from interactions with natural enemies between trophic levels, and these interactions limit grasshopper populations. Chemical control necessarily disrupts or otherwise affects these relationships in unpredictable ways. In the simplest case, other arthropods besides the target may also be killed, freeing up resources or reduc-



Figure 3. Workers spreading sodium arsenite dust for Mormon cricket control in Sheridan County, Wyoming, in 1935. Nonspecific and highly toxic arsenic-based compounds were the principal toxin used in grasshopper and Mormon cricket control programs from 1885 until the 1940s, when newer, more potent insecticides such as sodium fluosilicate and chlorinated hydrocarbons became widely available. After problems were discovered with the persistence and bioaccumulation of DDT in the 1960s, the organophosphate compound malathion became the most common insecticide used for grasshopper control; it is still used, along with the carbamate carbaryl, for grasshopper control programs in the United States. Over the last few years, Dimilin (diflubenzuron), which functions as a chitin inhibitor and prevents successful molting of insects, has seen increasing use in grasshopper control programs in the western United States because it has fewer nontarget effects on terrestrial insects and vertebrates. Photograph: US Department of Agriculture photo archive.

ing mortality from natural enemies. As interaction webs become more reticulated, it becomes increasingly difficult to predict responses to perturbation. Grasshopper control strategies have recently begun to take these factors into account, but the planning and actual application sometimes still proceed without incorporating the notion that feedbacks and indirect effects of intervention are important. The development of reduced area and agent treatments (Lockwood and Schell 1997), in which untreated swaths are included as refuges for natural enemies, recognizes the importance of density-based indirect interactions.

In addition to the range of indirect, density-dependent interactions embedded in natural food webs, available population models and empirical studies now identify discontinuous threshold conditions in grasshopper dynamics that are likely to be common and important (Belovsky and Joern 1995, Lockwood 1997). Combined, complex sets of indirect interactions coupled to thresholds challenge researchers' ability to predict not only the timing and spatial extent of outbreaks but also grasshopper population responses following chemical control programs. The failure of the climate release hypothesis to take account of these important ecological processes makes it an inappropriate framework for developing management programs, as natural limits to population abundances cannot be incorporated in this model. Because maintaining natural limits is a key ingredient in rational long-term management plans, this omission is critical.

Can scientists reconcile documented and unpredictable contributions from weather with feedback models? Fortunately, we can, as weather clearly interacts with biotic factors, especially in its effect on food plant availability and quality, or with temperature-driven physiologies that influence grasshopper digestion or species interactions (Logan et al. 2006). Although weather certainly affects demographic responses, negative feedbacks inherent in natural populations ultimately trump the direct contribution of weather in determining population dynamics for most of the population cycle (Ovadia and Schmitz 2004). Because a primary goal of grasshopper management should be to minimize opportunities for populations to reach critical density thresholds that facilitate outbreaks, we suggest that an appropriate conceptual model of grasshopper population dynamics, one that can be used as a sound foundation for ecologically based management, must include mechanistic insights that acknowledge thresholds even if they are difficult to specify with complete detail. In fact, we expect this to be true in making sound pest management decisions in general.

The sustainability of current strategies

Is waiting for outbreaks to occur and then responding to them with large-scale control programs a sustainable approach? Control tactics using chemicals or "biological insecticides" can be effective short-term practices for reducing outbreak populations of grasshoppers and providing immediate protection of treated grasslands and adjacent crops. The primary goal in chemical control is to kill a large fraction

of the collective grasshopper population and thus save forage in the current year, and potentially to reverse the direction of population increase so that the problem does not recur the next year. However, a number of drawbacks are associated with managing pest outbreaks in this manner in renewable resource systems. One of the most obvious is that the overwhelming majority of grasshopper species that are killed in control programs are not causing the problem and may be beneficial (Lockwood 1993, Belovsky et al. 2000a, 2000b). Of the approximately 400 grasshopper species in the western United States (Pfadt 2002), fewer than two dozen are estimated to be capable of causing significant economic damage to crops and forage (Parker 1952), and even fewer species are economically important on a regular basis. Some species, such as the snakeweed grasshopper (*Hesperotettix viridis*), may even help to control noxious rangeland plants and contribute to the success of mechanical or herbicide treatments designed to reduce these plants' abundance (Thompson et al. 1996). In addition, grasshoppers are a major food source for many grassland vertebrates and invertebrates. Finally, herbivory by grasshoppers may also have other important ecological consequences of interest to land managers and conservation organizations, including maintaining a diverse plant community and increasing rangeland productivity (Belovsky 2000, Belovsky et al. 2000a), all of which could be negatively affected by widespread chemical control activities.

Another problem of equal if not greater importance is that chemical control strategies can also kill many other arthropods, thus disrupting other important ecological interactions (Lockwood et al. 1988). The general public is becoming increasingly critical of large-scale chemical programs because of their harmful effects on biodiversity (Belovsky et al. 2000a, Joern 2000). Paradoxically, nontarget arthropods killed by chemical application include those with the greatest potential to help regulate grasshopper populations over the long term (Joern 2000). Fortunately, chemical control strategies have now evolved to incorporate the application of carbaryl bran bait, toxic only for organisms that consume wheat bran (Onsager 2000), along with untreated swaths that act as refuges for natural enemies in aerial spray programs to further maintain the presence of nontarget species (Lockwood and Schell 1997). By reducing grasshopper numbers in treated swaths, this strategy dilutes overall grasshopper densities, and the remaining natural enemies in untreated areas are more likely to impose a limit on grasshopper populations (Onsager et al. 1981, Belovsky and Joern 1995, Onsager and Olfert 2000). Targeted biological control of grasshoppers in the United States is currently not an option, as few specialized agents for biological control exist, and augmentative biocontrol with native parasites or pathogens appears both logistically and economically impractical (Onsager and Olfert 2000). The importation of nonnative agents to manage endemic grasshoppers in a neoclassical biocontrol scenario has not proved effective, and will justifiably meet strong resistance on ecological and environmental grounds (Lockwood 1993).

In addition to environmental drawbacks, there are also considerable economic costs associated with attempting to suppress large-scale grasshopper outbreaks with insecticides. These problems are often exacerbated by the geographic extent of the outbreak area (figure 2) and the high costs associated with the purchase and application of chemical control agents. During a major outbreak in 1985, over 22 million hectares of western US rangeland were heavily infested with grasshoppers. Of this, over 5 million hectares of rangeland were treated by the federal government with more than 2,900,000 kilograms of the active ingredients in malathion and carbaryl (Quinn et al. 2000). Comprehensive economic models suggest that traditional insecticide control programs for grasshoppers are cost-effective only under very restrictive conditions (Hewitt and Onsager 1983, Onsager and Olfert 2000). New chemical agents and application practices to reduce application rates of active ingredients rarely reach beyond benefit–cost ratios supporting economic justification for treatment (Onsager and Olfert 2000).

Perhaps even more disconcerting, from a sustainable management perspective, is that large-scale chemical applications often do not provide predictable long-term control (Zimmerman et al. 2004) and may even exacerbate grasshopper problems (Lockwood et al. 1988). As a result, the demonstration project on grasshopper integrated pest management conducted by the US Department of Agriculture's Animal and Plant Health Inspection Service from 1987 to 1994 concluded that there is an urgent need to develop management solutions that focus on outbreak prevention rather than suppression (Cunningham and Sampson 2000).

Can outbreaks be prevented?

The idea of managing grasshoppers and locusts in a preventative rather than a crisis-driven manner can be traced to Sir Boris Uvarov, who is known as the father of modern grasshopper and locust biology. In a 1969 talk presented shortly before his death, titled "Current and Future Problems of Acridology," Uvarov argued in favor of preventative management, stating that "such an approach to the problem could lead to the gradual replacement of the as yet essential direct control by the regulation of acridoid population dynamics by deliberate modification of the key ecological factors" (Uvarov 1977, p. 531). However, because of the historical emphasis on outbreak suppression and intervention using a climate-release framework, ecologically based preventative grasshopper management in renewable resource systems has received very limited attention since Uvarov's proposal. Few, if any, coordinated attempts have been made to exploit the many natural negative feedbacks that can limit grasshopper populations. A paradigm shift regarding the conceptual framework underlying grasshopper population dynamics and management tactics is needed to encourage alternative approaches.

The underlying conceptual basis of grasshopper management can be viewed as a three-tiered system of outbreak prevention, intervention, and suppression. Preventative approaches have a number of potential advantages in re-

newable resource systems. First, prevention can be sustainable, both economically and environmentally. Second, preventative approaches have the potential to be effective in preserving the biodiversity that can have beneficial effects on a variety of ecological processes (Joern 2000). Third, the preservation of biodiversity inherently maintains organisms that act as naturally regulating agents. Although there are advantages to preventative pest management approaches, such approaches must be economically viable and compatible with other management and conservation goals (Lockwood and Latchininsky 2000). It is also important to distinguish between prevention, intervention, and suppression as insect management goals, because they operate at different stages of the outbreak process. Preventing an outbreak from occurring in the first place, the primary focus of this article, differs from intervention or suppression, the aim of which is to prevent an existing outbreak from expanding, using chemical pesticides or biopesticides. The terms "preventive control" and "preventive management" are increasingly being used to describe control efforts at the start of pest outbreaks. However, this form of intervention omits the critical first step—prevention.

Do range scientists or ecologists have theoretical insights or empirical evidence to indicate that the implementation of preventative grasshopper management strategies will succeed? The development and application of truly preventative management techniques to reduce the likelihood of grasshopper outbreaks requires a sound ecological framework. A large body of ecological data relevant to the problem exists, but its synthesis and subsequent application remains unfinished. Although numerous interactions between food limitation, local weather, and natural enemies are responsible for determining grasshopper population densities (Joern and Gaines 1990, Belovsky and Joern 1995, Joern 2000), any factor that can limit grasshoppers on rangeland over the long term and keep population levels below this resource-based natural limit will reduce the likelihood of grasshopper outbreaks. By manipulating habitat characteristics that affect grasshopper population dynamics, it should be possible to use habitat manipulation to reduce the likelihood of grasshoppers reaching outbreak densities (Onsager 2000).

Grasshopper control often focuses on reducing local and regional densities of grasshoppers, with only lip service paid to actual forage loss in relation to the needs of large grazers. It is important to remember that the real focus of grasshopper management should be the management of the rangeland vegetation, including natural processes that structure native plant communities (Fuhlendorf and Engle 2001, 2004). High grasshopper abundances should not be a problem in a given year if vegetation is abundant, and increased ground cover during years with high vegetation production could lead to reduced grasshopper densities in the following year (Onsager 2000). By recognizing the importance of vegetation management in grasshopper control, we gain a new perspective as well as new management options. Vegetation management can be used both to optimize forage production for grazers and to manage grasshopper populations by

manipulating grasshopper habitat. Although much remains to be learned about the ecological processes underlying these techniques for application at large scales in a variety of different ecosystems, they hold considerable promise.

Ecological processes and habitat manipulation

Habitat manipulation is a promising starting point for developing preventive strategies. It is increasingly recognized that heterogeneity in grassland habitats plays an important role affecting almost all ecological processes and should be retained (Fuhlendorf and Engle 2001, 2004). Repeated large- and small-scale disturbances from habitat manipulations such as fire and grazing result in heterogeneous grassland vegetation structure and plant species composition (Fuhlendorf and Engle 2001, 2004). This in turn has important consequences for the abundance and species diversity of grasshoppers (Joern 2004, 2005) and other taxa (Fuhlendorf and Engle 2004). Insects are highly responsive to alterations and heterogeneity in habitat structure (Andow 1991, Tscharntke and Greiler 1995), providing significant opportunities for managing populations and communities through habitat manipulation. Patch grazing and discrete fires promote a heterogeneous, shifting mosaic of vegetation across the landscape (Fuhlendorf and Engle 2004). Grazing intensity can be maintained while managing landscapes for multiple objectives, including biodiversity, agricultural productivity, and prevention of insect outbreaks.

Although the impact of habitat manipulation on naturally occurring ecological processes that limit and regulate grasshopper populations has been the subject of limited empirical study, numerous processes can be modified through habitat manipulation to decrease the occurrence of grasshopper outbreaks in grassland systems. Habitat manipulation can directly affect the population dynamics of pest insects by slowing nymphal development, reducing survival and reproduction, or simply decreasing year-to-year variability in those life history characteristics (Onsager and Olfert 2000). In addition, both immediate and long-term direct effects of habitat management alter ecological interactions affecting grasshoppers. Habitats can be manipulated in ways that reduce grasshopper food abundance or availability at critical stages of the insects' life cycle (Belovsky et al. 2000b). Such manipulations could include introducing direct competition from mammalian herbivores such as livestock (Onsager 2000), altering food quality, manipulating plant composition, and increasing the abundance of natural enemies (Belovsky et al. 2000b, Joern 2000). Economically unimportant grasshopper species can limit the populations of economically important grasshopper species by competing directly for limited food or by increasing the success of shared natural enemies when they co-occur. The ability to manipulate specific competitive interactions and predict their outcomes is not yet well developed (Belovsky et al. 2000b, Joern 2000) but clearly warrants further study.

Habitat manipulation can also change microhabitat structure and availability in ways that directly affect the develop-

ment and survival of grasshoppers (Willott and Hassall 1998, Onsager 2000). For example, altering the availability of bare ground and canopy cover can affect insect thermal performance by modifying habitat available for optimal thermoregulation (Onsager 2000). Similarly, habitat management can result in longer-term changes to plant community composition (Fielding and Brusven 1996, Onsager 2000, O'Neill et al. 2003), affecting the food resource base and habitat structure. Much evidence now indicates that grasshoppers are food limited, which determines ceilings for the number of grasshoppers that can survive and reproduce (Belovsky and Joern 1995, Danner and Joern 2004). Altering vegetation structure also affects grasshopper numbers indirectly by increasing the abundance or efficiency of natural enemies. Both short- and long-term positive and negative feedbacks associated with food-limitation and natural enemies are quite strong in grassland systems, and their relevance to grasshopper population dynamics and management must be explored in much greater detail. As Joern (2000) noted, ecological processes can interact with each other and with weather conditions, so responses may not always be linear or predictable. Furthermore, given the range of variation among grasshopper species in phenology, habitats, and food plant preferences, any habitat management approach is unlikely to affect all grasshopper species in the same way (Onsager 2000).

Habitat manipulation: Some examples using ecosystem drivers

No comprehensive examinations exist that describe how various habitat management techniques might be used to manage pests in renewable grassland systems. Over the past 30 years, grasshopper densities and species composition have been sampled in rangeland systems undergoing numerous types of habitat manipulation, including mechanical manipulations, herbicide applications, rangeland reseeding, burning, and livestock grazing (table 1). Although the methodologies vary greatly, these studies illustrate that many different techniques can affect grasshopper densities or species composition, or both. Most existing studies have simply measured short-term responses of grasshopper densities or species composition, with little attempt to understand the underlying ecological mechanisms (table 1; Fielding and Brusven 1996, O'Neill et al. 2003). Notable exceptions are burning and grazing, both of which have been examined in greater depth in multiple ecosystems.

Fire. Fire can influence grasshopper population dynamics and community composition in a number of grassland ecosystems (table 1). The evidence to date suggests that fire is a strong candidate for use as a preventative pest management tactic in association with other vegetation management activities, and that both direct and indirect effects on grasshoppers will result. Direct effects of fire include killing adult and nymphal grasshoppers (Bock and Bock 1991) and increasing mortality for eggs near the soil surface by elevating soil temperatures. Many effects are indirect, including (a) fire-induced changes

in host plant quality and plant community composition that mediate the effects of burning on grasshoppers following a fire (table 1; Porter and Redak 1996, Vermeire et al. 2004); (b) negative impacts on natural enemy abundance or efficiency through changes in habitat structure; and (c) postfire differences in soil moisture or temperature regimes, leading to increased egg mortality or accelerated hatching phenology (Riegert and Varley 1972, Meyer et al. 2002).

As illustrated in table 1, the responses of grasshoppers to fire differ within and among ecosystems. In the northern and southern Great Plains, burning led to short-term reductions of grasshoppers in studies by Branson (2005) and Vermeire and colleagues (2004). In tallgrass prairie, by contrast, densities typically increase following fire, because nutrient availability in leaves and primary production increase after burning (table 1; Meyer et al. 2002, Joern 2004). Postfire

changes in plant species composition can also play an important role (Porter and Redak 1996, 1997). For example, populations of *H. viridis*, a specialist grasshopper, declined following a fire that killed most of the species' host plants in the family Asteraceae (table 1; Vermeire et al. 2004).

Some studies have addressed the potential for using fire in the southern and northern Great Plains to help reduce pest grasshopper species over the short term (Vermeire et al. 2004, Branson 2005). In these cases, however, reductions in grasshopper populations after fire persisted for only one to two years (table 1), which suggests the use of fire in a truly preventative fashion will remain limited. The timing and intensity of a fire largely determine whether grasshopper densities are reduced because of the direct and immediate effects of fire. (table 1; Branson 2005). Scientists' limited understanding of underlying mechanisms also constrains the ability to predict

Table 1. Representative case studies of the effects of grassland habitat manipulation on grasshopper population dynamics and species composition.

Habitat manipulation	Location	Result	Reference
Mechanical			
Three treatments: (1) contour furrowing, (2) rangeland scalping, (3) scalping and interseeding	Northern mixed-grass prairie, Montana	All three treatments generally reduced grasshopper densities compared with controls. Economically damaging grass-feeding species were less abundant on treated plots. The differences were hypothesized to result from changes in plant species composition and abundance. Grasshopper densities in all plots were less than one per square meter.	Hewitt and Rees 1974
Sagebrush removal and legume interseeding	Northern mixed grass prairie, Montana	Treatment had minimal effects compared with untreated controls. <i>Melanoplus sanguinipes</i> , a mixed-feeding economic species, increased in treated plots, but grass-feeding grasshoppers were unaffected.	Hewitt and Onsager 1988
Herbicide			
Spraying 2, 4-D for control of sagebrush	Northern mixed-grass prairie, Montana	Treatment had minimal effects on grasshopper densities. Grasshopper densities were very low during the study (less than one per square meter). All common grasshopper species were grass feeders or mixed feeders.	Hewitt and Rees 1974
Spraying 2, 4-D	Pasture habitats, Saskatchewan, Canada	Densities were approximately 8 times higher in plots treated 5 to 10 years previously than in untreated plots. Spraying strongly influenced grasshopper species composition. An economically damaging grasshopper species, <i>Camnula pellucida</i> , made up 43% of the grasshopper population in sprayed plots and 0% in unsprayed plots. Higher densities were hypothesized to result from the higher abundance of grasses (56% higher) and bare ground (2 times higher) with herbicide application.	Secoy et al. 1981
Fire			
Summer wildfire	Semiarid grassland, Arizona	Densities were 60% lower in the first year following a summer wildfire that occurred while the dominant grasshopper assemblage was alive. The species-specific reductions were hypothesized to result from direct mortality and reduced grass availability. Density differences disappeared in the second year postfire.	Bock and Bock 1991
Spring prescribed fire	Tallgrass prairie, Kansas	Grasshopper abundance increased (up to 6 times higher than the norm) in the same year following spring burning; longer burn intervals had no detectable effect overall, but responses by individual species to the burn interval were observed. Burning effects did not normally carry over to the next year. Abundances were greatest when plant biomass and canopy height was lowest and spatial heterogeneity greatest, a response that was greatest immediately following fire.	Joern 2004, 2005

(continued)

grasshopper responses to burning. The effects of fire on vegetation often interact with precipitation regimes in semiarid ecosystems (Lesica and Martin 2003), and as a result, insect responses may differ between years. A further complication is that grasshopper responses to fire are often species specific (Joern 2004, Vermeire et al. 2004). To facilitate grazing opportunities, researchers must focus on the response of vegetation to fire rather than on direct control of grasshoppers to use fire successfully as a long-term grassland management tool. The responses of vegetation to fire as a management tool must be compatible with long-term land management goals and will be dependent on local habitat conditions (Samson and Knopf 1996).

Grazing management. Livestock grazing can also affect grasshopper population densities and species composition

(table 1; reviewed in Fielding and Brusven 1996, O'Neill et al. 2003). In mechanistic terms, foraging by livestock may reduce food availability for grasshoppers either directly through competition or indirectly through changes in plant community composition (Fielding and Brusven 1996, Belovsky et al. 2000b, O'Neill et al. 2003). In addition, both grazing and trampling can affect the structure and microclimate of the grasshopper habitat (O'Neill et al. 2003). Unfortunately, differences in vegetation and habitat characteristics between rangeland management treatments have not been quantified in most studies.

A number of grazing system attributes can potentially be manipulated in the northern Great Plains of the United States, with both short- and long-term effects on grasshopper population dynamics (Onsager 2000). Many pest grasshopper species in the northern Great Plains thrive in response to

Table 1 (continued)

Habitat manipulation	Location	Result	Reference
Fall prescribed fire	Sand sagebrush–mixed prairie, Oklahoma	Total abundance was unaffected by fire. <i>Hesperotettix viridis</i> , a specialist on Asteraceae species, was reduced by more than 80%. <i>Ageneotettix deorum</i> , a species that lays shallow egg pods, was reduced by 65%. The differences were hypothesized to result from damage to host plants and egg mortality.	Vermeire et al. 2004
Spring prescribed fire	Native perennial grassland, California	Grasshopper abundance and biomass were lower for two years following the burn, with densities approximately 43% lower in the second year. Species diversity was higher following the fire, as a result of a reduction in the dominant grasshopper species. The differences were hypothesized to result from reduced forb cover.	Porter and Redak 1996
Fall wildfire	Northern mixed-grass prairie, North Dakota	Grasshopper densities were approximately 44% lower for one year following the fire, with much of the reduction due to a decline in species in the Gomphocerine subfamily. No differences were apparent in the second year postfire.	Branson 2005
Grazing Bison grazing	Tallgrass prairie, Kansas	Grasshopper densities were approximately 2.5 times higher in pastures with bison grazing than in ungrazed pastures. Species richness averaged approximately 45% higher in bison-grazed pastures. Species richness responded positively to vegetation heterogeneity created by grazing. Grazing had a much greater effect on densities than did fire, and there was no interaction between fire and grazing.	Joern 2004, 2005
Season-long and twice-over rotational cattle grazing management	Northern mixed-grass prairie, North Dakota	Densities averaged approximately 3.3 times higher over a five-year period in pastures with season-long grazing management than in pastures with twice-over rotational grazing management. Densities were approximately 6 times lower in rotational pastures during two years in which outbreak densities were reached under season-long grazing. Late-season grasshopper species did not reach economically damaging levels with rotational grazing, and no economically important grasshopper species were more abundant with rotational grazing. Differences were hypothesized to result from increased ground cover and shading in the rotational pastures.	Onsager 2000
Cattle grazing	Cheatgrass–sagebrush–bunchgrass grassland, Idaho	<i>Melanoplus sanguinipes</i> , an economically damaging species, was more abundant on ungrazed plots in three of four years. This species was more abundant in grazed plots in a year when above-average rainfall led to increased plant production and regrowth following grazing. Fielding and colleagues (2001) hypothesized that grazing during dry years increased food limitation for grasshoppers, whereas grazing during the cool, wet year led to more favorable habitat conditions for <i>M. sanguinipes</i> .	Fielding et al. 2001

enhanced capacity for thermoregulation in microhabitats with bare soil and little shade (Onsager 2000). Grazing management practices that vary the time and intensity of defoliation can serve to preserve or enhance canopy shading during critical parts of grasshopper development, as well as decreasing bare ground. Thus, grazing strategies that manipulate habitat structure can affect grasshopper performance by reducing the habitat available for thermoregulation and hence for optimal digestion (Onsager 2000, Logan et al. 2002).

Recent research on native rangeland also indicates that different intensities and schedules of cattle grazing (e.g., season-long versus twice-over rotational grazing) affect vegetation structure and species composition, which in turn influence grasshopper performance and the likelihood of population outbreaks (figure 4; Onsager 2000). Outbreak densities were observed in pastures with season-long grazing, but not in twice-over rotational pastures, in years in which outbreaks were likely (figure 4). In pastures with twice-over grazing, fewer nymphs of traditional outbreak species (e.g., *Melanoplus sanguinipes*) were observed, forage consumption by grasshoppers was considerably less, and both nymphal development and survival rates were lower. Differences in grasshopper responses were consistent with the hypothesis that differences in microhabitat structure resulting from the two grazing management practices (e.g., increased canopy cover during critical periods of grasshopper development and decreased amounts of bare ground in the rotational system) altered grasshopper thermoregulatory capacities and consequently affected development and survival (Onsager 2000).

Differences in the underlying nature of critical responses among grassland ecosystems experiencing different climatic conditions are an important consideration when using grazing as a grasshopper management strategy at different sites. Grasshopper responses to grazing have been shown to vary in important ways between ecosystems in western North America (table 1; Fielding and Brusven 1996, Onsager 2000, O'Neill et al. 2003). At southern Great Plains, high desert, or semidesert grassland sites, grasshoppers are typically more numerous in ungrazed settings (Capinera and Sechrist 1982, Fielding et al. 2001). In contrast, significantly higher densities are often associated with heavily grazed systems when compared with ungrazed systems in the northern Great Plains and tallgrass prairie (table 1; Onsager 2000, O'Neill et al. 2003, Joern 2004). These results parallel geographic differences in responses to weather conditions (Onsager 1987, Capinera and Horton 1989, Fielding and Brusven 1990, Kemp and Cigliano 1994): Southern or semidesert populations are more responsive to precipitation and northern populations are more responsive to temperature. As a result of this variation, there will be no global prescription for a single grazing management strategy; instead, managers must develop region-specific approaches.

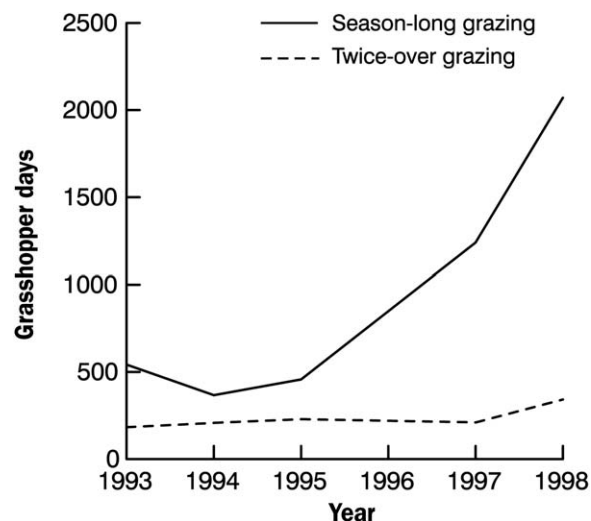


Figure 4. Grasshopper days, an index of cumulative seasonal abundance, in season-long (solid line) and twice-over rotational (dashed line) grazing management pastures in western North Dakota from 1993 to 1998. Grasshopper days were calculated by plotting population densities for third-instar or larger grasshoppers over the course of a summer and then determining the area under the resulting curve. Modified from Onsager (2000).

Developing new directions in preventative management

There are many potential constraints to the development and utilization of preventative management techniques in renewable rangeland systems in western North America, but we believe each is a solvable problem. The inherent variation in climate, vegetation, and grasshopper population densities in grassland systems necessitates the initiation of long-term habitat management experiments to determine whether a given type of habitat manipulation will be effective in reducing grasshopper outbreaks. Such large-scale, long-term, experimental examinations of habitat manipulation practices are expensive and require consistent management, making them logistically difficult. The cyclical nature of grasshopper populations makes it difficult to determine whether a given habitat management technique reduces the likelihood of grasshopper outbreaks—studies of which have yet to be done in earnest—and experiments must be conducted over a period when grasshopper populations are increasing in the region of the study.

It is unrealistic to think that land managers will implement grasshopper management systems to reduce outbreaks of a periodic pest unless such approaches provide additional benefits to grazers (Lockwood and Latchininsky 2000). Preventative pest management systems will be implemented only if they are compatible with other economic, conservation, and management objectives for ranchers, conservationists, and land managers in western North America. To be effective, preventative grasshopper management tools must be integrated

into multidisciplinary management systems, typically before a period of increasing grasshopper densities, as some habitat management techniques will have little or minimal effects after an outbreak occurs (Lockwood and Latchininsky 2000, Onsager 2000).

Fortunately, vegetation management practices known to affect grasshopper populations are already used as components of other land management strategies. For example, both grazing management and prescribed fires are widely used in a variety of different habitat types to manage the establishment and spread of invasive exotic weeds (Tu et al. 2001). Additional research will be required, often on an ecosystem-specific basis, to determine the proper habitat manipulation schemes required to yield synergistic benefits of grasshopper management and other desirable outcomes. Other land management objectives that could also be compatible with grasshopper management through habitat manipulation include improving grassland conditions, increasing plant production, increasing plant or insect biodiversity, and improving economic benefits for ranchers (Samson and Knopf 1996, WallisDeVries et al. 1998).

Is preventative management feasible?

The dynamics of grasshopper populations are highly variable and are determined by a variety of intrinsic (biotic) and extrinsic (e.g., climatic) interacting factors (Joern 2000, Ovadia and Schmitz 2004), many of which are unpredictable (Joern 2000). Although there has been much research on the components of grasshopper population dynamics, their feeding biology, the impacts of natural enemies, population forecasting, and control, a synthetic understanding of the problem still eludes researchers. For example, climate, soil, and vegetation patterns typically explain less than 30% of the variation in grasshopper densities within sites (Joern 2000). Given such complexity and the variation between ecosystems, can habitat management techniques that are compatible with ranching or conservation goals be widely used to mitigate grasshopper outbreaks?

We argue that the goal of sustainable and preventative management of grasshoppers is feasible and holds great promise. First, it is not necessary to understand all biotic and extrinsic interactions in the near term. Instead, we simply need to find complementary grassland management techniques that slow nymphal development, reduce survival and reproduction, or simply decrease year-to-year variability in those life history characteristics. Such approaches will greatly decrease the likelihood of grasshopper outbreaks. Second, the immediate effects of management tactics need not be dramatic to bring about large reductions in pest densities. Onsager (1987) demonstrated that because of their cumulative nature, small changes in mortality and development rates can result in large differences in grasshopper densities over the course of a season, and subtle adjustments in such rates through management activities appear feasible. Third, for a given type of habitat management, the same underlying ecological mechanisms are likely to interact in largely predictable ways. A chal-

lenge will be to understand how differences in weather among sites influence the action of underlying mechanisms. Comparative research is needed on habitat management practices and the underlying ecological processes across a range of ecosystem types. Finally, researchers and managers must pay additional attention to the many facets of range management in addition to pest insect management. As suggested by Fuhlendorf and Engle (2004), we need to develop rangeland management strategies that simultaneously benefit multiple objectives by searching for ecological indicators that serve many functions. Grasshopper outbreaks are an intermittent, cyclical problem, and no one will manage rangeland with the primary goal of reducing grasshopper outbreaks. Rather, we must develop mutually beneficial rangeland management strategies that minimize pest outbreaks and promote biodiversity while satisfying the needs of the grazing industry.

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