8. WHAT ARE THE CONSEQUENCES OF NON-LINEAR ECOLOGICAL INTERACTIONS FOR GRASSHOPPER CONTROL STRATEGIES?

A. JOERN
School of Biological Sciences
University of Nebraska-Lincoln
Lincoln, NE 68599-0118, USA

Abstract

Grasshopper populations from grasslands have been notoriously difficult to predict, a prerequisite for developing forecasting methods. In part, lack of good studies that uncover mechanisms driving population dynamics has contributed to this state of affairs. More importantly, grasshopper population dynamics may not follow the simple climate-driven, niche-based models that underlie most current explanations and control strategies. More likely, non-linear responses resulting from combined effects of abiotic forces (climate) and biotic interactions (e.g., competition, predation, parasitism) cause this unpredictability. A variety of examples is provided and a synthesis of new possible directions is described.

1. Problem

Complexes of grasshopper populations wax and wane in abundance, sometimes reaching sufficiently high densities to impact human resources. In parts of the world, legendary swarms of phase-polymorphic locusts engulf large areas and cause great economic damage before retreating to a fraction of the outbreak area and population size. In North America, fortunately, no phase polymorphic grasshopper species are known that exhibit such dramatic shifts in life cycle, population surges, or corresponding economic damage. However, grasshopper populations periodically reach high densities with resulting loss of forage causing economic impact [12]. In each of these situations, multiple factors collaborate to limit and regulate grasshopper populations [31]. In many cases, significant differences exist concerning the underlying ecological processes that actually apply, often making it difficult to assign causal relationships. Whatever the details, these multiple, natural processes critically affect the successful development of control policies and their success, but in reality are typically ignored as a serious backdrop for decision making.

Federal government sanctioned grasshopper control programs in North America emphasize western grassland regions, programs that focus on forage for cattle in rangeland. Agricultural crops in this region can also be at risk, but control of grasshoppers on crops

J. A. Lockwood et al. (eds.), Grasshoppers and Grassland Health, 131-144.
is typically left to individual farmers. Over the years, grasshopper control efforts in North America readily embraced the development of new technologies. Even so, this history is relatively short (since ca. 1880). Until the development of broad-spectrum chemical control capabilities, most technologies were environmentally benign, labor intensive and local in their impact. However, the problem captured national attention from the beginning. Grasshoppers and the need for their control were instrumental in the establishment of professional entomology in the United States in the late 1800s in response to widespread outbreaks of the Rocky Mountain Locust (*Melanoplus spectabilis*). However, even after this species went extinct early in the 1900s, other periods of significant, widespread grasshopper damage periodically occurred. Early control efforts relied on a variety of mechanical contraptions, simple chemical control including natural poisons and moats filled with fuel oil, or natural control agents. For example, an entire agency within the USDA was initially established to study and evaluate the importance of birds to insect pest control (including grasshoppers), although this group disbanded in the 1930s.

With the development of synthetic insecticides in mid-century, grasshopper control in North America shifted from local application to the wide-ranging, broad spectrum chemical control of grasshopper populations, with insecticides aerially sprayed over large areas (minimum 4 000 ha blocks). Recent chemical control guidelines were developed with application efficiency in mind, given the large expense and effort needed to apply insecticides. Costs were typically shared equally by rancher, state and federal governments on private land and by federal or state governments alone on public areas, a large fraction of the total land area in the western USA. Control action was considered when populations reached > ~9 individuals/m² although higher densities typically were needed to actually initiate action. All grasshoppers were included in the counts until recently despite the fact that only a tiny fraction of these species can be considered economically important; no effort was made to adjust estimates to include only those species that were likely to cause economic damage or to conditionally adjust risk of forage loss according to species composition. Moreover, no real effort was made to either assess the actual success of chemical methods on long-term grasshopper control, or to evaluate the impact of grasshopper chemical control technologies on non-target, often beneficial arthropod species, including the natural enemy complex that could be important in limiting grasshopper numbers in most years. After the demise of the “bird unit”, little thought was given to environmental risks in government circles except by some thoughtful USDA/ARS research scientists stationed at the Bozeman, MT lab (sometimes at career risk). What critical environmental risks to large-scale chemical control of grasshoppers exist in western North American range? What more needs to be done to pursue these issues?

Most current grasshopper control efforts in North America are based on a very simple underlying ecological model of grasshopper population dynamics. Unspecified environmental conditions (usually directly reflecting climate) lead to the rapid build-up of grasshopper densities using an exponential population growth model, requiring a 2-3 year period of a density buildup. At this point, grasshopper populations may cause sufficient damage to be economically important. The contribution of density-dependent or frequency-dependent factors, including more complex responses reflecting non-linear interactions among species within and among trophic levels, are seldom acknowledged.
Focused only on grasshopper population complexes, current strategy relies on repeated knock-down of population numbers, a successful approach that awaits the build-up of populations during periods of suitable environmental conditions until they once again require control. If the exponential population growth model applies to natural populations, this response is legitimate with regard to the specific goal: controlling grasshopper populations. The model simplifies ecological reality in a way that accommodates simple approaches to grasshopper control.

But, what if this simple underlying model is not an appropriate framework within which to design control? Will control efforts contribute to the problem? What if natural enemies are critically important to natural limitation and control? If so, not only does the current chemical-control strategy not work, it has negative environmental impact because broad-spectrum insecticides kill many native arthropods. Future grasshopper control efforts in North America must be sensitive to the possible degradation of biological diversity at local and regional scales, both because of current political and public pressure and because natural checks and balances can only be maintained by keeping these players in the system.

Recent historical analyses of grasshopper control suggest that the current model underlying control is incorrect, and that continued use of this model to justify large-scale grasshopper control may contribute to grasshopper problems. Long-term grasshopper population responses were compared between Wyoming with little chemical control and Montana with significant chemical control on government lands [34]. In Wyoming, where large-scale chemical control was not regularly applied, acute problems rapidly disappeared and long intervening periods of low grasshopper density persisted. Montana populations, on the other hand, exhibited chronic, long-term increases in grasshopper population densities after a history of control with associated economic significance. Despite that fact that these two regions are adjacent, contain essentially the same habitat, and experienced the same general climatic conditions during this period, very different population trajectories were observed after the period with extensive chemical control in Montana. More importantly, population responses from the two sites were the opposite of what one expects if the basic population model underlying control efforts is true.

Interactions among grasshopper species with other species in other trophic levels, and their non-linear consequences are largely ignored in the current ecological model underlying North American grasshopper control programs. In part, this reflects a lack of commitment by federal agencies responsible for grasshopper control programs to consciously incorporate basic ecological understanding of grasshopper population dynamics. Most funding has been directed at either chemical methods of control or bioinsecticides, and North American agencies have been quite successful in developing these methodologies. Less effort is directed at their long-term effectiveness and essentially no effort is allocated to the environmental impact of these policies. The irony here is that of these three important research priorities, two issues require basic understanding of grasshopper population processes in North American range systems. Clearly more research is required to work out the critical details, and future environmental risk from grasshopper control depends on these considerations.
I would like to emphasize the following take-home points:

(1) Successful control strategies must act in concert with natural processes or they will either fail at best and possibly exacerbate the problem at worst. In this context, better information is needed at all stages of the process, ranging from the basic understanding of what is going on in terms of species-specific population dynamics and multiple species assemblies, to having access to accurate data on which species are contributing to current conditions and why.

(2) New conceptual models of grasshopper population and community responses are needed that incorporate important non-linear interactions among species, with an emphasis on developing critical understanding at different temporal and spatial scales, including their linkage. Intense research should be directed at understanding how multiple sources of mortality contribute to basic population processes, including those resulting from multiple species interactions, within and among trophic levels.

(3) Natural enemies play an important role at all levels. While we are not always certain exactly what dynamic role these species play under specific but variable environmental conditions, it is certain that they are important. Moreover, it is certain that natural enemies play different dynamic roles under different environmental conditions and that different sites will exhibit different responses.

(4) Models that exhibit multiple equilibria with thresholds that define domains of attraction at low and high densities are currently attractive from my perspective. If such models result from complex density- and frequency-dependent, non-linear interactions among species and multiple domains of attraction, standard time-series analysis to search for density-dependent relationships will often fail to either project future change or uncover underlying ecological mechanisms.

(5) Protecting the biodiversity of native species must be a main consideration in developing grasshopper control programs in North American western rangeland. Not only will incorporation of this goal typically contribute to long-term, effective grasshopper management, but basic public concerns for protecting biodiversity can be met simultaneously.


Basic assumptions underlying insect population dynamics, including that for grasshoppers, often reflect basic propositions of Uvarov [55], ideas generalized by Andewartha and Birch [1]. In this "climatic release hypothesis" [36, 56], good and bad environmental periods occur because of changes in climate, affecting population growth parameters for a period of time until conditions switch. The length of this period determines if insect populations increase or decrease, and to what extent. Climate is a conspicuous possible determinant for such population responses, and it certainly plays a role no matter what the eventual mechanism underlying insect population dynamics proves to be. This view has utility in that it provides insect ecologists and economic entomologists with a simple, easily-recorded set of environmental variables that can be used to predict grasshopper
population changes. In addition, an unstated assumption that typically accompanies this view is that the process responsible for grasshopper population outbreaks is physiologically driven. Since grasshoppers are ectotherms, their key basic physiological processes are temperature driven and changes in climate can alter the ability to extract nutrients, and then allocate these to basic demographic attributes that affect fitness and population growth, among other possibilities. How far does this logic take us for understanding grasshopper population dynamics?

2.1 DIRECT EFFECTS OF CLIMATE

Repeated efforts have correlated grasshopper population changes with weather variables, including lagged effects [14, 21, 25, 35]. Significant correlations between weather variables and grasshopper population responses are often uncovered. As a rule of thumb, population densities tend to increase with hot, dry weather in northern US grasslands and decrease with these same conditions in southern plains [12, 14]. However, despite the significant relationships, correlations between climate variables and populations typically explain only a small fraction of the variance associated with the relationship, usually less than about 30%; the 70% or so of the variance in the relationship unexplained. It is almost always acknowledged that weather data from standard recording stations are used for convenience. Moreover, the data themselves are only correlated with the actual environment occupied by individual insects, especially given the regional rather than local nature of the data. Thus, significant correlations probably do reflect real relationships. At issue, however, is the causal nature of the interaction underlying the relationship. Unless underlying ecological mechanisms can be described, the relationship between grasshopper population change and weather provides only a tenuous link with which to direct control programs, even if the underlying dynamics eventually prove to be logically simple and straightforward. Effective control programs will work only when they operate in concert with natural mechanisms and processes!

Several examples document the important influence of climate on mechanistic population processes, including the clear fact that temperature does play a role! For example, food processing strongly interacts with temperature [60]. Coxwell & Bock [1995] documented a positive relationship between grasshopper abundance and distribution and diurnal surface temperatures in alpine situations. Ritchie [46] finds a significant correlation between grasshopper density and food quality, but only in warm years. In a food web context, Chase [15] documented how thermal conditions profoundly alter trophic cascades. And finally, Carruthers et al. [14a] document the adaptive consequences of increasing grasshopper body temperature to thwart disease and increase survival. There is no question that abiotic factors emanating from a variable climate are important. At issue is the need to understand exactly how they influence dynamic responses by grasshoppers at the population level in a varying environment.

2.2 CLIMATE AND FOOD PLANT QUALITY

Climate also directly affects food plant quality, thus indirectly influencing grasshopper
population dynamics. Stressed food plants often contain higher concentrations of key nutrients, especially N-containing compounds such as protein, that are often limiting to insect herbivores [37, 38, 57, 58]. There may be a direct link between climatic variation, food quality and grasshopper population dynamics. If so, increased food quality under extreme environmental conditions may lead to increased survival and reproduction, with consequent increases in grasshopper population size.

Physiological, behavioural and demographic responses in grasshoppers are sensitive to changes in food quality, especially N [3, 4, 27, 29, 30, 60-62]. These various responses are consistent with predictions from a nutrient quality hypothesis of population dynamics. Densities of grass-feeding grasshoppers often increase with increased fertilization levels under otherwise natural conditions [27]. At the behavioural level, grasshoppers select food based on the presence of limiting amino acids in a remarkably specific manner [3, 4], among many other factors that affect diet selection [9]. Grasshopper demographic responses often respond positively to total-N content of food, but not always [29, 30]. For all grasshopper species studied, maximal egg production rate occurred at ca. 4% total-N for the diets used, mostly reflecting the rate at which egg pods were produced and laid rather than the number of eggs per pod. Survival, development and weight gain often respond positively to increased total-N in the food, although this can be highly species-specific [29, 30]. Food processing capabilities strongly vary with food quality [60-62], compensating for suboptimal diets. However, the main point of these examples is that food quality has repeatedly been shown to influence physiological and demographic responses at the individual level. The next critical question is whether these individual-level responses translate into population-level responses.

Have we identified the key mechanistic link between grasshopper population dynamics and climatic variation based on food quality as just described? If true, two key predictions must be satisfied. The first is that there is a link between physiological stress and plant nutritional quality. This appears to be satisfied, even for the system in which the above species occur (Joem & Mole, unpublished data). Second, there should be strong positive relationships between increased N-concentrations in host plants and population size. Table 1 provides correlation coefficients for the most common species for 10 years of available plant quality data from a sandhills grassland site (Arthur Co., Nebraska, USA). Significant correlations exist but most explain relatively small proportions of the observed variance in grasshopper population size. Moreover, many of the correlations between population size and average total-N are negative (although not necessarily significantly different from zero), counter to predictions of the plant stress-nutrient quality hypothesis. Like investigations of the direct relationships between climate and grasshopper population dynamics, critical mechanisms are ignored in this type of analysis.


Grasshopper populations do not occur in an ecological vacuum, and species from many trophic levels routinely interact in a variety of ways: plant-plant, plant-grasshopper, grasshopper-grasshopper, and grasshopper-natural enemy. Basic density- and frequency-
dependent processes guide most of these species interactions within and between trophic levels. Moreover, a wide variety of direct and indirect responses that affect grasshopper populations cannot be detected and certainly not predicted except within this complete set of interactions. These relationships in all of their complexity are seldom recognized much less accommodated by the prevailing grasshopper control policies in North America. This may prove to be a big mistake if grasshopper management unknowingly disrupts critical links.

3.1 COMPETITION

Naturally occurring species are embedded in food webs in all natural communities [45]. Many grasshopper species (20-50 species) regularly coexist at a single site, providing significant opportunities for interactions, including competition [7, 16, 17, 20, 43] for limited food. Contrary to previous views [54], it is now recognized that insect herbivores regularly compete [20] and many opportunities exist for competition among grasshoppers in some years when quality food is limited. Ironically, the complex of relatively uncommon, non-economically important grasshoppers may keep damaging species in check by the diffuse effects of competitive interactions from many species [7]. However, competition among grasshoppers is variable and may not occur at all times and places [22, 23].

3.2 PREDATION

Natural enemies have widespread impact in most natural communities [18]. Grasshoppers are routinely preyed upon by a long list of arthropod and vertebrate predators [16, 8, 11, 28, 31, 32, 41, 42]. Many fungal, bacterial and viral pathogens attack grasshoppers as well
[53]. This combined natural enemy complex is well recognized but largely underappreciated in terms of its importance for the limitation and regulation of North American grasshopper populations. Recent results from a variety of studies indicate the importance of understanding grasshopper population dynamics in the context of food web dynamics if we are to understand primary sources of mortality and how these sources of mortality interact [2, 15, 47, 48, 49, 50]. Many of these responses will be strongly convoluted and difficult to predict based on correlation analysis and simple linear responses.

Many studies have documented the role of natural enemies in limiting grasshopper populations [6, 11, 24, 28, 48, 50], although this role is not always easy to demonstrate [7]. In Nebraska sandhills grassland (USA), arthropods and vertebrates provide significant impact [28, 32, 41, 42]. Specifically, nymphs are most susceptible to predation from wandering spiders. Moreover, while nymphs experience significant predation pressure, they also experience many other sources of mortality, with younger nymphs most affected. Adults are primarily taken by large predators such as birds and occasionally robber flies and large orb web spiders [6, 41, 42]. Avian predation on adults is variable in time and space [28]. Direct depressing effects of bird predation on adult grasshoppers are routinely observed in Nebraska grasslands [28, Joern unpublished] but seldom observed in Montana Palouse grassland [6]. However, even when direct effects of bird predation are not observed, the impact on grasshopper dynamics can be quite pronounced, including responses in the Montana system [see multiple stable states below, 5].

3.3 COMPENSATORY VS. ADDITIVE MORTALITY

Multiple sources of mortality undoubtedly combine to limit grasshopper populations. How do these factors combine to determine final densities? When all mortality sources contribute to mortality in a largely independent fashion, mortality is considered additive. However, sources of mortality often interact in a nonlinear fashion where the final population density may reach the same level independent of the number of factors involved, a compensatory response. Understanding how mortality factors interact is critical in that increasing mortality pressure at one life stage may have the effect of decreasing it at a later stage with the consequence that there is no real impact for overall population level dynamics, just where and how mortality occurs. These types of interactions routinely occur in grasshopper populations [42]. Food quality (starvation) and spider predation interact as multiple mortality factors to affect final population sizes. Under ambient food quality conditions, predation and starvation act in a compensatory fashion. However, when plots are fertilized and food quality increases, the impact on mortality is non-compensatory and the effects of both are evident in the final population numbers. In a separate experiment, Oedekoven & Joern [42] showed that survivors in treatments that included spider predation were better able to withstand starvation, suggesting that particular qualities of individuals within a population shift in response to interacting sources of mortality.
3.4 TROPHIC CASCADES

Interacting sources of mortality operating within food webs exhibit a series of indirect interactions among trophic levels referred to as trophic cascades [48-50]. Presence or absence of the top predator in a food web [chain] results in different impacts on the basal food level [45, 48, 50]. The key point is that final densities in natural food webs reflect the combined set of dynamic interactions among populations at different levels of a food web, the combined impact of within trophic level effects of competition, and the between trophic level effects of consumption (both herbivory and predation). Both direct and indirect interactions combine to determine final densities, often in complex ways.

For grasshoppers, the control target should be focused on the plant forage base of the food web, not the absolute number of grasshoppers. If true, and if the presence of predators can increase forage biomass over the long term, all efforts should be focused on maintaining the complete system. Moreover, the nature of interactions among trophic levels in food webs is wildly difficult to predict. Indirect interactions can often be disentangled only through careful experimentation [2, 47, 48, 49, 50], and the sources of indirect interactions that contribute to final population densities are highly nonlinear.

3.5 MULTIPLE EQUILIBRIA

The standard explanation for grasshopper outbreaks follows from Andrewartha & Birch [2]: unpredictable but regular changes in climate make environmental conditions more or less suitable for grasshopper population growth. Are there alternate explanations for the existence of sometimes low vs. high grasshopper densities other than merely changing climate? Are population responses more regulated than they appear to be and not merely results of unpredictable environmental conditions?

There is good evidence that complex, nonlinear dynamics account for endemic vs. epidemic population levels in insect herbivores, including grasshoppers [5, 10, 44, 51, 52]. Basic biotic interactions (e.g., competition, predation, herbivory) in association with climatic state variables can determine response thresholds between grasshopper population responses over short temporal and spatial scales [5]. Threshold boundaries prescribe multiple equilibria, determining which domain the system will lie in. Identifying which ecological factors drive the dynamics of the system and which parameters (and their values) determine the location of thresholds defining domains of attraction is important. Deriving these responses in natural systems becomes an important empirical challenge, especially when trying to manage a grasshopper population. As described in Belovsky & Joern [5], there are good reasons to believe that multiple equilibria occur in North American grasshopper populations, and any feasible control strategy must take this new view into account. Much research remains to be performed on this important topic, however.
4. Solutions

North American grasshopper control programs in western rangeland have reached a critical juncture: programs must preserve and conserve natural occurring biodiversity, including the majority of grasshopper species which should not be targeted for control under any situation. Current grasshopper control approaches present significant risk to many species, particularly other arthropods. These risks must be explicitly addressed and increasing public pressure will demand that this be done. Moreover, the primary goal of grasshopper control policy must shift from one of control to one of management, a mindset very similar to that required for managing renewable resources.

4.1 COMPETING ECOLOGICAL HYPOTHESES UNDERLIE CURRENT GRASSHOPPER CONTROL POLICY

Recent research focused on dynamic food web interactions illustrates the complex set of direct and indirect interactions that underlie grasshopper population dynamics. Density- and frequency-dependent interactions among species coupled to unpredictable climatic forcing functions lead to a wide range of largely unpredictable responses. However, the causal mechanisms can be uncovered and their consequences evaluated in the context of intervention policies. Unfortunately, the current population dynamics model underlying past and most current grasshopper control philosophies in North America will not accommodate these new ecological findings. The current model harkens back to Andewartha and Birch [1], requiring nothing more than exponential population growth and unpredictable weather. This theoretical underpinning is clearly insufficient, even inappropriate, to develop grasshopper control programs and new approaches should be explored now.

Results of these recent studies suggest additional, important outcomes. While predictive models are desired to provide necessary lead time to organize grasshopper control programs, it seems unlikely that truly predictive models of future grasshopper population trends based on the current model can be developed. In particular, the existence of non-linearities strongly affects population dynamics. These relationships challenge the utility of time series analyses based on sequences of annual population data for either predictive purposes or for purposes of uncovering critical ecological mechanisms responsible for grasshopper population dynamics. Finally, we should shift our focus regarding grasshopper control in North America. Currently we emphasize grasshopper control, presuming that our efforts can control grasshopper outbreaks according to human desires and needs. More considerations must be included in the decision.

Scale-dependent responses for understanding grasshopper population dynamics have not been adequately evaluated and these really need attention. Small and large-scale visions are needed. However, it is clear that the emphasis on the 4 000 ha control block is arbitrary and population dynamics at this spatial scale should be ignored until it can be shown to be meaningful for ecological reasons rather than used in response to the economic needs of control agencies. Large-scale dynamics will probably be meaningful
and a scale-dependent spatial hierarchy should be developed that reflects appropriate ecological dynamics.

4.2 AMELIORATION OF RISK TO RANGELAND BIODIVERSITY FROM GRASSHOPPER CONTROL IS GOOD POLICY

Heightened public interest and pressure in North America to preserve biodiversity now requires that grasshopper control strategies on western rangeland protect native species even during periods of grasshopper outbreaks. Public concern for preserving biodiversity will most likely continue to grow. From a political view, this is reality. However, protecting biodiversity will be good management as well, given the important contributions of biotic interactions to the grasshopper population dynamics.

Natural controls that limit and regulate grasshopper populations in rangeland ecosystems must be accommodated. These natural limits are part of any rational grasshopper management program and most chemical control programs disrupt these processes, sometimes permanently. Interspecific competition and effects of natural enemies each have the potential to contribute significantly to grasshopper management programs. It is not yet clear how these processes can be brought to bear on the problem despite the fact that the basic interactions have been studied for decades. Ironically, these critical interactions are only now being described in sufficient detail, in just a few situations. Do otherwise non-economically important grasshopper species compete in such a way that economic species are limited? In what way are natural enemies a critical feature of these interactions? Managing grasshopper populations will require that these important limiting factors be maintained while managing for biodiversity at the same time. This is a win-win situation as both contribute to the same goal. Developing policy that builds on this assumption will provide the necessary balance for preserving biodiversity while appropriately addressing grasshopper issues, with both needs benefiting.

A look to the future is also worthwhile for assessing the relationship between grasshopper management and biodiversity. How will situations change in response to changing land use, or to global climate change? Each of these issues potentially influences grasshopper population dynamics: e.g., fragmentation of habitats that disrupt naturally limiting agents or altered climate that results in changed species distributions or altered temperature-dependent population-level mechanisms. I sense that these issues cannot be addressed based on current knowledge and there is no indication that appropriate actions are under consideration. Significant research on these types is warranted.

In sum, a significant paradigm shift is underway regarding the way in which grasshopper populations in North America will be managed. Past and current control policy now presents a significant risk to non-target native species on native rangeland if it continues as always. Preserving biodiversity in rangeland systems must be included as a major goal in the final package, both because it will retain natural controls on grasshopper populations and because the public demands that this be done. Unfortunately, much critical information regarding the basic ecological interactions are unknown. A high priority should be placed on developing the basic ecological framework that underlies grasshopper population dynamics.
5. References


