Linking Rangeland Management with the Nutritional Physiology and Ecology of Locusts

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Linking rangeland management with the nutritional physiology and ecology of locusts

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Abstract. Rangeland management practices alter soil and plant characteristics and communities. These changes have implications for the success of pests common to grass and forage systems. Understanding how pests respond to anthropogenic influences is a key variable for the development of sustainable pest management strategies that minimize potential risk and severity of pest damage. For example, heavy livestock grazing in northeast China promotes locust outbreaks by lowering plant nitrogen content. This in turn likely decreases the amount of protein, relative to carbohydrate, that locusts receive. In this case, a low protein/high carbohydrate diet is just what this locust species needs to thrive. While many environmental factors influence locust outbreaks and plagues around the globe, understanding the interactions between livestock grazing, range quality, and locust populations is central to developing integrated control practices.

Keywords: Rangeland ecology, integrated pest management, coupled natural-human systems.

Introduction

Rangeland practices alter plant communities via changes in soil structure and chemistry, species composition, and plant nutrient content (McLauchlan 2006; Wani, Rupela *et al.* 1995; Welbaum, Sturz *et al.* 2004). These changes affect insect herbivore growth, behavior, and reproduction with consequences for population dynamics and large-scale outbreaks (Mattson 1980; White 1993). Increases in herbivorous insect populations can then translate to elevated rangeland and crop damage and pest control costs, affecting range profitability and subsequent land management practices. This feedback loop can occur on local rangelands at small spatial scales, but can also be linked externally to other regions through pest migration (*e.g.* locust swarms), and can impact broader societal groups by causing food scarcity and rising food costs.

Understanding the organismal perspective can yield significant insights into the effects of local land use on broad, landscape scales. Plant quality strongly affects herbivore performance (Awmack and Leather 2002). Plant nitrogen (N) content is frequently used as an index of plant quality that connects multiple ecological levels (*e.g.* ecosystem nutrient cycling to herbivore ecology). Most plant N is in the form of protein. A common perception is that increasing plant N content will increase herbivore performance by relieving a protein limitation. A number of studies have found correlational and experimental evidence for N-limitation of insect herbivores (Mattson 1980; Scriber and Slansky 1981; White 1993). However, this concept is increasingly being questioned. A variety of studies have shown that, depending on the species, increasing plant N content can enhance, impede, or have no effect on herbivore growth and performance (Berner *et al.* 2005; Harrison *et al.* 2012; Scriber and Slansky 1981; Scriber 1984).

A change in the relative amounts of nutrients that insects can obtain from plants is likely a strong factor in determining the responses of these herbivores to changing plant N content. Extensive research has shown that different species of animals have distinct optimal *balances* of dietary nutrients that depend on their physiological and life history traits (Simpson and Raubenheimer 2012; Sterner and Elser 2002). Herbivorous insects, including locusts, strongly regulate the *ratio* of protein:carbohydrate they obtain from plants—not the absolute amount of protein *per se* (Simpson and Raubenheimer 2012). Thus, changes in nutrient landscapes available to insect herbivores will have different effects on different species. Indeed, nutrient imbalance is a critical factor regulating some plant-insect interactions (Behmer 2009). To develop sustainable pest and agricultural land management strategies we must understand how land use affects key plant-insect interactions and incorporate these mechanisms into coupled socioeconomic-ecological models used to guide policy.

Mongolian locust-livestock system

The Inner Mongolian rangeland system is one of the most important grassland-based animal husbandry areas in China. This region is located in northeast China and, along with the vast semi-arid region of central Eurasia, it makes up the largest continuous grassland in the world (DAHV and CISNR 1994). Land use in these regions has intensified during recent decades. For example, the Xilin River Basin (near the city of Xilinhot, Inner Mongolia) alone saw an increase in the number of livestock from 618,000 to 1.1 million from 1985 to 1999 (IMSB 1986; IMSB 2000). Such land use intensification is likely the dominant cause of rapid steppe degradation in many areas of the Eurasian steppe belt (Han, Zhang *et al.* 2008). Steppe degradation decreases biodiversity, productivity, and sometimes leads to desertification (Tong, Wu *et al.* 2004; Wu and Overton 2002). Globally, grasslands store about a third of the total terrestrial carbon (Lal 2001). Thus, degradation not only negatively impacts on the livelihood of local communities and regional economies, but also has far-reaching implications for global carbon (C) and nitrogen (N) pools. Hence, understanding how land use affects N and C dynamics has become an important area of ecological research in Inner Mongolia.

Giese *et al.* (2013) recently published a comprehensive study quantifying N pools and fluxes on three sites with different grazing intensities near the Inner Mongolia Grassland Ecosystem Research Station. Heavily-grazed sites had reduced pool sizes of organic N in the topsoil and in above- and below-ground biomass, consistent with previous studies (Wu *et al.* 2008). Major pathways of N loss from the heavily grazed sites included hay-making and sheep excrement export, for use as fodder and winter fuel, respectively, and increased risk of wind erosion.

This reduction of N pools has a paradoxical effect on the dominant locust species in the region. Heavy livestock grazing actually promotes locust outbreaks by lowering plant N content and creating protein-poor forage (Cease *et al.* 2012). In contrast to the commonly-held hypothesis that herbivores are ubiquitously protein-limited (White 1993), the Mongolian locust, *Oedaleus asiaticus*, preferred and performed best on low-protein plants found in pastures heavily-grazed by livestock (Figure 1). Not only were high-protein grasses avoided, they were detrimental to the growth and survival of this species. Although the precise physiological mechanisms by which plants with high N exert negative effects on this locust remain to be elucidated, data from synthetic diet studies strongly suggest that protein excess is playing a role. These experiments showed that *O. asiaticus* had a protein:carbohydrate intake target

Figure 1. A Mongolian locust (*Oedaleus asiaticus*) in its preferred habitat, a field heavily grazed by sheep (background) near the Inner Mongolia Grassland Ecological Research Station in northeast China. Heavy livestock grazing enhances soil erosion and nitrogen depletion which promotes outbreaks of this locust by shifting plant nutrient content toward lower nitrogen conditions favorable to *O. asiaticus*. In contrast to paradigms for nitrogen limitation in herbivores, higher nitrogen diets decrease growth and survival of this locust.

of 1:2 (Cease *et al.* 2012); among the lowest of any acridid studied (Behmer 2009)

Further experiments have shown that *O. asiaticus'* preference for low-N plants is a dominant feeding rule and consistent across multiple inter- and intra-specific host plant preference comparisons (Cease *et al.* in review Ecological Entomology). These studies, along with similar findings for some North American and Australian acridids (Berner *et al.* 2005; Clissold *et al.* 2006), support the hypothesis that N-excess, rather than N-limitation, is a potentially critical nutritional factor regulating plant-insect interactions (Joern and Behmer 1997). This may be especially true for herbivores that have experienced long-term adaptation to N-limited grassland environments. Such low protein preference may enable *O. asiaticus* and perhaps other herbivores to exploit degraded areas with low nutrient availability.

Rangeland management impacts on formation of migratory locust swarms

All locusts are grasshoppers (family: Acrididae), and here I use the term "locust" to indicate grasshopper species in which the larval environment triggers development of alternate phenotypes (reviewed in Pener and Simpson 2009). High population density plays a primary role in triggering the transformation to the swarming gregarious phase. Thus factors that promote population growth and aggregation can be expected to increase development of migratory swarms. For example, increased heterogeneity in vegetation patches, as is often found in heavily-grazed range, can lead to locusts clumping together and also switching between patches to obtain adequate balances of nutrients (Babah and Sword 2004; Bouaichi *et al.* 1996; Despland and Simpson 2000). These behaviors enhance the interactions between locusts that promote gregarization - a distinct behavioral shift that marks the beginning of larger group formations, leading to swarms. The potential for other environmental factors to modulate the effects of density are less understood.

In addition to regulating growth and survival, the relative amounts of protein and soluble carbohydrates which locusts obtain from their host plants may influence migratory polyphenism. Indeed, changes in plant quality influence development of migratory phenotypes in many insects. For example, the wing dimorphic planthopper (*Prokelisia marginata*) had decreased expression of long-winged phenotypes when fed high N (performance-enhancing) host plants, even when reared at high population density (Denno *et al.* 1985). Velvet bean caterpillars (*Anticarsia gemmatalis*) had a higher percentage of dark, migratory forms when fed diets that decreased their performance (Fescemyer and Erlandson 1993). Gaines (1989) tested the interactive effects of host plant N-fertilization and population density on the non-swarming but wing-dimorphic grasshopper (*Phoetaliotes nebrascensis*). She reared eggs from short-winged adults in a 2x2 factorial experiment (two levels of population density and two levels of fertilized grass). The one combination to produce long-winged offspring (25%) was high density and unfertilized grass (Gaines 1989). Later, Joern and Behmer

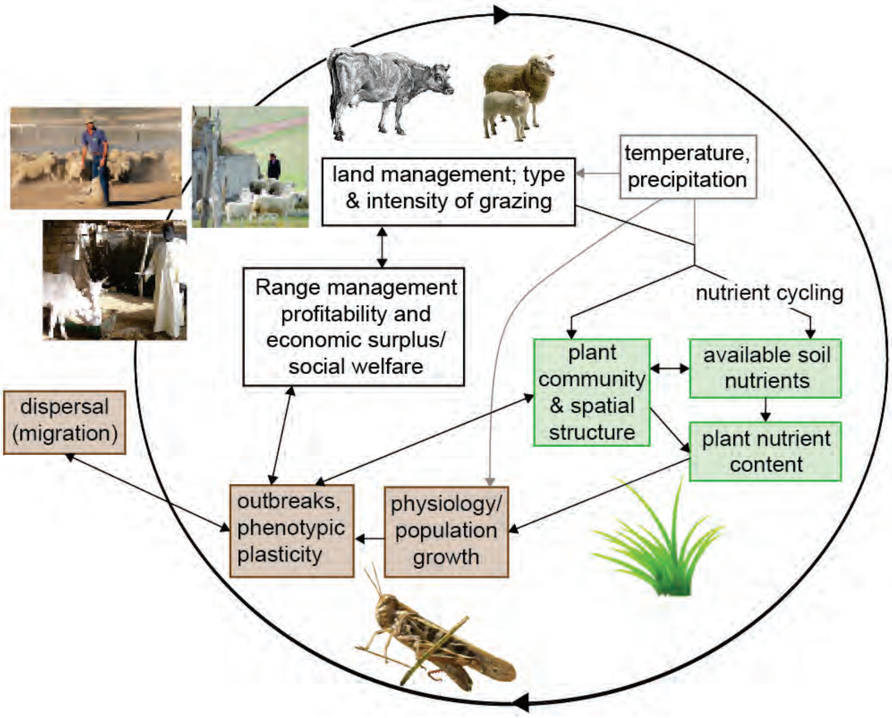

Figure 2. Conceptual model of the human-livestock-locust system

(1998) demonstrated that diets with increasing N content decreased survival rate in *P. nebrascensis* (but not in another abundant and co-existing acridid, *Melanoplus sanguinipes*). Therefore, the unfertilized grass in Gaines' 1989 study likely reflected performance-enhancing food, which, in conjunction with high density, promoted development of long-winged adults. Performance-degrading food (high N content in this case) suppressed this response to high density.

Recently, we found similar results for the Mongolian locust *O. asiaticus*. In addition to promoting population growth, low-protein plants increased the propensity for locusts to develop into migratory phenotypes (Cease *et al.* in review Oecologia). Locusts reared at high population density and fed on the more nutritionally balanced low-N plants had the most enhanced migratory characteristics, whereas locusts fed high-N plants consistently had decreased expression of migratory characteristics. These results are counter to conventional wisdom that deteriorating plant quality should promote migration to seek out better resources. Instead, these results suggest that the Mongolian locust, and perhaps other migratory insects, fit an alternative scenario where access to food that enhances growth and survival may be necessary to support development of migratory phenotypes that require high performances. In terms of rangeland management, this research suggests that excessive grazing depletes soil nitrogen, yielding lower quality forage for livestock but also better quality forage for locusts. This in turn stimulates outbreaks and increases the propensity of locusts to form migratory swarms, thereby exporting the problem to other regions (Figure 2).

Future directions and broader implications

Future aims of this research are to develop innovative, sustainable strategies to understand and manage locust outbreaks accounting for feedbacks among ecological, agricultural, and economic systems by engaging a multidisciplinary team of scientists and applied agricultural and food security agencies. Understanding the interactions between livestock grazing, range quality, and locust populations is central to developing integrated control practices. To investigate these interactions, we will compare related locusts from different regions around the world including East Asia, Australia, and West Africa. Arid grasslands in these regions share livestock production as an important source of livelihood support and also similar patterns of locust outbreaks on degraded pastures. However, each region employs unique ways of allocating property rights and faces unique challenges for maintaining healthy rangelands.

Oedaleus locusts are associated with overgrazed pastures worldwide; a clear human-environment interaction. These locusts are major pests on several continents. For example, *O. senegalensis* is often considered the main pest of the African Sahel; over a period of 7 years (1986-1992), $US177 million was spent on control (Cheke 1990; Popov 1996). *O. asiaticus* is a similarly dominant pest of grasses and crops in northern China (Kang *et al.* 2007). In Australia, *O. australis* is a secondary pest to a similar locust, *Chortoicetes terminifera*—the most serious pest species in the country. These Australian species are closely related, overlap in spatial distribution, even frequently being found in the same fields forming mixed but cohesive migratory groups, and both species are likely promoted by livestock overgrazing (Bailey 2007; Deveson 2012). Preliminary studies have shown that field-collected adult *C. terminifera* and *O. australis* have particularly low protein: carbohydrate requirements (1:2.1 and 1:1.8, respectively) (AJ Cease *et al.* unpublished data). The concordance of these patterns with *O. asiaticus* in China suggests that by lowering plant N content, and therefore the dietary protein:carbohydrate ratio available to locusts, overgrazing may stimulate locust outbreaks in grasslands across the globe.

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