DISSERTATION

# SPATIAL AND MULTIVARIATE ANALYSES OF COLORADO RANGELAND GRASSHOPPER ABUNDANCES: PATTERN AND PROCESS

Submitted by

Kerri M. Skinner

Department of Rangeland Ecosystem Science

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY KERRI M. SKINNER ENTITLED SPATIAL AND MULTIVARIATE ANALYSIS OF COLORADO RANGELAND GRASSHOPPER ABUNDANCES: PATTERN AND PROCESS BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

Committee on Graduate Work

~~Co-~~Adviser

Co-~~Adviser~~, Department Head

ABSTRACT OF DISSERTATION

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Grasshoppers are important agricultural pests which inhabit a broad variety of crop and rangeland ecosystems. Despite more than a century of research, little is known of the factors which control the spatio-temporal dynamics of rangeland grasshopper densities. This study (1) reviews the history of grasshopper problems in the western United States, outlines the efforts which have been made to control and understand grasshopper population changes, and discusses the complexities which preclude our best efforts to predict and control rangeland grasshopper outbreaks; (2) identifies and characterizes spatial patterns in Colorado grasshopper abundances; and (3) determines the environmental factors which are most closely linked with changes in grasshopper population densities. Exploratory data analysis and geostatistical techniques were used to identify and characterize spatial dependence among grasshopper counts for 1993 through 1997. Variograms were computed for each year and used with kriging to interpolate grasshopper densities in unsampled areas. Results are compared with previous spatial analyses of grasshoppers in Montana, Idaho, and Alberta. Grasshopper densities showed spatial patterning at scales larger than those reported for other areas of the Great Plains. The results indicate that the current grasshopper survey techniques may be more useful in detecting large-scale (regional) infestations than in identifying localized areas which may require control.

To determine the environmental factors which are most closely linked with changes in grasshopper population densities, grasshopper sampling sites were grouped by direction and magnitude of change in density from 1995 to 1996. Multiple regression and stepwise discriminant analysis were used to identify the soil and weather variables which best distinguished among groups. Grasshopper density in 1995 was the most important variable in the discriminant analysis, followed by mean precipitation for April, 1993, and mean temperature in October, 1993. These results indicate that soil characteristics in Colorado are not as important to changes in density as are population level and stochastic weather events and confirm the presence of time lags in the effects of weather conditions on population changes.

Kerri M. Skinner
Department of Rangeland Ecosystem Science
Colorado State University
Fort Collins, CO 80523
Spring 1999

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# CHAPTER I

## THE PAST, PRESENT, AND FUTURE OF RANGELAND GRASSHOPPER MANAGEMENT

*"Knowledge is power in protecting our crops against the ravages of a tiny insect, as in all other undertakings; and according as accurate knowledge regarding this locust plague is disseminated among our people, will they be able to vanquish the common foe."*

- C.V. Riley, 1877

Grasshoppers are important range animals which have long been regarded as serious agricultural pests. Grasshoppers have undoubtedly made large historical impacts on the rangelands of the United States through their reputedly voracious appetites and sheer numbers. Like other species whose habits conflict with human interests, efforts to understand the biology and ecology of grasshoppers have been driven by the quest for better ways to suppress their numbers. While there are good reasons for this approach to grasshopper research, it has not resulted in a thorough understanding of the biology, ecology, and population dynamics of these insect herbivores, nor the ability to accurately predict or prevent outbreaks. The objectives of this chapter are to 1) review the basic biology of grasshoppers and the history of grasshopper problems in the western United

States, 2) outline the efforts which have been made to control and understand grasshopper population changes, and 3) discuss the complexities which preclude our best efforts to predict and control rangeland grasshopper outbreaks.

**Basic biology.** There are more than 600 species of grasshoppers in North America (Hewitt and Onsager 1983), belonging to the family Acrididae in the insect order Orthoptera (Uvarov 1966). Grasshoppers are distinguished from katydids by their short antennae and differ from locusts in that grasshoppers generally do not exhibit the gregarious behavior which results in migratory swarms or "plagues" (Riley 1877, Uvarov 1966). Occasionally, rangeland grasshoppers develop high population numbers which are commonly called "outbreaks" or "infestations." Under these conditions, nongregarious grasshoppers may be more serious agricultural pests than locusts (Uvarov 1966). While a local grasshopper community consists of many species, only a portion of those species contributes to outbreak densities (Kemp 1992). Only about a dozen grasshopper species frequently develop high densities on rangelands (Hewitt and Onsager 1983).

As herbivores, grasshoppers are infamous for their appetites, although their destructiveness may be as much due to clipping vegetation (without eating the severed portion) as to actually consuming it (Mitchell and Pfadt 1974). Although grasshoppers are mainly herbivorous, cannibalism of sick or dead individuals may be an important source of moisture (Lockwood 1988). Species vary in diet breadth from polyphagy, as for the generalist feeder and sometime pest *Melanoplus sanguinipes* (Fabricius), to monophagy, such as in *Hypochlora alba* (Dodge), which feeds exclusively on *Artemisia ludoviciana* Nutt. (Mulkern et al. 1969). The ecological functions of grasshoppers have largely been neglected by researchers and land managers but include important roles as litter producers (Mitchell and Pfadt 1974), food sources for grassland birds and other wildlife (Wiens 1973, Miller et al. 1994), and biological control agents for weeds (Parker 1984).

Grasshoppers are textbook examples of hemimetabolous insects, which develop through the process of incomplete metamorphosis and lack the wormlike larval stage that characterizes holometabolous species such as flies, beetles, and butterflies. The immature stages resemble miniature adults, but lack mature wings and reproductive organs. Immature grasshoppers are called nymphs and pass through four to six developmental stages, called instars, before reaching the adult stage (Capinera and Sechrist 1982, Vickery and Kevan 1985). Hatchlings of most species reach adulthood in 30-40 days, the rate of development being temperature dependent, and adults live an average of about 51 days (Pfadt 1994).

In most species, the female grasshoppers lay their eggs in late summer. Egg-laying is formally termed "oviposition." Female grasshoppers choose their oviposition sites judiciously. Soil moisture, salinity, pH, and texture are important factors in determining where eggs are laid (Edwards and Epp 1965, Hewitt 1985). The number of eggs per pod, number of egg pods laid, and frequency of oviposition vary by species and with diet (Hewitt 1985, Pfadt 1994). Embryos begin development in the late summer and fall, then enter a stage of arrested development called diapause. Development resumes when soil temperatures exceed about 50° F (Pfadt 1994). The eggs hatch in spring or early summer and the emerged hatchlings are the first instar nymphs. In some species, the eggs hatch in the fall and the grasshoppers overwinter as nymphs (Capinera and Sechrist 1982, Vickery and Kevan 1985).

**A troubled history.** Grasshoppers and humans have been at cross purposes since the earliest days of agriculture in the American heartland. Most early records of grasshopper problems in America can be ascribed to one species: *Melanoplus spretus* (Walsh), the Rocky Mountain grasshopper or "locust." Unlike other acridid species in North America, *M. spretus* periodically formed migrating swarms which moved between permanent breeding grounds in the Rocky Mountain states and the fertile farmlands of the Mississippi valley (Riley 1877, Lockwood and DeBrey 1990). Six major swarms of this species, covering large regions of the Great Plains and lasting two or more years, were reported between 1818 and 1875 (Riley 1877). The "plague" of 1857 covered 12,000 square miles, over most of which "every green thing cultivated by man was consumed" (Riley 1877). In 1876, estimated crop losses for Minnesota alone totaled more than seven million dollars (USEC 1878).

The plight of human settlers in the prairie domain was exacerbated by the fact that *M. spretus* was not the only species to cause problems. In his treatise on the occurrence of *M. spretus* east of the Rocky Mountains, C.V. Riley wrote, "Yet, while no other species possesses such wonderful migratory habits, several [grasshopper species] become so enormously multiplied during certain years in their native homes as to commit very serious injury to vegetation. Some of them are also capable of extended flight (1877, p. 89)."

For reasons which remain largely unknown, the Rocky Mountain grasshopper is apparently extinct (see Cohn 1994). The last living specimen was collected in 1902, following a population decline that started in the 1880s (Turnbull 1980). Lockwood and DeBrey (1990) have theorized that agriculture and other human activities, especially in riparian areas where egg-laying and nymphal development took place, contributed to the extinction of this species. Their paper points out the irony that habitat loss, not pesticide use, was responsible for the extermination of the most pestiferous species encountered on western rangelands. It is unknown how the loss of such a widely distributed and numerous insect species has impacted the ecosystems of the Great Plains.

Despite the disappearance of *M. spretus*, its effects on entomology in America were long-lasting. It is probable that grasshopper plagues drove a shift from grain farming to cattle ranching, influenced tillage practices, fostered turkey production, and led to increasing dependence of agriculture on subsidies and aid provided by the federal government (Schlebecker 1953, Atkins 1984).

In 1877, an act of Congress created the United States Entomological Commission in response to the plight of farmers caused by the widespread grasshopper plagues of the preceding years (USEC 1878, Atkins 1984, Smith and Smith 1996). The Commission, directed by Charles Valentine Riley, was charged with reporting on Rocky Mountain grasshopper infestations and "the best practicable method of preventing their recurrence or guarding against their invasions (USEC 1878)." This shift in the focus of federally funded entomology from a naturalistic approach to one concerned with injurious insects may be viewed as the origin of applied (economic) entomology in the United States (Metcalf 1996).

**Dealing with infestations.** The Rocky Mountain locust probably swarmed over the Great Plains long before white settlers brought their wheat and cattle (Giles 1886). Outbreaks would have provided an easily gathered source of nutrients for indigenous people (Madsen 1989; see also Vickery and Kevan 1983). Indeed, grasshoppers were regularly included in the diets of many Native American tribes (Sutton 1988). Large quantities could be collected during cold weather or by using fire to drive bands toward collection pits (Sutton 1988). Fire was later used by white farmers to destroy grasshopper nymphs (Riley 1891).

During the late nineteenth century, several methods were developed to help remove grasshoppers from agricultural lands. Preventive measures which were advocated included conservation of game birds, crop rotation, irrigation, planting the resistant crop sorghum, and prayer (USEC 1878, Riley 1891, Schlebecker 1953). Means of destroying the pests during outbreaks included collection with nets, plowing and harrowing to destroy eggs, and the use of turkeys and other domestic fowl. Various manifestations of the "hopperdozer," usually consisting of a pan of tar or coil oil mounted behind a horse or tractor, were used to collect very large numbers of wingless nymphs, a practice which was encouraged by bounties (USEC 1878, Riley 1891, Schlebecker 1953). Many experiments were undertaken to find new methods to destroy eggs, nymphs and adults. Chemicals such as Paris green were tested and a South African fungus was imported to spread disease among the insects in a notable early effort at biological control (Schlebecker 1953). Smudging and concussion were also tried (USEC 1878).

By the 1930's, chemical control became "the most generally accepted method of grasshopper control in the United States (Parker 1937)." Mixtures of arsenic with bran or sawdust were recommended for poisoning nymphs and adults by ingestion (Parker 1939). New chemical insecticides supplanted the arsenic bait, and in 1950, the new insecticides were used to suppress a threatening outbreak (Schlebecker 1953). Insecticide sprays such as Malathion and carbaryl were recommended for grasshopper control by the United States Department of Agriculture (USDA 1977). Later, these chemicals were incorporated into bran baits (Onsager et al. 1980) and used with biological control agents for both short- and long-term population effects (Johnson and Henry 1987).

Concerns over the use of toxic pesticides in agriculture drove the development of biological means to reduce insect pests, including grasshoppers. The most well-known biological control agent for grasshoppers is the pathogen *Nosema locustae* Canning. Extensive research and field testing were done to investigate the feasibility of using *N. locustae* as a long-term solution for grasshopper outbreaks (e.g., Henry 1982, Oma and Hewitt 1984, Onsager 1988; see also Senft 1989). While pathogens may provide a means of managing grasshopper populations at levels below the threshold for economic damage, their use and success in the field have been limited. Additional efforts to import and release a parasitic wasp for biological control of grasshoppers have been dropped following much debate and controversy (Carruthers and Onsager 1993, Lockwood 1993).

Until the 1950's, the concern was to protect crops, not rangeland, from grasshopper damage (Hewitt 1977). Devastating plagues lead to a shift from farming to ranching and the advent of federal funding for rangeland grasshopper control (Schlebecker 1953, USDA 1982). Management of grasshoppers on rangelands is different than on crop lands because the cost-benefit ratio differs. The cost of a control measure on rangeland often cannot be justified given the low value of forage; other options, such as selling off livestock or buying hay, may be more economical alternatives (Davis et al. 1992, Skold et al. 1995). Currently, rangeland grasshopper densities (the number of individuals per unit of area) must exceed eight grasshoppers per square meter before federal funding is made available for control measures (Davis et al. 1992).

**The scientific approach.** The focus of federal grasshopper management programs has remained relatively unchanged for the last 120 years. From the start, entomologists have looked for practical ways to prevent grasshopper damage and control populations. The geographic distribution, life cycles, behavior and diets of pest species have been described in detail (e.g., Anderson and Wright 1952, Mulkern et al. 1969, Pfadt and Smith 1972, Vickery and Kevan 1985, Fielding and Brusven 1992), in an effort to provide the knowledge that Riley (1877) believed would vanquish the foe. Additionally, many researchers have noted relationships between grasshopper abundances and various environmental factors and have investigated the influences of weather, fire, sunspots and even earthquakes on grasshopper outbreaks (USEC 1878, 1880, 1883; Criddle 1932).

Interest in predicting grasshopper population levels and preparing for outbreaks goes back to the earliest days of grasshopper research. The second report of the U.S.

Entomological Commission (1880) proposed the establishment of "a permanent system of [locust] observations and warnings" and daily bulletins to publish information on swarms. In the third report, the forecast for the coming summer was based on the "widely scattered" infestations of the previous year (USEC 1883). Grasshopper surveys were taken annually for many western states, and hazard maps were drawn, based on the field observations, to estimate the probability that grasshopper numbers would approach or exceed the economic threshold.

In the late 1980's, new techniques and computing power helped fortify efforts to predict and prepare for high grasshopper numbers. A computer simulation model called HOPPER was developed to improve decision-making when selecting between grasshopper treatment options (Kemp et al. 1988). Kriging was used to improve the predictive power of the grasshopper outlook maps (Kemp et al. 1989). In applied research, the emphasis was on readiness for outbreaks and early intervention.

As the search for patterns continued, population models for phenology and density-dependence were constructed (Kemp 1987, Kemp et al. 1989, Kemp and Dennis 1993). An individual-based population model was recently proposed by Carter and coworkers (1998). Joern and Gaines (1990) provide a review of the mechanisms which are thought to drive grasshopper population dynamics, only a few of which have been incorporated into modeling efforts. Research also has been conducted on grasshopper community characteristics, such as species composition (Kemp et al. 1990, Quinn et al. 1991, Kemp 1992, Fielding and Brusven 1993) and competition (Evans 1989, Ritchie and Tilman 1992, Belovsky and Slade 1995).

Recognition and analysis of spatio-temporal dynamics in grasshopper communities has come about only recently. Most studies have focused on patterns in abundance during outbreak years (Cigliano et al. 1995, Lockwood and Schell 1995, Schell and Lockwood 1997), some of which have addressed the debate concerning whether grasshopper outbreaks exhibit eruptive or gradient characteristics. Several studies have related abundance and species composition with habitat characteristics (Johnson 1989, Kemp et al. 1990, Fielding and Brusven 1993, Skinner 1995), while others examined temporal changes in grasshopper numbers (Johnson and Worobec 1988, Przybyszewski and Capinera 1990, Kemp 1992). However, explicit attention to spatio-temporal patterns and increasingly sophisticated methodologies have not yet yielded complete understanding of the factors governing grasshopper population ecology.

**Difficulties.** Despite more than 120 years of study on rangeland grasshopper ecology and population dynamics, we are still unable to accurately predict when or where the next grasshopper outbreak will occur. There are a number of reasons why outbreak prediction is difficult. First, the grasshopper species complex is composed of multiple species; upward of 10 species may cohabit a single habitat type (Kemp 1992). Each species has particular habitat requirements, behaviors, adaptations, vulnerabilities and reproductive capacities.

Irrespective of this heterogeneity, grasshopper communities are often treated as if composed of a single species. Control efforts frequently use a single treatment to manage all species, with varying success. For example, bran bait is not accepted equally among grasshopper species, and some economically damaging species are not as readily controlled by this method (Onsager et al. 1980). The efficacy of biological control agents is also likely to differ among grasshopper species and sexes (Oma and Hewitt 1984).

Grasshopper outbreaks are the result of combined changes in grasshopper abundances and community proportions working over the whole community. The factors which lead to increased abundance operate within the context of the biology and ecology of differing species, and different outcomes can be expected. The forces which allow pest species to increase may conversely lead to decreases in other grasshopper species (Flaherty 1995, Kemp 1992). Given a set of environmental conditions, there is likely to be at least one species in the community which can respond independently to those conditions and increase in abundance (Mulkern 1980).

Similarly, efforts to model grasshopper biology, ecology, or dynamics must focus either on a single species for which adequate information is available or on a generalized grasshopper model (e.g. Onsager 1983, Berry et al. 1995). Modeling a single species is insufficient for predicting the dynamics of the entire feeding guild. Modeling a generalized grasshopper may provide a guess at the composite dynamics of the entire community but is unlikely to accurately predict the dynamics of any of the "real" species. There also may be emergent properties of the community which cannot be modeled by reductionism. Achieving accurate and tractable simulation models is thus extremely difficult, complicated by the natural variability of the grasshopper community.

In some cases, information gained from laboratory studies may not be applicable under field conditions. For example, natural reproductive rates are probably much lower than the rates obtained from studies of caged grasshoppers (J.A. Onsager, Agricultural

Research Service, personal communication; see also Pfadt and Smith 1972). Practical difficulties in measuring parameters such as egg mortality contribute to the intractability of grasshopper modeling and research.

Another complicating factor is that grasshopper populations fluctuate largely over both space and time (Cigliano et al. 1995, Schell and Lockwood 1997). Many studies of grasshopper populations have ignored change over either time or space for practical reasons, but this approach cannot produce accurate predictions of outbreak dynamics. Grasshopper infestations, their expansion and collapse, are spatiotemporal in nature. In addition, multiple species may be at different population levels at a given time, complicating the dynamics of the community as a whole (see Capinera and Thompson 1987). As the pest species increase, do the less common and/or non-economic species increase as well?

Adding to the complexity is the fact that grasshoppers are managed over multiple spatial scales. On the field scale, local landowners and leaseholders may control grasshoppers by spraying fields and roadsides. Species composition, microhabitat use, and diet breadth are likely to influence the success of those management efforts. At the habitat-type or watershed scale, changes in species composition and abundance influence the effectiveness of treatment. Over statewide areas, surveys and hazard maps are used to assess the chances of damage, but the probability that an outbreak will develop changes from one county to another (Kemp 1987). On a regional scale, rangeland grasshopper management efforts have been coordinated by the USDA Animal and Plant Health

Inspection Service-Plant Protection and Quarantine (USDA 1987, 1991), and national agricultural policies are as important to consider as abundance and infestation dynamics.

**The future.** How can these obstacles be overcome? Riley may have been correct in stating that accurate knowledge is the key to living comfortably with grasshoppers in agricultural settings. However, vital information is still missing. Basic biological and ecological information is unavailable for many acridids, especially non-economic species. Phylogenetic relationships need to be clarified (but see Otte and Naskrecki 1997). Issues such as aposematism, competition, community assembly, and niche partitioning need to be more fully investigated. In addition, the relative impacts of abiotic and biotic factors on population growth have been speculated but are largely unknown (Capinera 1987). It is probable that the environmental factors which are most important to grasshopper population changes will differ from one area of the Great Plains to another (Capinera and Horton 1989).

With regard to grasshopper outbreaks, several basic questions remain unanswered. Perhaps the most crucial question is whether grasshopper outbreaks can be predicted or recognized early enough to intervene. One approach to finding the answer is to look for temporal or spatial patterns in outbreak occurrences. Outbreaks have long been assumed to be cyclic, but the return period has been estimated to be anywhere from four to 22 years (Criddle 1932, Parker 1940, Anderson 1964, Smith 1954, Capinera and Sechrist 1982) and other work suggests that outbreaks are aperiodic (Cigliano et al. 1995). Investigation into the development of grasshopper outbreaks has shown that expansion of high density areas over space does not follow any specific pattern (Cigliano et al. 1995).

An alternative approach to predicting grasshopper abundances is to employ population models. The pitfalls of this approach have been discussed above. A third approach is to look for correlations between grasshopper infestations and auxiliary variables, such as drought or sunspot activity. The success of this approach has been minimal, and whether outbreaks primarily result from changes in reproductive rates, precipitation regimes or resource availability is unknown. A combination of these approaches may be necessary. Elucidating the abiotic and biotic factors which are most closely linked with increases in grasshopper abundance, and incorporating those variables into population models, may be the key to accurately predicting outbreaks.

The future of grasshopper management rests on our understanding of this complex system. There is a need to generate new hypotheses and test them in the field, consider time lags in driving variables, and examine combinations of factors instead of looking for one-at-a-time correlations. Population-level studies of individual species, coupled with community-level studies, at multiple spatial and temporal scales are necessary to address the gaps in our knowledge. In a time of changing agricultural practices, reduced federal funding for control efforts, and uncertainty regarding the impacts of global temperature change, the need to understand the ecology of grasshoppers is likely to grow more urgent.

It is surprising that so much remains to be learned about a group of insects which have been so important in American agricultural history. This may be the legacy of an outlook which fails to recognize the heterogeneity of the grasshopper complex. Representative of this mentality is the fact that the disappearance of *Melanoplus spretus,* one of the West's most serious pests, has been overlooked even by historians:

Schlebecker (1953) states that while conversion of the Great Plains to agriculture has decimated bison, wolves, beavers, and Native Americans, grasshopper communities remain largely unchanged.

This dissertation attempts to inform the current approach to grasshopper research by examining the dynamics of abundance over space and in relation to environmental factors. My objectives are to characterize the scale of spatial patterns in grasshopper abundances and to determine which soil and climate variables can be used to distinguish areas where grasshopper densities increase from areas where populations decline or remain constant. The results will clarify the ecological relationships between grasshoppers and their surroundings and the scale at which they interact. While this research may lead to improvements in grasshopper monitoring and control programs, in the end our most important lesson is likely to be that which teaches us how to see grasshoppers not as a "foe" but as a natural part of agroecosystems.

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## CHAPTER II

## SPATIAL ANALYSIS OF COLORADO GRASSHOPPER ABUNDANCES

### Abstract

Grasshoppers are important agricultural pests which inhabit a broad variety of crop and rangeland ecosystems. While the dynamics of grasshopper outbreaks have been studied in several parts of North America, little is known of the spatial dynamics of rangeland grasshopper densities under non-outbreak conditions. The objective of this study was to identify and characterize spatial patterns in grasshopper abundance. Exploratory data analysis and geostatistical techniques were used to identify and characterize spatial dependence among grasshopper counts for 1993 through 1997. Variograms were computed for each year and used with kriging to interpolate grasshopper densities in unsampled areas. Results are compared with previous spatial analyses of grasshoppers in Montana, Idaho, and Alberta. For all years, spherical models provided the best fit to the sample variograms, showing that similar processes influenced grasshopper densities over the years studied. However, the parameters of the variogram models differed among years, indicating that the scale of spatial dependence changed over time. Grasshopper densities showed spatial patterning at scales larger than those reported for other areas of the Great Plains. Given these results, current grasshopper

survey techniques may be more useful in detecting large-scale (regional) infestations than in identifying localized areas which may require control.

**Introduction**

Grasshoppers are important range animals which have long been regarded as serious agricultural pests. These herbivores are capable of causing severe losses to grazing and crop agroecosystems, especially during the periods of high population numbers which are commonly called outbreaks (Cigliano et al. 1995, Davis et al. 1992, Hewitt 1977). However, destruction by grasshoppers is concentrated in both time and space (Lockwood and Schell 1995) and outbreaks are the exception rather than the rule.

To ensure preparedness for impending rangeland grasshopper outbreaks, the United States Department of Agriculture's (USDA) Animal and Plant Health Inspection Service, Plant Protection and Quarantine (APHIS-PPQ) conducts annual surveys of adult grasshoppers in seventeen western states (USDA 1982). Until 1995, the Colorado survey sampled sites at 5 mile intervals; in recent years, the survey has been scaled down and less than 150 representative rangeland sites are visited each year. The goal of the survey is to monitor grasshopper densities and determine the likelihood of economically damaging densities (more than 9.6 grasshoppers per $m^2$). Because "...it is important to use grasshopper sampling intervals appropriate to the habitat patch size... (Fielding and Brusven 1993, p. 45)," description of the scale at which grasshopper abundances are patterned (i.e., the patch size) is critical to reaching this goal.

Despite more than a century of grasshopper research, we still do not fully understand why or how outbreaks develop. Questions which remain unanswered include why some areas develop outbreaks more frequently than others and what triggers the shift from endemic population levels to outbreak densities. One of the approaches to finding answers to these questions has been to describe the characteristics and development of grasshopper infestations over both time and space (Cigliano et al. 1995, Lockwood and Schell 1995, Schell and Lockwood 1997).

While outbreak dynamics have been studied in several parts of North America, little is known of the spatial dynamics of rangeland grasshopper densities under non-outbreak conditions. Such knowledge is necessary to more fully understand their ecology, accurately forecast population changes, and improve hazard maps. Analysis of the spatial dependence in endemic grasshopper densities can also help to assess the adequacy of current survey methods for detecting infestations.

The description and analysis of spatial patterns is essential to understanding the spatial distribution of an ecological phenomenon and the processes which produce that distribution (Chou 1993). Spatial patterns of abundance make it possible to describe, understand, and predict grasshopper population growth over both time and space and can give clues to the factors involved in the initiation, development, and subsidence of outbreaks. Indeed, pest outbreaks in general have been characterized and classified (Berryman 1987) based on their temporal and spatial dynamics. Examination of patterns of abundance can also aid in identifying habitats prone to high densities.

Methods of detecting and describing spatial patterns have been developed in the field of geology and have recently been applied to ecological phenomena. These methods are collectively referred to as geostatistics or spatial statistics. While spatial statistics are already being used to produce grasshopper hazard maps via kriging (Kemp et al. 1989), improving readiness for outbreaks, a fundamental description of spatial variability and patterning in grasshopper abundances has not been undertaken until now.

Previous studies of grasshopper communities through time and space have examined a number of ecological phenomena. Kemp (1992) found high spatial variability in grasshopper species composition at low regional densities and over different habitat types. Cigliano et al. (1995) established that grasshopper outbreaks vary widely in geographic extent, and may remain stable, expand, or collapse with time. The dynamics and prevention of outbreaks were investigated during an interoutbreak period by Lockwood and Schell (1995), who found that localized infestations averaged 820 ha in size. Schell and Lockwood (1997) quantified the scope and frequency of grasshopper outbreaks in Wyoming, showing that in most years grasshoppers do not cause economic damage: only 6% of Wyoming had been infested more than five times in their 31 years of data. Kemp and coworkers (1989) applied geostatistics to counts of Montana grasshoppers and showed that patterns differed across three environmental regions of the state. In Idaho, Fielding and Brusven (1993) found that ecological condition did not strongly influence kriged grasshopper densities; Johnson and Worobec related spatial autocorrelation to contour maps of grasshopper densities in Alberta, Canada.

Despite a growing number of spatially-explicit studies, much of the fundamental details of grasshopper community distribution remains unknown. This paper addresses this knowledge gap by characterizing spatial and temporal patterns in Colorado grasshoppers at low to moderate densities of an interoutbreak period using geostatistical methods. Geostatistics have been used to characterize and model distributions of insects across space (e.g., Johnson and Worobec 1988, Johnson 1989, Kemp et al. 1989, Liebhold et al. 1991, Fielding and Brusven 1993, Hohn et al.1993, Gribko et al. 1995).

However, these ecological applications often lack the foundation needed to examine underlying assumptions and theory of the techniques used (Rossi et al. 1992). In this paper, an exploratory data analysis (EDA) is conducted to determine whether grasshopper densities exhibit spatial patterning. Geostatistical techniques were used to test for and determine the scale of spatial dependence among grasshopper counts. Results are compared with previous spatial analyses of grasshoppers in Montana, Idaho, and Canada to determine whether the scale of spatial patterns differs over regions of the Great Plains. The scale of spatial patterning is key to determining whether the APHIS-PPQ survey is effective in detecting incipient outbreaks.

**Objectives.** The primary objective of this study was to determine the adequacy of current grasshopper survey techniques for detecting both large-scale (regional) and small-scale (field) infestations (Objective 1). To achieve this objective, I pursued two related objectives: to determine whether Colorado grasshopper abundances exhibit spatial patterning (Objective 2) and to identify the scale of spatial dependence in Colorado grasshopper abundances (Objective 3).

## Methods

**Grasshopper data.** Each site in the APHIS-PPQ survey is sampled by taking 50 visual checks for presence of one or more grasshoppers in a 0.1 $m^2$ area (E. Danielson-Buffington, Colorado State University, personal communication). Grasshopper densities are estimated from incidence through the use of the Poisson probability density function (Onsager 1991, Legg et al. 1993).

APHIS grasshopper survey data for 1993 through 1997 were acquired in digital form and inspected for outliers. One site from each of the 1995 and 1997 data sets were reported to have longitudes near -120° west. Because these values would put the sites outside of the state of Colorado, the longitudes were suspected to be erroneous and the sites were removed from their respective data sets. Grasshopper densities were also inspected and two sites with questionably high densities (approx. 200 grasshoppers per $yd^2$) were removed from the 1996 data set. Densities were converted from numbers per $yd^2$ to numbers per $m^2$ where necessary.

The locations for sites sampled in 1994 were recorded in Universal Transverse Mercator (UTM) system. Locations for all other years were recorded in latitude and longitude. Because the UTM projection minimizes distortion of area, distance, and direction, all site locations were transformed to UTM meters for zone 13 using PC ARC/INFO 3.5.1 (ESRI 1997). Point coverages were generated from the UTM site locations for each year of grasshopper data.

**Ecoregions.** Ecologists are often interested in categorizing landscapes into habitat types, biomes or ecological regions (ecoregions). The classification scheme may be based on climate, climax vegetation, or other variables. The result is often a map which delineates areas within which physical and biological characteristics are expected to be similar. Omernik's (1987) ecoregion map is one such classification scheme, compiled from potential vegetation, land use, topography, and soil maps to delineate ecological regions at a map scale of 1:7,500,000 for the conterminous United States. Because the ecoregions are defined based on a combination of physical and biotic variables, they integrate the large-scale ecological processes which give context to smaller-scale interactions.

To assess whether grasshopper densities show similar patterns across different ecological regions of Colorado, a digital map of Omernik's (1987,1995) Level III Ecoregions of the Conterminous Unites States was obtained from <ftp://ftp.epa.gov/pub/spdata>. This map was imported into PC ARC/INFO 3.5.1 (ESRI 1997) and overlaid with the boundaries of the state of Colorado, which were downloaded from <http://www.landuse.com>. The resulting coverage (Figure 2.1), containing only ecoregions of Colorado, was overlain with each of the grasshopper site coverages, resulting in a coverage for each year which contains site locations, grasshopper densities, and the ecoregion in which each sampled site lies.

The ecoregions of interest are the two which comprise the eastern plains of Colorado: ecoregion 25, the Western High Plains, and ecoregion 26, the Southwestern Tablelands (Omernik 1987, 1995). Ecoregion 25 consists of smooth to irregular plains dominated by grama and buffalo grasses (*Bouteloua gracilis* (H.B.K.) Lag. *ex* Steudel, *Buchloe dactyloides* (Nutt.) Engelmann) on dry mollisol soils. The land is used for dryland crops, grazing, and irrigated agriculture. Ecoregion 26 comprises semiarid tablelands with moderate relief where the natural vegetation includes grama, buffalo, and bluestem grasses (*Andropogon gerardii* Vitman, *Bouteloua gracilis* (H.B.K.) Lag. *ex* Steudel, *Buchloe dactyloides* (Nutt.) Engelmann, *Shizachyrium scoparium* (Michx.) Nash) with some sandsage (*Artemisia filifolia* Torrey). Land use includes grazing and dryland agriculture.

**Geostatistics.** When using conventional statistical methods, one must frequently assume that all data are independent and identically distributed. These assumptions are violated when data are spatially or temporally correlated. This is the case for many ecological data, in which samples taken close to one another may be expected to have more similar values than samples taken farther apart (Rossi et al. 1992), a phenomenon variously referred to as spatial dependence, spatial continuity, and autocorrelation. Alternative statistical tools are needed when dealing with autocorrelated data. A body of such tools has been developed in the field of geology, and subsequently applied in ecology, for modeling spatial dependence. These tools are collectively known as geostatistics. Geostatistical tools include tests for spatial autocorrelation, *h*-scattergrams, variograms, correlograms and kriging (Rossi et al. 1992). The spatial analysis functions used here were provided by Reich and Davis (1998) and were performed in S-PLUS 4.0 for Windows (MathSoft 1997).

**Exploratory data analysis.** Although several studies have applied geostatistics to grasshopper data, none have conducted the supporting exploratory data analyses (EDA) described by Rossi and coworkers (1992) as necessary for proper ecological interpretation of spatial patterns and to guide subsequent analyses. In this study, various EDA techniques were used to detect and describe spatial patterns in Colorado grasshopper densities. Univariate summary statistics and standard two-sample *t*-tests between means were also performed to determine whether differences exist in grasshopper densities between ecoregions and years.

To assess the sampling distribution of the grasshopper data, frequency histograms were made for each year's densities. The histograms showed that the grasshopper densities were positively skewed in all years sampled, with many zero or low values and few high values (Figure 2.2). For better approximation to the Normal distribution, a ln(density + 1) transformation was performed before proceeding with the spatial analyses.

Data posting is a simple visual tool for spatial display and description (Isaaks and Srivastava 1989). A map of data values is made by plotting sampled sites using the grasshopper density of each site as the display symbol. The plotted data are examined, noting the highest and lowest values, trends, and outliers. If similar values map close together, there may be spatial dependence in the posted variable. Data posting can also show patterns in how data were collected, as areas of interest may be represented by more samples.

Bivariate scatterplots are another useful way to display spatial data. The data can be graphed with one axis corresponding to the data values and another axis corresponding to a locational coordinate or the value of a second variable measured at the same site (Rossi et al. 1992, Isaaks and Srivastava 1989). Scatterplots are used to look for a nonrandom distribution of the data and to check for outliers. Bivariate scatterplots of grasshopper density by longitude and latitude were examined to reveal spatial trends and give visual clues to the presence and direction of spatial dependence.

**Spatial autocorrelation.** Spatial autocorrelation is the degree to which the value of a variable at a given sampled site is correlated with the values for the same variable at neighboring sites (Sokal and Oden 1978a). Positive spatial autocorrelation produces a pattern where sites of similar values tend to be clustered and negative autocorrelation indicates a spatial pattern in which sites with similar values are dispersed (Chou 1993). When there is no significant spatial autocorrelation, the pattern is random.

Tests for spatial autocorrelation include a number of indices which measure the degree to which a variable is correlated with itself, the most common of which is Moran's I statistic (Moran 1950). Moran's I was used to test for autocorrelation among grasshopper densities for all sites (COLO data), eastern Colorado sites (EAST data), and each ecoregion (E25 and E26 data) within each sampled year.

Moran's I statistic is analogous to a correlation coefficient, ranges between -1 and 1, and its sign indicates whether the spatial correlation is positive or negative. The statistic is calculated under the null hypothesis of spatial independence (no spatial autocorrelation) as:

$$I = \frac{n}{2A} \frac{\sum_{i=1}^{n}\sum_{j=1}^{n} \delta_{ij} (Z_i - \overline{Z})(Z_j - \overline{Z})}{\sum_{i=1}^{n} (Z_i - \overline{Z})^2}$$

where n is the number of sampled points; 2A is $\Sigma_i\Sigma_j\ \delta_{ij}$, the total number of pairs of points; $\delta_{ij}$ is the matrix of weights based on the inverse distance between the *i*th and *j*th points; and $Z_i$ is the observed value of the variable of interest at the *i*th sampled point (Cliff and Ord 1973, Chou 1993).

When Moran's I statistic is calculated under the randomization assumption, one does not have to know the true distribution of the data because I is calculated under all n! random permutations of the data. In this case, I is asymptotically Normal for $n \geq 25$, provided the distribution is not markedly non-Normal and no sites dominate the "lattice" (Cliff and Ord 1973, Ord 1979). Thus, critical values for hypothesis testing are calculated from the standard deviation of I (see Sokal and Oden 1978a) using the standard Normal distribution. For this reason, Moran's I was calculated for natural log-transformed grasshopper densities, as their distribution more closely resembled the Normal. *P*-values for I were calculated for 500 random permutations of the data and the test statistic was rescaled so each row of the spatial weights matrix $\delta_{ij}$ summed to 1. Moran's I tests were performed separately on the COLO, EAST, E25 and E26 data sets.

The expected value of Moran's I under the null hypothesis of no spatial autocorrelation is not necessarily zero; it is determined from the spatial weights matrix of the data. The difference between the observed and expected values of I are tested for significance. If no spatial autocorrelation was detected using Moran's I, then variography and kriging were not performed on the data set.

Moran's I was also calculated for increasing distances around sample points and summed to find the cumulative value of I at each distance class (0-5 km, 5-10 km, ..., 95-100 km). The cumulative value of the I statistic can be graphed against the distance classes to identify the scale of autocorrelation (Reich et al. 1994; see also Greig-Smith

1952). If the cumulative value of I decreases with increasing distance, the spatial pattern is one of regularly distributed patches. The plot of cumulative I against distance will reach an asymptote when patches are aggregated or randomly distributed (Reich et al. 1994). The distance at which the curve levels off indicates the scale of the spatial pattern (R. Reich, Colorado State University, personal communication). The peak of the cumulative value of Moran's I is analogous to the range for the sample variogram, and can be expected to have a similar value.

**Variography.** One of the methods traditionally used to describe and quantify spatial autocorrelation is the variogram, also called the semivariogram. A variogram summarizes the degree of similarity between data values, for all possible pairings of the data, as a function of the distance between the samples (Rossi et al. 1992, Liebhold et al. 1993). The sample variogram is calculated as:

$$\gamma(\mathbf{h}) = \frac{1}{2N(\mathbf{h})} \sum_{i=1}^{N(\mathbf{h})} [z(x_i) - z(x_i + \mathbf{h})]^2$$

where $\gamma(\mathbf{h})$ is the semivariance for lag distance **h**, $N(\mathbf{h})$ is the number of pairs of sampled points separated by **h**, and $z(x_i)$ is the observed data value at location $x_i$ (Rossi et al. 1992).

Several characteristics of the variogram are used to describe its structure. The value at which the variogram levels off is known as the sill and is equivalent to the sample variance. The distance at which the variogram reaches the sill is called the range; this represents the average distance to which samples are spatially autocorrelated (Isaaks and Srivastava 1989, Rossi et al. 1992, Liebhold et al. 1993). Thus, the range is analogous to the asymptote of the cumulative plot of Moran's I statistic.

The value of the variogram is strictly zero for zero distance, since there can be no variability between a sampled point and itself. In practice, however, the value of the sample variogram may not be zero at very small distances, causing a discontinuity at zero called the nugget effect (Isaaks and Srivastava 1989). The positive value at which the variogram appears to intercept the ordinate is called the nugget and represents either sampling error or spatial variability at distances smaller than the minimum sampling distance (Rossi et al. 1992, Liebhold et al 1993).

The sample variogram was calculated for each year of the COLO data using the spatial library for S-Plus developed by Reich and Davis (1998). Each variogram was calculated to about half the maximum distance between points (Liebhold et al. 1993). Variograms were calculated for all directions about the sampled sites (omnidirectional/isotropic). The nugget, range and sill of each sample variogram were estimated and used as parameters to iteratively fit a linear, spherical, exponential, or Gaussian model to the sample variogram. The model with the lowest corrected Akaike Information Criterion (AIC) was selected as the best fit to the sample variogram.

**Kriging.** The fitted variogram models specify the spatial correlation for different distances between data points (Liebhold et al. 1993). Once this covariance structure has been quantified through variography, the shape and parameters of the fitted variogram can be used to interpolate values of the variable of interest at unsampled points through kriging. Kriging uses the variogram model to weight the known samples and provide estimates for unsampled locations. The kriged estimates are weighted linear combinations of the sampled data, calculated such that the mean squared error of prediction is minimized (Isaaks and Srivastava 1989, Liebhold et al. 1993). Each interpolated value is calculated as:

$$V^*(x_0) = \sum_{i=1}^{n} w_i \cdot V(x_i)$$

where $V^*(x_0)$ is the value to be estimated at location $x_0$ and $w_i$ are the weights given each sampled value $V(x_i)$ (Isaaks and Srivastava 1989, Liebhold et al. 1993).

To produce interpolated surfaces of grasshopper densities from the sample data, I used the variogram parameters and model with best fit, iteratively selected the number of neighbors that produced the surface with most relief (n=4 for most surfaces), and plotted the surface on a 25x25 grid. The standard error of the estimated surface was also plotted. Kriging was done on log-transformed grasshopper densities.

## Results and Discussion

**Exploratory Data Analysis.** Summary statistics for grasshopper densities are given in Table 2.1. The mean grasshopper density over all sites differed among years, and in 1996 densities were highest, with a median density more than twice that of any other year. However, populations remained at the moderate mean density of about eight grasshoppers per $m^2$, which is below the traditional economic threshold of 9.6 grasshoppers per $m^2$ for control activities (Davis et al. 1992). In all years of data, densities remained below the regional carrying capacities of 8.6 to 8.9 grasshoppers per

$m^2$ calculated by Kemp and Dennis for plains regions of Montana (1993), although the carrying capacity for grasshoppers on Colorado rangeland may differ from that of Montana.

Two-sample *t*-tests between mean grasshopper densities resulted in no significant differences between ecoregions in any of the five years sampled (Table 2.2). These results contrast with those of Skinner (1995), who found significant differences in grasshopper abundance among three ecoregions in Montana. It may be that the two ecoregions of eastern Colorado are very similar in grasshopper species composition or influenced by common large-scale processes, and thus exhibit similar densities. Further study is necessary to determine whether ecoregions differ in grasshopper abundance when populations are at higher, economically damaging densities.

The histograms of grasshopper densities (Figure 2.2) show positive skewness, as discussed above, and comparison of histograms shows that the maximum measured grasshopper density differed between years. The highest maximum density was 42.5 grasshoppers/$m^2$ in 1996 and the lowest was 12.5 grasshoppers/$m^2$ in 1997 (Table 2.1). The cause of this abrupt reduction in mean grasshopper density is unknown but may be related to increased precipitation in the summer of 1997 (pers. obs.), since moist conditions increase nymphal mortality rates both directly and as a result of increased incidence of pathogens (Dempster 1963).

Data posting (Figure 2.3) reflected the respective histogram for each year in that there are many sites with low densities scattered across the state. Areas of moderate to high densities are somewhat clustered but are also scattered among low density sites, as can be seen in Figure 2.3. In general, densities were low in the western half of Colorado and higher densities were well dispersed among lower densities in eastern Colorado. This pattern suggests that positive spatial autocorrelation may be detected when the COLO data are tested but densities may exhibit a random pattern when only the eastern sites (EAST data) are analyzed.

The posted data show that sampling is more intense in the eastern half of Colorado, indicating a higher interest in monitoring grasshopper populations, probably as a result of historical outbreak frequencies, differences in land use, and the value of agricultural productivity. Very few samples are taken in the middle longitudes, which correspond to the mountainous areas of the state. The mapped data also showed high overlap in site locations from year to year, such that many sites were revisited annually.

The bivariate scatterplots (Figure 2.4) revealed a weak relationship between density and longitude for all years, with high densities located mostly between about -104° and -102° longitude. These locations correspond to the eastern plains of Colorado, where drier climatic conditions would generally favor grasshopper populations (Gage and Mukerji 1977). However, correlations between density and locational coordinates were generally low (Table 2.2). This result is supported by the findings of Kemp et al. (1989), who examined Montana grasshopper counts for anisotropy and concluded that isotropic variograms were appropriate for kriging purposes. For this reason, only omni-directional (isotropic) variograms were computed.

**Spatial autocorrelation.** Tests using Moran's I statistic on the COLO data revealed significant positive spatial autocorrelation for all years (Table 2.3). When

Moran's I was calculated for the sites in eastern Colorado only, significant positive autocorrelation was found in all years except 1995. For the sites in ecoregion 25, significant positive autocorrelation was found in years 1993 and 1997, while in ecoregion 26, autocorrelation was significant and positive for 1993 and 1994. Because spatial autocorrelation was not significant for all years in the ecoregion data sets, variography and kriging were performed only on the COLO and EAST data sets.

Cumulative calculations of Moran's I are plotted against distance in Figure 2.5 and results are reported in Table 2.4. In 1993, the peak of the cumulative curve occurred at 20 km, while in all other years, the curves leveled off at distances of 300 km or more. The results for 1993 compare with those of Johnson (1989) and Johnson and Worobec (1988) for Alberta, where significant positive spatial autocorrelation occurred out to distances of 20-50 km. For 1994 through 1997, the curves indicate spatial patterning at distances greater than those found for plains areas of Montana by Kemp and coworkers (1989), where ranges of variograms were 90-112 m. Indeed, the curves for 1996 and 1997 indicate that there may be larger spatial patterns in density which could only be detected by sampling grasshopper densities in both Colorado and adjacent states (Figure 2.5). This hypothesis is supported by the work of Capinera and Horton (1989), who found that "infestation levels were positively correlated between adjacent states." Characterization of spatial patterning in grasshopper abundances at a larger, regional scale would help to identify and understand regional outbreak patterns.

Although the peaks of cumulative values of Moran's I for 1994 and later indicate spatial autocorrelation at larger scales than have previously been reported for other areas in the Great Plains, this may be a result of the number of sites sampled. Over a thousand sampled sites were taken over a 200,000 $km^2$ area for Johnson and Worobec's (1988) calculations and Kemp and coworkers (1989) used over 400 sites in computing variograms for Montana's plains, while only about 100 samples were used for this study. The smaller number of samples for a comparable spatial area (267,000 $km^2$) results in poorer resolution and changes in grasshopper densities at scales of less than 50 km may be present but not detected.

The lack of strong spatial autocorrelation at smaller scales may also be a result of the low to moderate population levels in the years sampled. When grasshopper densities are high, populations show strongly clumped patterns, in time as well as in space. Infestations are not uniformly distributed across suitable habitat but instead form "hot spots" of high densities (Schell and Lockwood 1997). At the lower densities seen here, however, autocorrelation is less pronounced. The distribution of the data may have influenced the results of Moran's I statistic, because even the log-transformed data are positively skewed and the few sites with high densities may "dominate the lattice," violating the assumption that the statistic is asymptotically Normal.

These results show that the current scheme for surveying grasshopper populations is not adequate for detecting localized infestations. The average distance between points (from weight matrices) was between 219 and 264 km for the years 1993 to 1997 and the smallest scale at which autocorrelation was detected was 20 km (Table 2.4). These distances would have to be greatly reduced to detect incipient infestations, based on Lockwood and Schell's (1995) finding that the average size of "hot spots" is 8.2 $km^2$.

Since 1934, the U.S. Department of Agriculture's Animal and Plant Health Inspection Service (APHIS), has funded management efforts on rangeland (USDA 1982). The Federal criteria for grasshopper control include treating blocks of infested rangeland at least 10,000 acres (40.5 $km^2$) in size. An infestation covering more than twice that area might still be missed using the current APHIS survey methods. An improved sampling protocol would include more sites at closer distances to reduce the average distance between points and thus increase the probability of sampling within a developing infestation. More intensive sampling would be more likely to meet the objective of the survey, which is to assess the potential for grasshopper densities which may require treatment on a local or county basis (USDA 1982).

**Variograms.** Table 2.4 lists the best-fitting variogram model and parameter estimates for each data set in which significant spatial autocorrelation was found for every year tested. The model shape differed only slightly between years. For the COLO data, the spherical model gave the best fit in all years. When variograms were calculated for the EAST data, the spherical model again gave the best fit except in 1994, when the Gaussian model gave a slightly better fit. Thus, it is likely that the same processes are influencing grasshopper densities and their spatial patterns over the five years studied (Sokal and Oden 1978b), although the specific characteristics of the spatial structure varied (Table 2.4).

The parameters of the fitted variogram models differed over time. The range, for example, varied between 60 and 125 km for the COLO data and between 25 and 160 km for EAST sites. While the range represents the average distance to which data are spatially autocorrelated (Rossi et al. 1992), these ranges do not match the peaks of the cumulative Moran's I plots. This could occur if there are larger-scale patterns which were not modelled because the sample variograms were calculated only to half the maximum distance between points. The variograms did show signs of larger scale patterns: sample variation tended to increase at the largest lags, but since variograms were only modelled to half the maximum distance, any larger-scale patterning was not investigated.

Grasshopper densities may exhibit spatial patterns at multiple scales, which may be nested, such that autocorrelation at smaller scales are masked by patterns at larger scales. Indeed, the posted data (Figure 2.3) indicate positive autocorrelation when sites across the state are examined, but a random pattern is seen among the eastern sites. Thus, grasshopper densities in Colorado exhibit spatial patterning at both small (local) and large (regional) scales.

Comparison of the fitted variograms with those of previous studies is problematic. The work of Fielding and Brusven (1993b) in Idaho fitted only exponential models, while Kemp and coworkers (1989) fitted only spherical models, so comparison based on the shape of the best fitting model is not possible. The spatial structure (e.g. sill, and nugget values) is also difficult to compare unless variograms are standardized (Rossi et al. 1992), although ranges may be directly compared. The ranges reported in Table A.5 are comparable to the ranges of 43 to 112 km which Kemp et al. (1989) estimated for regions of Montana. In a smaller study area (15,000 $km^2$) in Idaho, Fielding and Brusven (1993) reported shorter ranges of 14 to 53 km. These ranges are comparable with the smaller-scale patterns detected using the cumulative values of Moran's I.

**Kriging.** The kriged surfaces and standard error surfaces for the COLO and EAST data sets for 1995 are shown in Figures 2.8 and 2.9. The Z axis represents log-transformed grasshopper densities. All kriged surfaces showed higher densities with increasing distance along the abscissa, corresponding to the expected higher population levels in Colorado's eastern plains. The standard error surfaces showed that errors of prediction were highest for the middle distances, a result expected from the fact that few samples were taken in the mountainous mid-longitudes of the state. Kriging only the eastern Colorado sites (EAST data) removed these large errors and resulted in a more readily interpreted surface which showed that the estimated grasshopper densities were spatially autocorrelated, with areas of higher densities forming hills and areas of lower densities forming valleys (Figure 2.9).

## Summary

Colorado grasshopper densities exhibited spatial patterning at two spatial scales. Positive spatial autocorrelation was detected at scales up to 300 km. The scale differed from year to year and with the geostatistical method used. The average distance between sampled points was an order of magnitude larger than the smallest scale at which autocorrelation was detected. These results show that while current grasshopper survey techniques may be adequate for detecting large-scale outbreaks, local infestations are likely to be missed. The presence of more than one scale of spatial autocorrelation in the grasshopper densities indicates that sampling for monitoring purposes should be done at frequent spatial intervals and coordinated over large geographic areas. More extensive sampling would capture the variability in abundance which results from ecological processes operating at both the field and regional scales.

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Table 2.1. Summary statistics for grasshopper densities (number per $m^2$) at all sampled sites (COLO data). IQR is the inter-quartile range; CV is the coefficient of variation.

| | Year | | | | |
|---|---|---|---|---|---|
| | 1993 | 1994 | 1995 | 1996 | 1997 |
| N | 106 | 99 | 98 | 132 | 118 |
| Minimum | 0 | 0 | 0 | 0 | 0 |
| Maximum | 23.4 | 32.6 | 26.8 | 42.5 | 12.5 |
| Mean | 4.20 | 4.90 | 3.18 | 7.97 | 2.43 |
| Median | 2.5 | 2.1 | 1.5 | 5.6 | 1.6 |
| Std Dev | 4.77 | 7.13 | 4.87 | 8.11 | 2.54 |
| IQR | 4.20 | 4.50 | 2.00 | 8.23 | 2.60 |
| CV | 1.14 | 1.45 | 1.53 | 1.02 | 1.05 |

Table 2.2. Standard two-sample *t*-tests for mean grasshopper densities.

| | Year | | | | |
|---|---|---|---|---|---|
| | 1993 | 1994 | 1995 | 1996 | 1997 |
| **Ecoregion 25 x 26** | | | | | |
| *t* | 1.426 | -1.524 | 1.277 | 0.315 | 1.344 |
| d.f. | 90 | 87 | 76 | 110 | 94 |
| *P*-value | 0.157 | 0.131 | 0.206 | 0.754 | 0.182 |

Table 2.3. Results of tests for spatial autocorrelation using Moran's I statistic.

| | | Year | | | | |
|---|---|---|---|---|---|---|
| | | 1993 | 1994 | 1995 | 1996 | 1997 |
| **All sites** | | | | | | |
| | Dimension | 106 | 99 | 98 | 132 | 118 |
| | Moran's I | 0.179 | 0.0802 | 0.0899 | 0.161 | 0.129 |
| | Mean of I | -0.0112 | -0.00970 | -0.0114 | -0.00692 | -0.00804 |
| | Std Dev | 0.0370 | 0.0189 | 0.0207 | 0.0374 | 0.0165 |
| | *P*-value | 0* | 0* | 0* | 0* | 0* |
| **Eastern Colorado sites** | | | | | | |
| | Dimension | 88 | 91 | 79 | 113 | 98 |
| | Moran's I | 0.232 | 0.0639 | 0.0318 | 0.0916 | 0.0694 |
| | Mean of I | -0.0133 | -0.0118 | -0.0131 | -0.00912 | -0.0103 |
| | Std Dev | 0.0453 | 0.0211 | 0.0208 | 0.0467 | 0.0164 |
| | *P*-value | 0* | 0.008* | 0.056 | 0.036** | 0* |
| **Ecoregion 25 sites** | | | | | | |
| | Dimension | 43 | 46 | 37 | 52 | 48 |
| | Moran's I | 0.171 | 0.0175 | 0.0693 | 0.0691 | 0.114 |
| | Mean of I | -0.0223 | -0.0221 | -0.0275 | -0.0180 | -0.0203 |
| | Std Dev | 0.0746 | 0.0472 | 0.0537 | 0.0657 | 0.0395 |
| | *P*-value | 0.012** | 0.328 | 0.104 | 0.196 | 0.008* |

| | Year | | | | | |
|---|---|---|---|---|---|---|
| **Ecoregion 26 sites** | | | | | | |
| | Dimension | 42 | 43 | 41 | 60 | 48 |
| | Moran's I | 0.233 | 0.0642 | -0.0141 | 0.133 | 0.0142 |
| | Mean of I | -0.0217 | -0.0242 | -0.0251 | -0.0187 | -0.0222 |
| | Std Dev | 0.0458 | 0.0327 | 0.0293 | 0.0839 | 0.0260 |
| | *P*-value | 0* | 0.028** | 0.592 | 0.072 | 0.16 |

Tests for spatial autocorrelation using natural log transformed grasshopper densities. The mean and standard deviation (std dev) of I are calculated under the null hypothesis of no spatial autocorrelation. Tests were performed on 500 random permutations of the data. *P*-values are for a two-sided test of the hypothesis.

* Significant at $\propto$=0.01 level.
** Significant at $\propto$=0.05 level.

Table 2.4. Spatial dependence in grasshopper populations.

| | Year | | | | |
|---|---|---|---|---|---|
| | 1993 | 1994 | 1995 | 1996 | 1997 |
| **All sites** | | | | | |
| Peak of cumulative Moran's I (km) | 20 | 300 | 400 | 400 | 400 |
| Value of cumulative Moran's I at peak | 8.5 | 0.80 | 1.4 | 4.5 | 4.2 |
| Variogram model | Spherical | Spherical | Spherical | Spherical | Spherical |
| Nugget | 0.214 | 0.164 | 0.163 | 0.231 | 0.124 |
| Range (km) | 125 | 60 | 100 | 70 | 60 |
| Sill | 0.548 | 0.705 | 0.592 | 0.614 | 0.355 |
| **Eastern Colorado sites** | | | | | |
| Variogram model | Spherical | Gaussian | Spherical | Spherical | Spherical |
| Nugget | 0.235 | 0.140 | 0.134 | 0.261 | 0.106 |
| Range (km) | 160 | 25 | 75 | 60 | 50 |
| Sill | 0.551 | 0.706 | 0.598 | 0.605 | 0.345 |

Figure 2.1. Omernik's ecoregions for Colorado.

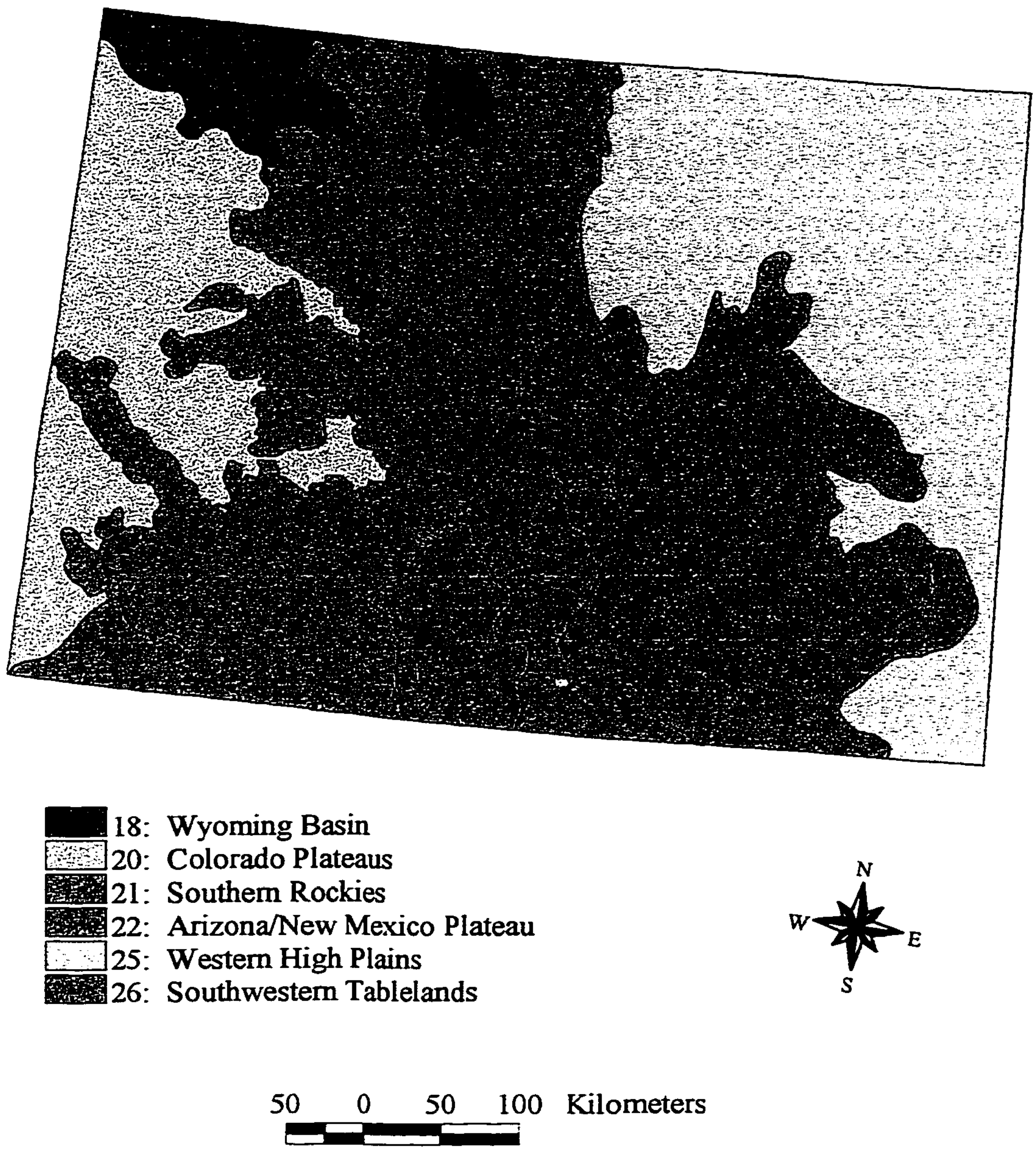


Figure 2.2. Histogram of 1993 grasshopper densities (number of individuals per $m^2$).

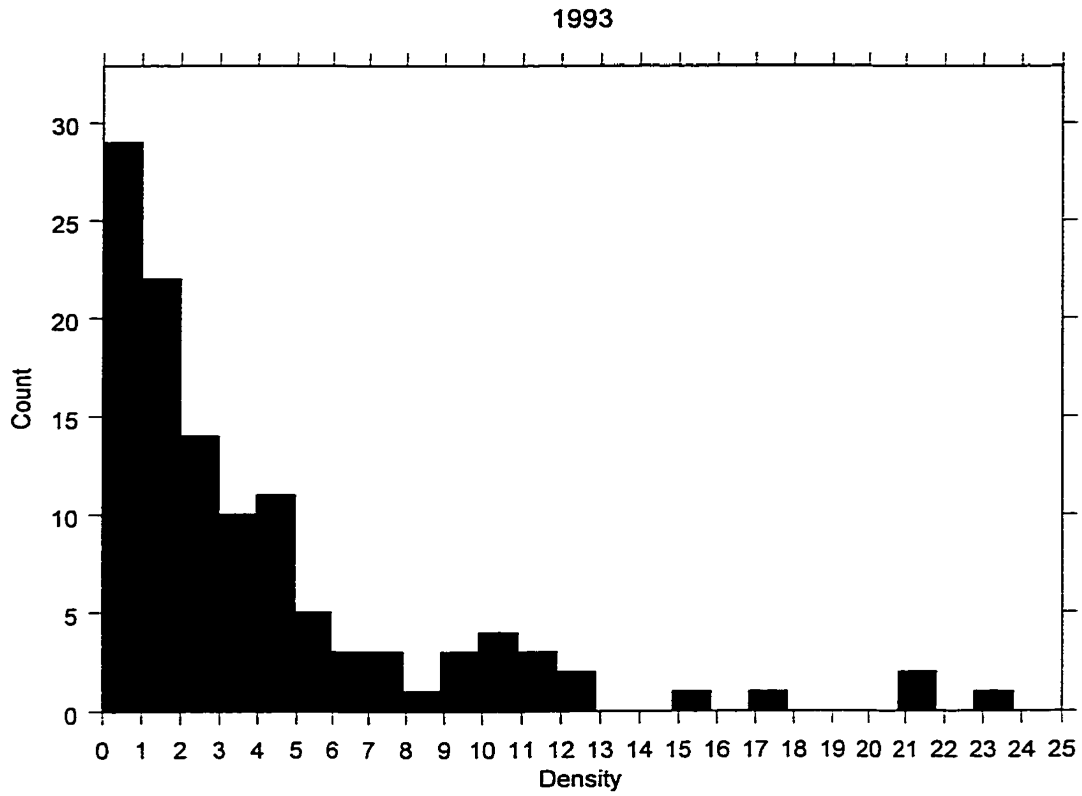


Figure 2.3. Posted grasshopper densities for 1996. Some sites have been moved or omitted for legibility.

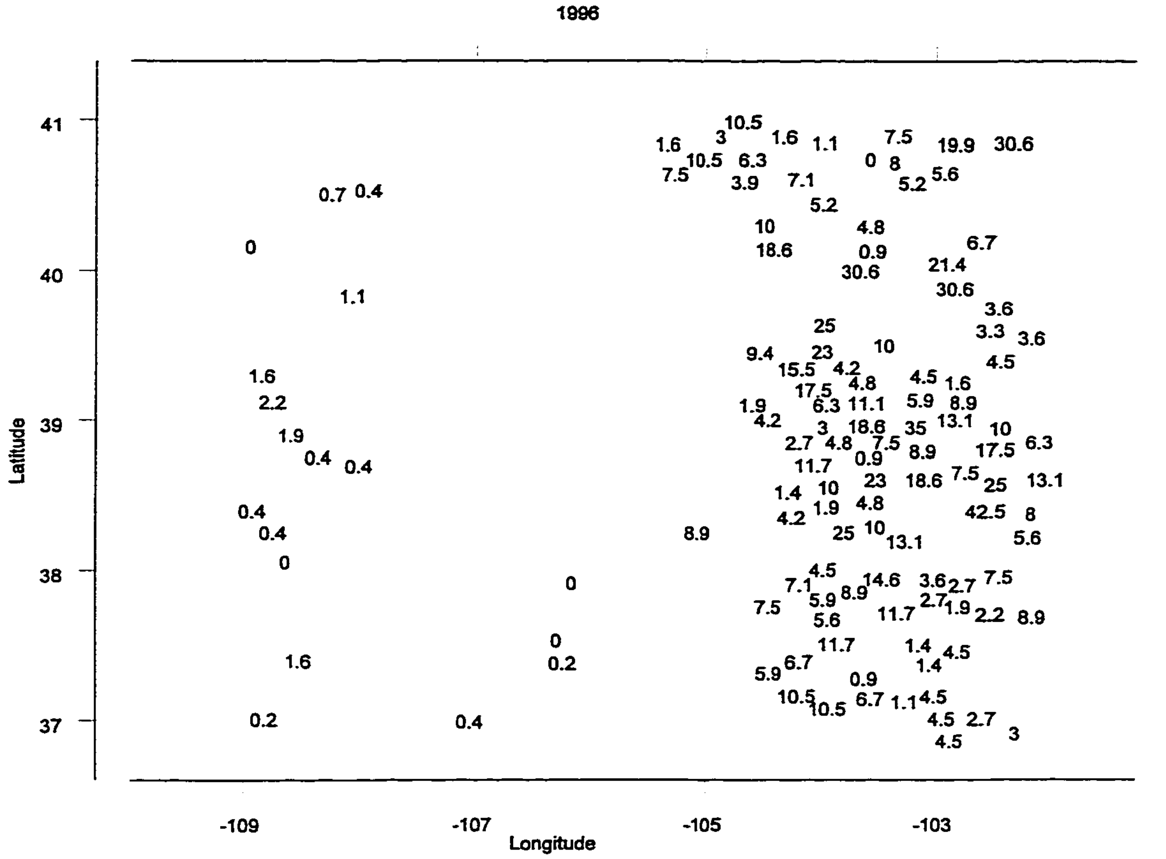


Figure 2.4. Bivariate scatterplots (density vs. location) for 1994. Grasshopper density is given in number of individuals per $m^2$.

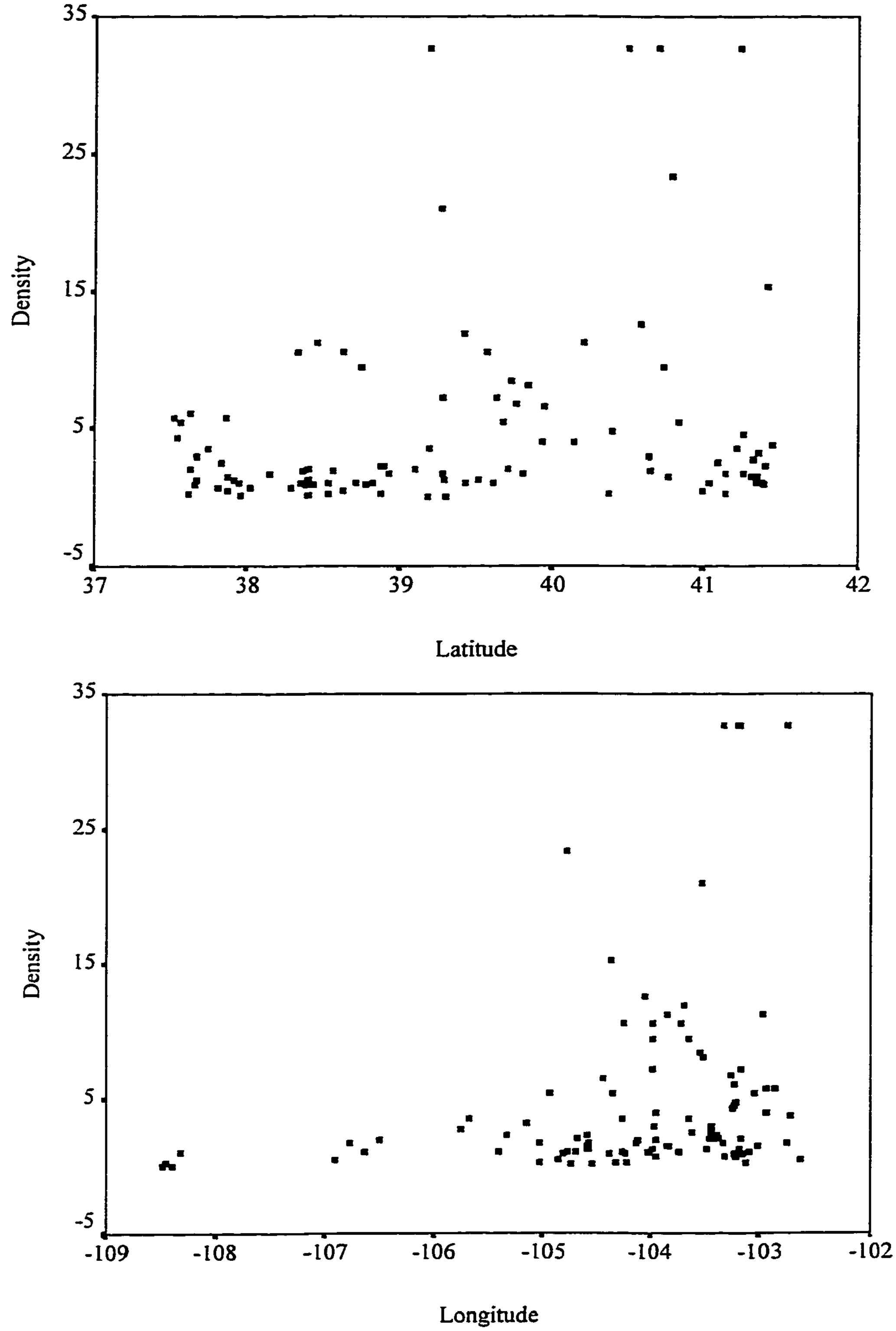


Figure 2.5. Cumulative Moran's I plotted against distance.

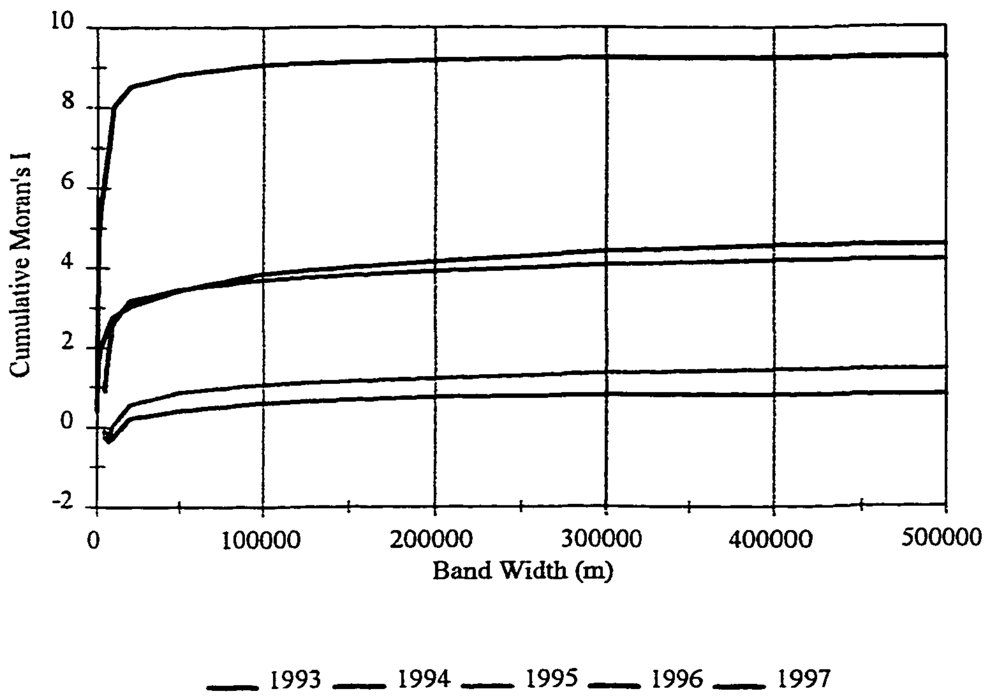
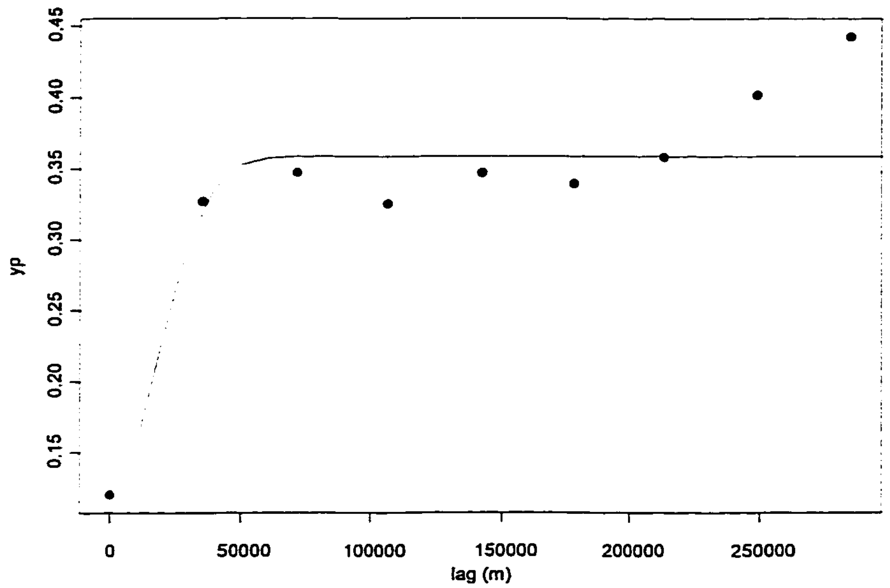


Figure 2.6. A. Variogram for 1997 grasshopper densities, all sites. B. Variogram for 1997 grasshopper densities, eastern Colorado sites only.

A




B

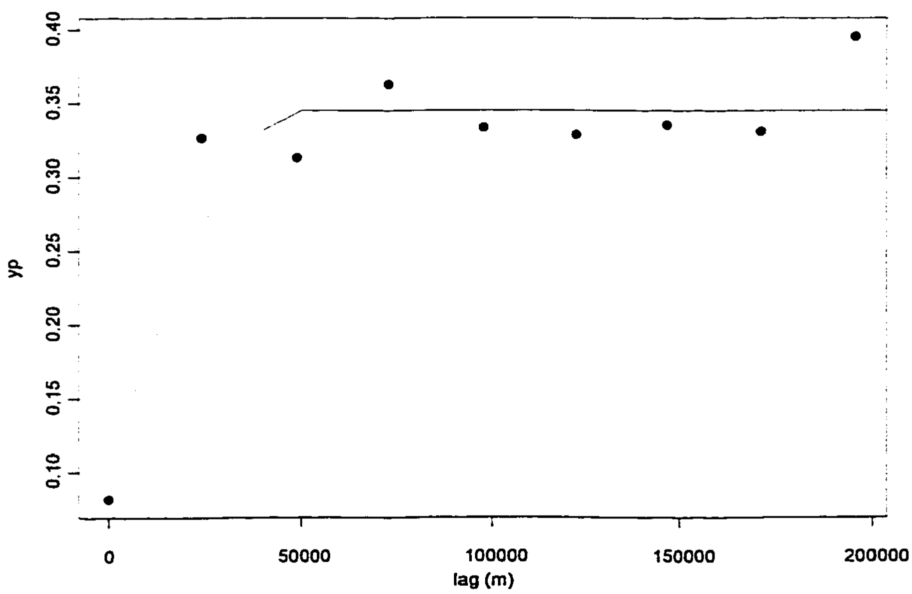
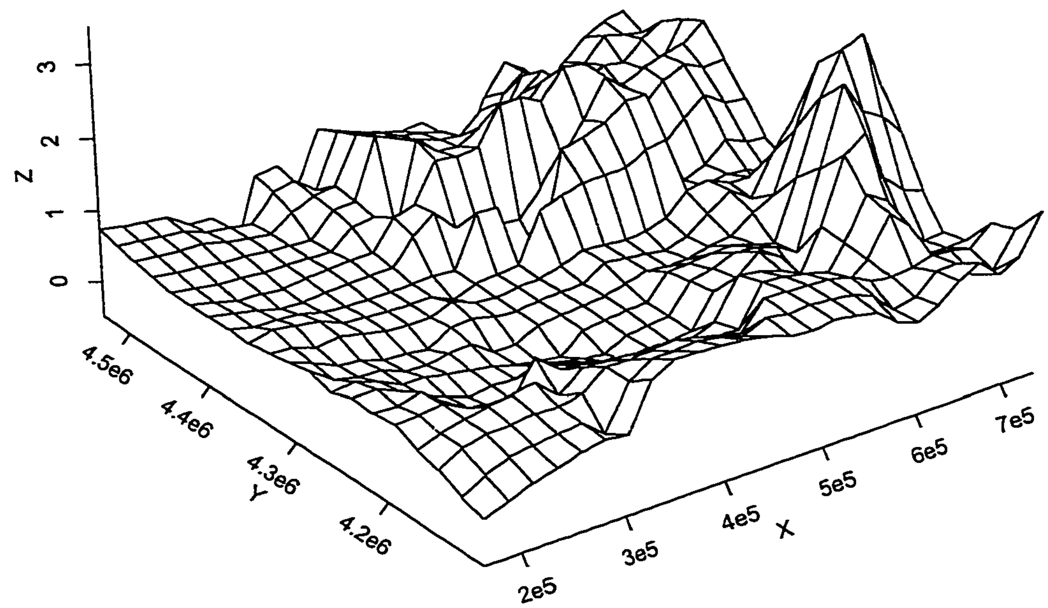
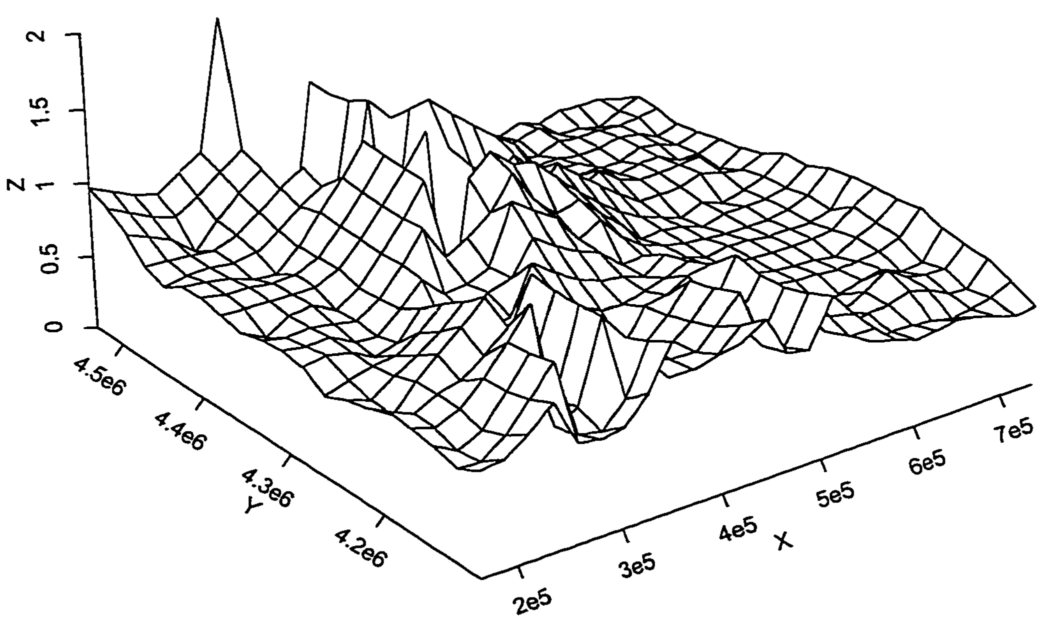


Figure 2.7. Kriging results for all Colorado sites. A. Kriged surface for 1995 grasshopper densities. B. Standard error surface for 1995 grasshopper densities.

A




B



## CHAPTER III

## MULTIVARIATE ANALYSIS OF THE FACTORS INFLUENCING CHANGES IN COLORADO GRASSHOPPER ABUNDANCES

### Abstract

Although the correlation between grasshopper densities and environmental conditions has long been recognized, the relationship is not well understood and may involve very complex interactions. The primary objective of this study was to determine the environmental factors which are most closely linked with changes in grasshopper population densities. Grasshopper sampling sites were grouped by direction and magnitude of change in density from 1995 to 1996. Multiple regression and stepwise discriminant analysis were used to identify the soil and weather variables which best distinguished among groups. Grasshopper density in 1995 was the most important variable in the discriminant analysis, followed by mean precipitation for April, 1993, and mean temperature in October, 1993. These results indicate that soil characteristics in Colorado are not as important to changes in density as are population level and stochastic weather events and confirm the presence of time lags in the effects of weather conditions on population changes.

## Introduction

Since the early days of agriculture in the United States, there has been great interest in preventing and predicting grasshopper outbreaks. The earliest observers of grasshopper population dynamics recognized a relationship between hot, dry weather and grasshopper numbers (Riley 1877, 1891; USEC 1878, 1880). Attempts have also been made to link grasshopper numbers to prairie fires, sun spots, earthquakes, and volcanic activity (USEC 1883, Criddle 1932), with little success. Nonetheless, the correlation between grasshopper densities and weather conditions has been confirmed by numerous studies (e.g., Gage and Mukerji 1977, Capinera and Horton 1989, Fielding and Brusven 1990, Belovsky and Slade 1995).

Despite this large body of evidence, the relationship between the population biology of rangeland grasshoppers and weather phenomena is not well understood and may involve very complex interactions (Joern and Gaines 1990). For example, the effects of weather may operate synergistically with other ecological factors such as habitat characteristics or population density to produce the observed change in abundance. In addition, it may be the accumulated or combined effects of several weather events which occur over more than one season which result in a change in the population trajectory (see Gage and Mukerji 1977, Johnson and Worobec 1988). Because temperature and precipitation have both direct and indirect effects on grasshopper development and survival (Edwards 1964, Hewitt 1979, Joern and Gaines 1990), it is likely that the several mechanisms operate simultaneously to influence grasshopper population dynamics.

There is evidence that the climate variables which are important to changes in grasshopper densities vary with latitude (Capinera and Horton 1989). In the shortgrass steppe, precipitation appears to be more important to grasshopper abundances than temperature, presumably because grasshoppers are more limited by food resources than by developmental rates (Nerney 1961, Capinera and Horton 1989, Lockwood and Lockwood 1991). By contrast, grasshopper populations in Alberta are negatively correlated with precipitation, perhaps because cooler temperatures accompany rainfall event and thus inhibit nymphal development (Gage and Mukerji 1977).

Soils are also purported to be important to grasshopper populations through their effect on oviposition behavior, embryonic development, and egg survival. Although soil type, texture, pH, and moisture have been shown to be important in certain species, the effects are probably species-specific (Mukerji and Randell 1975, Hewitt 1985, Johnson 1989). The relative importance of soil characteristics, in comparison with other abiotic and biotic factors, on population dynamics is unknown.

The extensive body of research into the relationships between grasshopper abundances and environmental factors has not yielded satisfactory models for predicting grasshopper population changes. One reason for this may be that most previous work has been done using simple correlations or regressions on individual variables. While relationships may be found between the variables, univariate analyses are not adequate when the dependence between variables is the source of significance (Horton et al. 1968). Thus, multivariate methods must be used to investigate relationships which are based on interactions among factors. Presumably, conditional interactions among biotic and abiotic factors drive changes in grasshopper populations (Joern and Gaines 1990).

**Objectives.** The primary objective of this study was to determine the environmental factors which are most closely linked with changes in grasshopper population densities and thus may be causal factors ("triggers") for outbreaks. Specific objectives were to:

1. Identify areas in which grasshopper densities and direction of population change (increase, decrease, no change) differ between 1995 and 1996.
2. Identify the environmental factors which best distinguish among those areas
3. Characterize the relationships between selected environmental factors and changes in grasshopper density.

## Methods

**Grasshopper data.** To predict grasshopper outbreaks, the United States Department of Agriculture's (USDA) Animal and Plant Health Inspection Service (APHIS) conducts annual surveys of adult grasshoppers in Colorado. Each site is sampled by taking 50 visual checks for presence of one or more grasshoppers in a 0.1 $m^2$ area (E. Danielson-Buffington, Colorado State University, personal communication). Grasshopper densities are estimated from these presence/absence counts through the use of the Poisson probability density function (Onsager 1991, Legg et al. 1993).

APHIS grasshopper survey data for 1995 and 1996 were acquired in digital form and inspected for outliers. One site from the 1995 data set was reported to have longitude near 120° west. Because this value would be outside of the state of Colorado, the longitude was suspected to be erroneous and the site was removed from the data set. Grasshopper densities were also inspected and two sites with questionably high densities (approx. 200 grasshoppers per $yd^2$) were removed from the 1996 data set. For consistency, densities for 1996 were converted from numbers per $yard^2$ to numbers per $meter^2$.

Although grasshopper data for 1993 through 1997 were available, I selected 1995 and 1996 for this analysis because differences were greatest between these two consecutive years. The mean density increased from about 3 to 8 grasshoppers per $m^2$ from 1995 to 1996 and the maximum density increased from about 27 to 43 grasshoppers per $m^2$. These increases, and inspection of kriged surfaces produced in Chapter II, indicated the likelihood that there were areas where grasshopper abundances increased between the two years, as well as areas where grasshopper numbers decreased or stayed constant.

The locations for all grasshopper sites sampled in 1995 and 1996 were recorded in latitude and longitude. Point coverages were generated from the locations for sampling sites using PC ARC/INFO 3.5.1 (ESRI 1997a) and transformed to Albers Equal Area Conic projection to match the STATSGO coverage.

**STATSGO.** A state soil geographic data base (STATSGO) is available for Colorado. This data base contains soil survey information compiled at a scale of 1:250,000 and saved as a digital map (USDA 1991). The Colorado STATSGO coverage was downloaded from <ftp://boralf.agsci.colostate.edu/pub/statsgo/co/> and imported to PC ARC/INFO 3.5.1 (ESRI 1997a).

The STATSGO coverage was overlain with the point coverages of the grasshopper sampling sites using the IDENTITY command in ARC/INFO. The resulting coverages for 1995 and 1996 included the number of the STATSGO map unit in which each site lies as an attribute of the sampling site. This map unit identification number (MUID) was used to link each site with the soil attribute files and extract specific soil variables.

Each STATSGO data base includes a number of tabular data files which contain information about the soil (and other characteristics) within each map unit. Each map unit may encompass up to 21 components (soii series), each component is composed of several soil layers, and components are not spatially referenced; thus, there is no one map unit value for a given soil variable (USDA 1991). To reduce this one-to-many relationship, the weighted average of each soil attribute was calculated to find a single value for the entire mapping unit (MUID).

To ensure the sites for 1996 matched sites sampled in 1995, I joined the 1995 and 1996 coverage attribute tables in Arc's TABLESW on site number. I then re-selected only the records for 1995 which were revisited in 1996 and whose STATSGO MUIDs matched were retained. The soil attributes for those sites were exported for regression and discriminant analysis.

Seven soil attributes (Table 3.1) were selected for analysis. For available water capacity (AWC) and permeability rate (PERM), means were calculated for the first meter of soil; for all other soil variables, only values for the surface (uppermost) layer of soil were used. Areas where PERM=0 were excluded. For each of the soil attributes, STATSGO lists a maximum and minimum value for each soil layer. All attribute values were averaged by adding the minimum and maximum and dividing by two. For AWC and PERM, this value was multiplied by the thickness of the soil layer; layer values were summed over the soil profile for AWC and averaged for PERM. The results were then weighted by the percent of the map unit covered by each component to find the average for then entire map unit.

**Weather data.** Monthly mean temperature and total monthly precipitation for 1993 through 1996 at all active weather stations were downloaded from the Colorado Climate Center at http://ccc.atmos.colostate.edu/mly_form.html. The latitude and longitude for each weather station was used to build a coverage in PC ARC/INFO 3.5.1 (ESRI 1997a). The coverage was projected to match the grasshopper site and STATSGO coverages, then overlain with the coverage containing those 1995 sites which were revisited in 1996. The closest weather station to each grasshopper sampling site was determined using the Measure tool of ArcView GIS Version 3.0a (ESRI 1997b). The list of grasshopper sampling sites and closest weather station was merged with the weather station files and soil data by matching station and sampling site numbers.

**Analysis.** Multiple linear regression was used to reduce the number of variables to be entered into the discriminant analysis. For better approximation to the Normal distribution, a ln(density + 1) transformation was performed before proceeding with the regression analyses. The 1996 transformed densities were then subtracted from the 1995 values to find the change in log density from 1995 to 1996.

Separate multiple regression analyses were performed on STATSGO variables (Table B.1), mean monthly temperature, and mean monthly precipitation. Regressions on weather data were performed for April through October of the years 1993 through 1996. The probability of F to enter a variable was set at .10 (after Capinera and Horton 1989). All statistical analyses were conducted in SPSS for Windows (SPSS, Inc. 1997). Variables which were entered into the multiple regression models were used in subsequent discriminant analyses.

Discriminant analysis (DA) is a multivariate technique which uses a set of measurements to classify observations into distinct groups, where one knows to which group a given observation belongs at the outset (Afifi and Clark 1996). DA can be used to distinguish among populations or communities, to classify new observations for which the group is unknown, or to test whether the addition of each variable improves the discrimination among groups (Afifi and Clark 1996). The analysis examines two or more groups (or populations) which differ with respect to several measurable variables and combines the variables into mathematical equations called linear discriminant functions (LDFs).

In this analysis, the groups were defined based on the magnitude and direction of change in grasshopper densities between 1995 and 1996. The group definitions are listed in Table 3.2. In addition to soil and weather variables, the log-transformed density for 1995 was also entered into the DA (Table 3.3). As in the multiple regressions, the probability of F to enter was set a 0.10. Prior probabilities for group membership were calculated from group sizes.

DA can be performed by entering all the classification variables at once or by adding them in stepwise fashion, such that only variables which improve the classification are added. The results of the stepwise discriminant analysis indicate which variables were most useful in distinguishing between the categories of change in grasshopper density. The DA used Wilk's lambda statistic as the criterion for entering variables.

**Results and Discussion**

Multiple regression analysis resulted in selection of three soil variables, three months of temperature data, and four months of precipitation data for DA (Table 3.3). Coefficients for each of the selected variables are given in Tables 3.4 and 3.5. Correlations were generally low (<0.35) for all variables. Although the regression results for 1996 included October in the precipitation model (Table 3.5), these data could not be relevant to changes in grasshopper densities because sites were sampled previous to that time. Thus, the October 1996 precipitation data were not included in the DA. This spurious correlation suggests that all relationships between grasshopper densities and environmental variables should be interpreted cautiously.

The three soil attributes which were entered from the regression results were clay content, organic matter, and salinity. These variables may impact grasshopper populations through the choice of oviposition sites or indirectly through plant community composition. However, because grasshoppers are mobile and sampling was not done immediately after hatching, a relationship between soil characteristics, oviposition sites, and density cannot be inferred from this analysis. However, the positive correlation between density and clay content contrasts with Johnson's (1989) finding that grasshopper distributions in Alberta vary with soil type but not with soil texture (sand, silt, clay content). These opposite results may be due to differences in grasshopper species composition between Alberta and Colorado.

All the significant correlations between precipitation and density were negative except for July, 1993 (Table 3.5). These results contrast with previous studies which found positive correlations between spring rainfall and abundance (Capinera and Thompson 1987, Johnson and Worobec 1988) but agree well with the results of Gage and Mukerji (1977) for Alberta, where they found a negative correlation between precipitation and density at time lags up to 3 years. This negative relationship may be due to increased prevalence and effectiveness of pathogens during cool, moist weather.

It is curious that correlations between fall temperatures and grasshopper density were also negative (Table 3.5), contrary to the work of Edwards (1964, Edwards and Epp 1965) in Saskatchewan, where temperature during oviposition activity was the most important factor in determining population abundance in following season.

Discriminant analysis of the ten environmental variables and 1995 density resulted in identification of previous year's grasshopper abundance as the most important variable in discriminating among groups. Stepwise discriminant analysis identified 1995 density, precipitation for April of 1993, and temperature for October of 1993 as the three variables which contributed most to discrimination between groups (Tables 3.6 and 3.7). None of the soil variables contributed significantly to the ability to distinguish among groups.

Inspection of the discriminant functions in Table 3.7 reveals the inability of single variables to distinguish among all groups. For example, the coefficients for April 1993 precipitation were very similar for groups 0 and 1 (and likewise for groups -1 and 2), such that DA separated the observations into only two groups using this variable. Thus, combinations of three variables were necessary to distinguish between all four groups. This result highlights the importance of using a multivariate approach.

The discriminant functions gave correct classifications for 67.5% of the original data. Forty-five percent of observations from group 0 were misclassified into group 1 and 83.3% of group 2 sites were incorrectly classified into group 1, including three sites for which the change in density was over 24 grasshoppers per $m^2$. Clearly, the variables used in the DA did not sufficiently distinguish sites with large increases in density and further research should be conducted to identify the factors which characterize these sites.

The contributions of weather variables from two years previous to the time of increased density highlights the need to further investigate time lags in the effects of environmental factors of grasshopper densities. It has long been recognized that the cumulative effects of weather are important in the development of high densities. Smith (1954) concluded that grasshopper outbreaks in Kansas followed two or more consecutive dry years. Similar results were obtained by Edwards (1960) in Canada. In Colorado, the work of both Pfadt (1977) and Carter and co-workers (1998) suggests that several years of favorable precipitation conditions may be necessary before populations reach economic levels and the timing and magnitude of rainfall events are probably important. My results confirm this hypothesis and indicate that a single year of favorable spring precipitation and fall temperatures may produce changes in density which appear at a later time. Thus, models of grasshopper population dynamics should incorporate the occurrence of stochastic events for at least three previous seasons.

Like most multivariate analyses, this study did not explicitly address issues of scale. However, the results might be interpreted to show how local-scale processes such as density-dependent population levels interact with larger-scale processes (climatic events) to produce ecological patterns of abundance (Menge and Olson 1990). Further research is required to determine the relative importance of biotic and abiotic factors at differing spatial scales and to elucidate the mechanisms by which their interactions influence grasshopper populations (Joern and Gaines 1990).

**Summary**

Soil characteristics were not as important to changes in density as were weather effects, indicating that stochastic events have more influence on grasshopper populations than habitat differences. Spring precipitation and fall temperatures from previous seasons, coupled with grasshopper abundance levels, may be good indicators of whether densities will increase, decrease, or stay constant. These environmental variables are good candidates for modeling population dynamics, for inclusion in decision-support systems, and for further research, including field experimentation to elucidate the mechanisms responsible for these relationships.

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Table 3.1. Colorado STATSGO soil variables used for multiple regression analysis.

| Variable Name | Abbreviation | Units/Description |
|---|---|---|
| available water capacity | awc | inches per inch of soil |
| bulk density | bd | g per cc of moist soil |
| clay content | clay | percentage of the material less than 2 mm in size |
| organic matter | om | percent by weight |
| permeability rate | perm | inches per hour |
| soil reaction (pH) | ph | NA |
| salinity | salin | electrical conductivity at saturation in mmhos/cm |

Table 3.2. Definitions of groups for discriminant analysis. "Diff" is the difference between 1995 and 1996 grasshopper densities.

| Group Name | Density Range |
|---|---|
| -2 | diff < -10 |
| -1 | -10 ≤ diff < -1 |
| 0 | -1 ≤ diff ≤ 1 |
| 1 | 1 < diff ≤ 10 |
| 2 | diff > 10 |

Table 3.3. Variables used in discriminant analysis.

| Variable Name | Abbreviation | Units/Description |
|---|---|---|
| log-transformed grasshopper density for 1995 | lngh95 | number per $m^2$ |
| clay content | clay | percentage of the material less than 2 mm in size |
| organic matter | om | percent by weight |
| salinity | salin | electrical conductivity at saturation in mmhos/cm |
| mean precipitation for April, 1993 | aprp93 | 0.01 inches |
| mean precipitation for July, 1993 | julp93 | 0.01 inches |
| mean precipitation for October, 1995 | octp95 | 0.01 inches |
| mean precipitation for June, 1996 | junp96 | 0.01 inches |
| mean temperature for June, 1993 | junt93 | 0.1°F |
| mean temperature for October, 1993 | octt93 | 0.1°F |
| mean temperature for September, 1994 | sept94 | 0.1°F |

Table 3.4. Results of multiple regression on Colorado STATSGO soil variables. Variable abbreviations are given in Table 3.1.

| Variable | B | Std. Error | t | Sig. | Partial Correlation |
|---|---|---|---|---|---|
| constant | -1.71 | .233 | -7.34 | .000 | --- |
| clay | 0.0315 | .009 | 3.37 | .001 | .169 |
| om | .437 | .143 | 3.06 | .002 | .153 |
| salin | .103 | .052 | 2.00 | .046 | .101 |

Table 3.5. Results of multiple regression on weather variables. Variable abbreviations are given in Table 3.1.

| Variable | B | Std. Error | t | Sig. | Partial Correlation |
|---|---|---|---|---|---|
| **1993 precipitation** | | | | | |
| constant | -.323 | .279 | -1.16 | .251 | — |
| julp | .00326 | .001 | 3.12 | .003 | .331 |
| aprp | -.00423 | .002 | -2.31 | .023 | -.252 |
| **1993 temperature** | | | | | |
| constant | 2.81 | 2.22 | 1.27 | .210 | — |
| octt | -.034 | .013 | -2.69 | .009 | -.312 |
| junt | .0201 | .009 | 2.20 | .031 | .260 |
| **1994 temperature** | | | | | |
| constant | 5.94 | 2.62 | 2.27 | .026 | — |
| sept | -.00993 | .004 | -2.42 | .018 | -.273 |
| **1995 precipitation** | | | | | |
| constant | -.230 | .178 | -1.30 | .199 | --- |
| octp | -.00807 | .005 | -1.78 | .079 | -.195 |
| **1996 precipitation** | | | | | |
| constant | .314 | .319 | .985 | .328 | — |
| junp | -.00272 | .001 | -2.26 | .027 | -.248 |
| octp | -.00346 | .002 | -1.96 | .053 | -.220 |

Table 3.6. Results of discriminant analysis: linear discriminant functions. Variable abbreviations are given in Table 3.1. Group definitions are given in Table 3.2; group -2 was omitted because N=1.

| | **Group** | | | |
|---|---|---|---|---|
| **Variable** | **-1** | **0** | **1** | **2** |
| lngh95 | 1.008 | -2.091 | -1.136 | .672 |
| octt93 | .666 | .712 | .685 | .674 |
| aprp93 | .0628 | .0426 | .0420 | .0616 |
| constant | -167.08 | -181.24 | -168.18 | -169.83 |

Table 3.7. Results of canonical discriminant analysis: stepwise statistics. Variable abbreviations are given in Table 3.1. Note that F level is approximate for step 3.

| **Step** | **Entered** | **Wilks' Lambda** | | | |
|---|---|---|---|---|---|
| | | **F Statistic** | **df1** | **df2** | **Sig.** |
| 1 | aprp93 | 5.542 | 3 | 60 | .002 |
| 2 | lngh95 | 4.310 | 6 | 118 | .001 |
| 3 | octt93 | 3.723 | 9 | 141.3 | .000 |

# CHAPTER IV

# SUMMARY AND CONCLUSIONS

In the preceding chapters, I have reviewed rangeland grasshopper ecology and used novel techniques to examine patterns and processes associated with Colorado grasshopper abundances. The analyses presented in Chapters II and III determined that:

- Colorado grasshopper densities exhibit spatial patterning at very large scales
- current grasshopper survey methods are not adequate for detecting localized, small-scale infestations
- previous year's grasshopper density is more important than soils or weather events in determining abundance
- there are time lags in the effects of weather events on grasshopper populations

These results will be useful to rangeland pest managers and insect ecologists in monitoring and modeling grasshopper populations. In addition, these findings highlight critical ecological relationships which should be examined and clarified with further research.

Rangeland grasshopper communities provide excellent opportunities for the study of community ecology, spatial and temporal patterning, landscape ecology, and ecosystem functioning. The heterogeneity in grasshopper communities, their spatiotemporal complexity, and their broad distribution allow the testing of myriad hypotheses. Although grasshoppers were among the first insect groups on this continent to be studied intensively by economic entomologists, numerous aspects of their biology and ecology remain obscure.

**The importance of scale.** As in other areas of ecology, the issue of scale has, until recently, been largely ignored in grasshopper research (see Chapter I). Population and community dynamics operate over multiple temporal and spatial scales, contributing to the complex nature of this system. The difficulties come to the foreground when attempts are made at predicting grasshopper outbreaks or determining what triggers them. Simply correlating changes in grasshopper density with the factors which may drive their increase does not elucidate the problem (Joern and Gaines 1990). The need to address grasshopper population dynamics through consideration of the multiple factors involved and their interactions is surpassed only by the need to place the contributions of those factors within the framework of scale.

If progress is to be made in the study of grasshopper population dynamics, a new paradigm must be adopted. To date, research on grasshoppers has been structured by the traditional, hierarchical levels of organization: organism, population, community, ecosystem, biome. A shift to using scale-defined levels of organization would help to clarify the processes which provide the context for changes in abundance (Allen and Hoekstra 1990). In addition, the recognition and use of scale would direct research and management efforts toward the most appropriate levels for study and monitoring.

A spatial model of grasshopper dynamics is likely to be intricate. Grasshopper populations in Colorado are structured at more than one spatial scale, implying the influence of at least two classes of processes in structuring densities over space. Biotic factors may be dominant in producing spatial patterns at local scales, through canopy structure, plant community composition, interspecific competition, density-dependent population dynamics, predation and parasitism. Abiotic habitat characteristics such as slope, aspect, and soil properties may be influential in selection of microhabitat but less important to population change.

At larger spatial scales, it is more likely that abiotic factors such as stochastic weather events influence the distribution of abundances over space. The effects of topography are likely to be seen at landscape and larger scales, as the rain shadow of mountain ranges, for example. At regional spatial scales, the influence of both abiotic and biotic processes are integrated into ecosystems or biomes which differ in their suitability for individual grasshopper species.

The importance of any of these processes depends on scale, the condition of the population, and interactions among the factors. For example, the ability of parasites to keep grasshopper numbers low depends on weather events, population density, and age-structure (Streett and McGuire 1990). Additionally, a single factor may influence the system in multiple ways. Precipitation, for example, impacts grasshopper populations both directly, through nymphal mortality, and indirectly, by providing green food or favoring pathogens (Capinera and Sechrist 1982). Thus, the behavior of the system cannot be described using a single ecological theory such as resource limitation or topdown population control. Because these various factors act on populations simultaneously, a multivariate approach is necessary to fully understand grasshopper dynamics.

Ideally, efforts to model grasshopper dynamics at any scale should incorporate both biotic and abiotic factors. However, the factors which are most important are likely to differ with scale. At large scales, it is necessary to remember that the species composition of grasshopper communities changes from region to region. The dominant and economically important species in each community differ, and there may be different limiting factors which determine whether populations reach outbreak levels (see Capinera and Horton 1989). Ecoregions, such as those used in Chapter II, can be used to delineate areas where species composition and habitat are relatively homogeneous and within which similar processes are likely to determine population dynamics.

To fully examine grasshopper dynamics, temporal scaling must also be considered, although the range of scales important through time is probably smaller than across space. As Edwards emphasized in 1964, "The underlying causes of [grasshopper] outbreaks are of interest not only as an academic problem in insect population dynamics but also as a practical problem in modern agriculture.... Grasshopper populations reach their annual low point in early July when they are in the adult stage and increase sharply in the fall at the time of oviposition. Any factor that influences the grasshopper during this period may have a marked effect on the outbreak of the following year (Edwards 1964, p. 307)." The effects of weather or other factors may also be delayed, producing a time lag between causal events and their results (see Chapter III).

The rangeland grasshopper species complex is thus structured by multiple driving variables operating over multiple temporal and spatial scales. There may also be multiple equilibria (Belovsky and Joern 1995) which produce stable populations at more than one density as a result of differing dominant processes. Because even simple models can result in complex interactions (Costantino et al. 1995, Dwyer 1995), it is not surprising that efforts to accurately predict population dynamics in this system are plagued with difficulties. In addition, the predictability of the system varies with scale, and efforts to model grasshopper populations may be pseudo-predictions if only fine temporal scales are examined (Wiens 1989).

**A new paradigm.** One way to bring order to this complexity is to adopt a hierarchical, scale-referenced model of grasshopper dynamics. Figure 4.1 depicts one possible model which organizes the several spatial scales at which grasshopper abundances are patterned into levels of a hierarchy. Scale increases with higher levels of the hierarchy. At each level, some ecological processes will be more important than others and will seem to dominate population dynamics. Processes at lower levels are encompassed by higher levels. For example, at level 3, climatic events have the most impact on population changes but interact with finer scale processes such as parasitism and vegetation to produce the observed abundances. This model highlights the interaction of diverse processes which operate at multiple spatial scales (Menge and Olson 1990) to affect grasshopper densities.

The model shown in Figure 4.1 is analogous to a metapopulation model, where "patches" are occupied by local grasshopper communities. Metapopulation models recognize scale and explicitly "separate within-patch and among-patch dynamics" (Levin 1992, p. 1955) and may provide a workable framework for predicting regional populations if modified to incorporate time lags and spatial structure (see Gotelli 1995).

Viewing rangeland grasshopper communities from a scale orientation would be beneficial to managers by determining the proper scale for survey, monitoring, and control efforts. Grasshopper densities are managed on at least four spatial scales: the field scale (1) is managed by the individual landowner or lessee; if the land is publically owned, then state and federal interests may also be involved in monitoring and treating rangelands on a county-wide (2) or state-wide (3) basis. Grasshopper treatment programs, such as the Grasshopper Integrated Pest Management Program (GHIPM), across Great Plains region (4) have been managed by federal agencies such as the U.S. Department of Agriculture's Animal and Plant Heath Inspection Service-Plant Protection and Quarantine (APHIS-PPQ; USDA 1991). Elucidating the processes important to increases in grasshopper abundance at each of these scales would help to focus management efforts at each level and result in more effective cooperative treatment programs.

A prototype for such a management scheme was proposed by C.V. Riley and his colleagues in 1880 (USEC 1880) in a lengthy report on the Rocky Mountain Locust (*Melanoplus spretus* Walsh), a species which exhibited extremely large-scale habitat use. Their suggestion was to establish "a permanent system of observations and warnings" throughout the affected region, which could provide regular reports on "the situation and extent of egg-deposits; the time of hatching of the young locusts; their movements both on foot and on wing" (USEC 1880, p. 318). The information was to be disseminated by the local press and updated daily during severe outbreaks.

The devastation caused by the Rocky Mountain Locust would certainly have merited the establishment of such a system, had the species not disappeared as a threat to western agriculture. The current losses by grasshoppers may not generate the same urgency for monitoring activities, but a coordinated system of regular surveys would be easily implemented. The APHIS surveys already canvass agricultural lands across seventeen western states and the National Agricultural Pest Information System (NAPIS) could serve as a central clearinghouse for the information gathered.

Because grasshopper surveys are conducted by individual offices in each of the seventeen western states, sampling methods differ. Standardization of sampling methods, frequency, and timing are necessary. Additionally, the current funding climate for grasshopper monitoring, management, and research casts doubt on the future of the surveys. Despite these obstacles, the benefits of coordinating annual grasshopper surveys across the Great Plains would far outweigh the costs. A single, very large scale data set would be created which would allow researchers to investigate grasshopper dynamics over a range of spatial and, as additional years of data are collected, temporal resolutions. Comparison of infested areas across habitat types and with non-infested areas during the same season would yield insights into the mechanisms which regulate population dynamics.

The use of scale-explicit models has already been adopted in many areas of ecology. As tools for handling and analyzing spatially-explicit data, such as GIS, become more commonplace, models based on scale-defined levels of organization will become increasingly widespread. The incorporation of multivariate data into scale-based models promises to be useful in the study of grasshopper communities.

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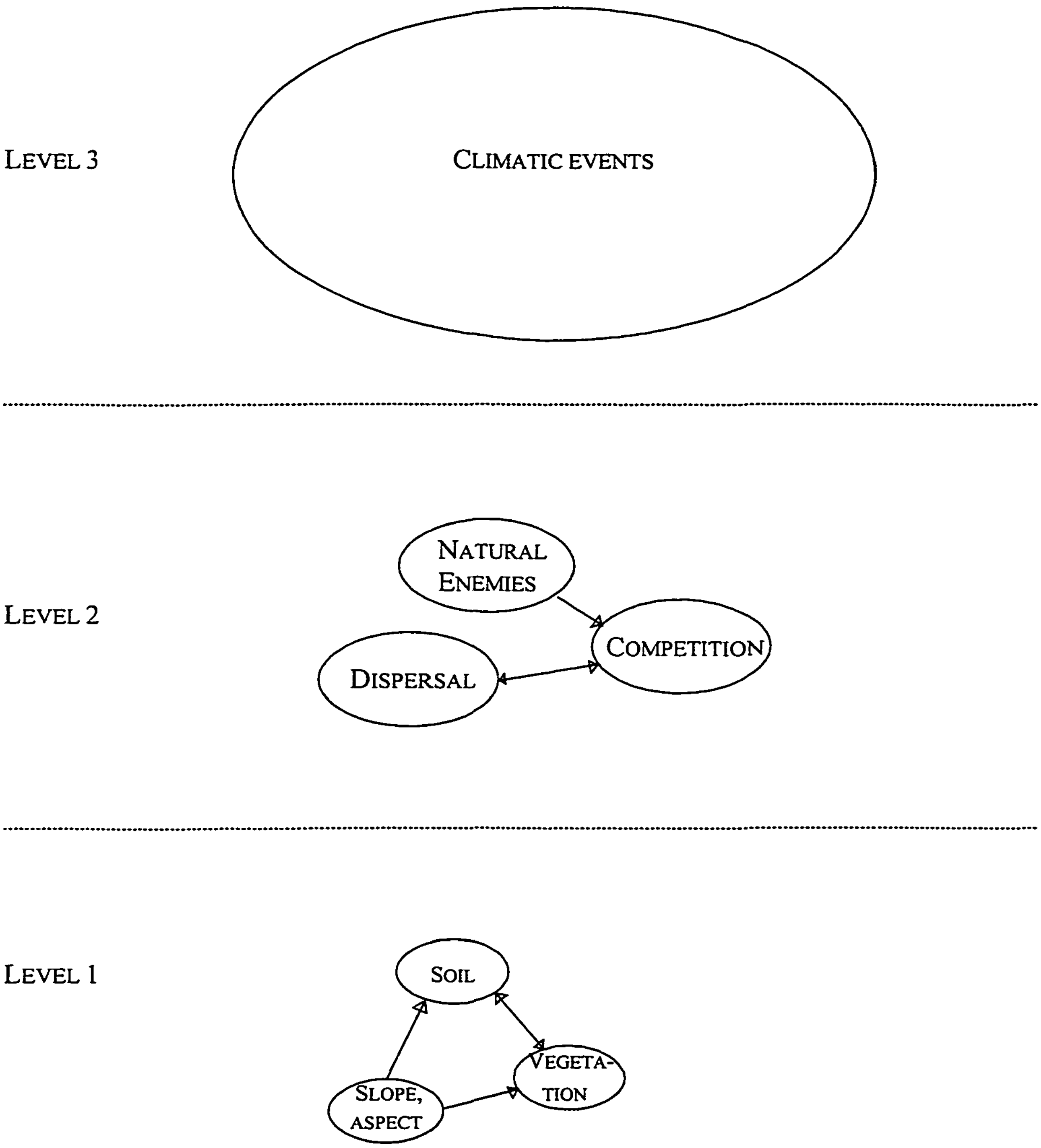
Figure 4.1. Diagrammatic representation of a scale-explicit, hierarchical model for grasshopper dynamics. Hierarchical levels represent increasing spatial scales, from microhabitats to continents; upper levels encompass lower levels. Arrows represent interactions. The ecological processes which most influence grasshopper abundance differ with spatial scale. (After Urban et al. 1987.)



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# APPENDIX: DIAGRAMS

Figure A.1. Histograms of 1994 and 1995 grasshopper densities (number of individuals per $m^2$).

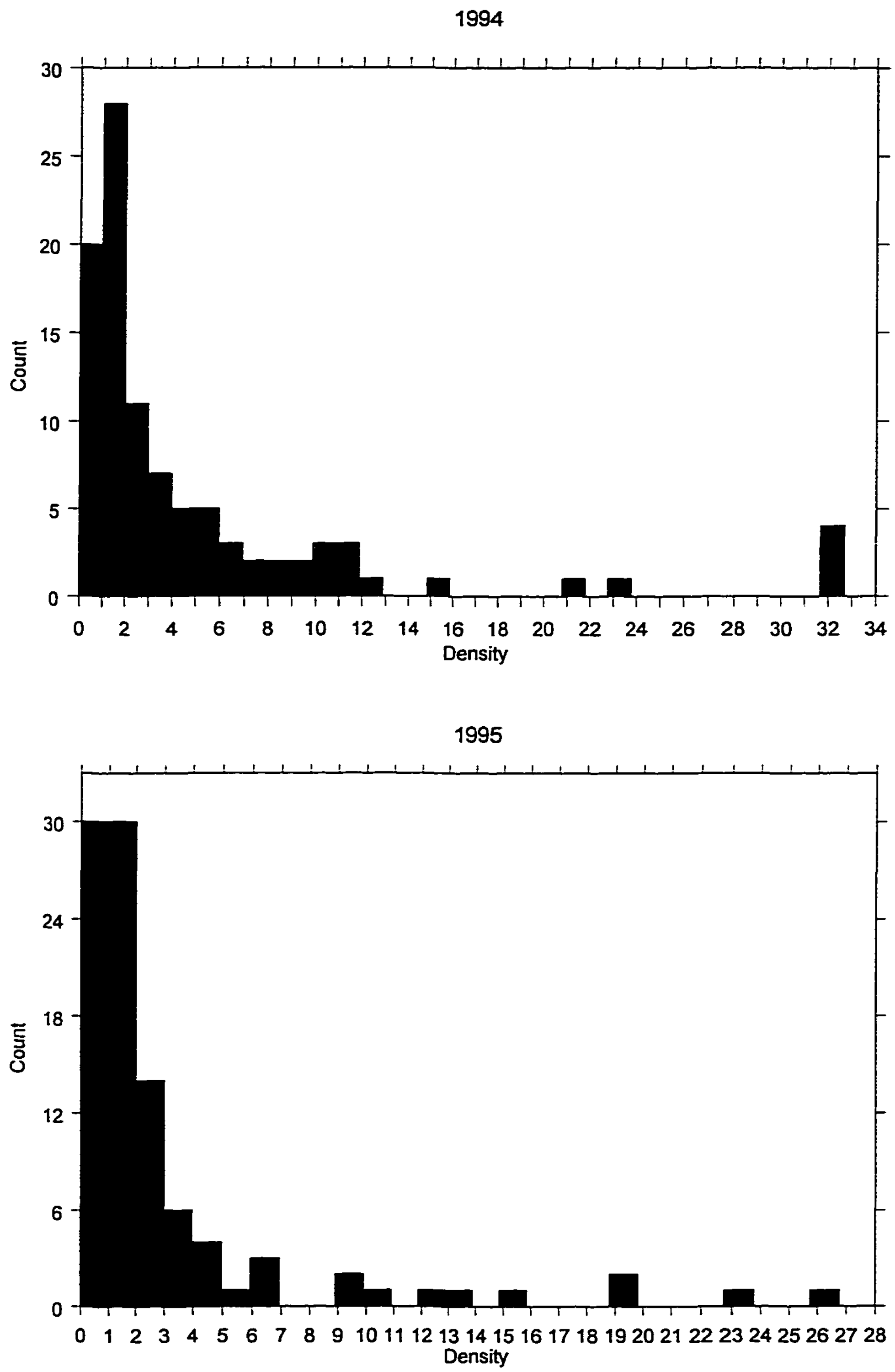
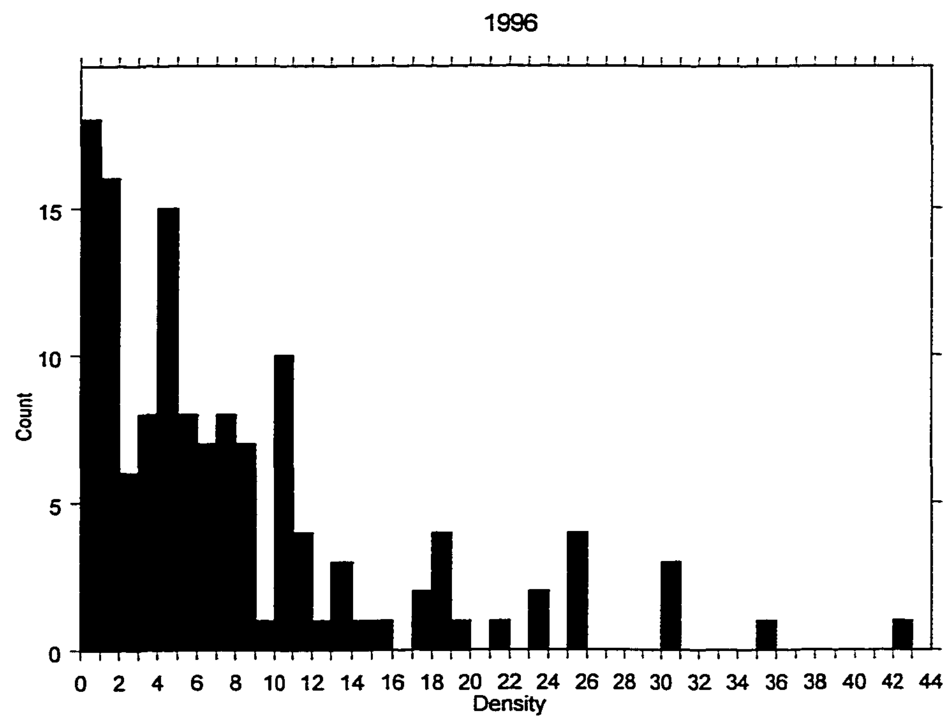


Figure A.2. Histograms of 1996 and 1997 grasshopper densities (number of individuals per $m^2$).



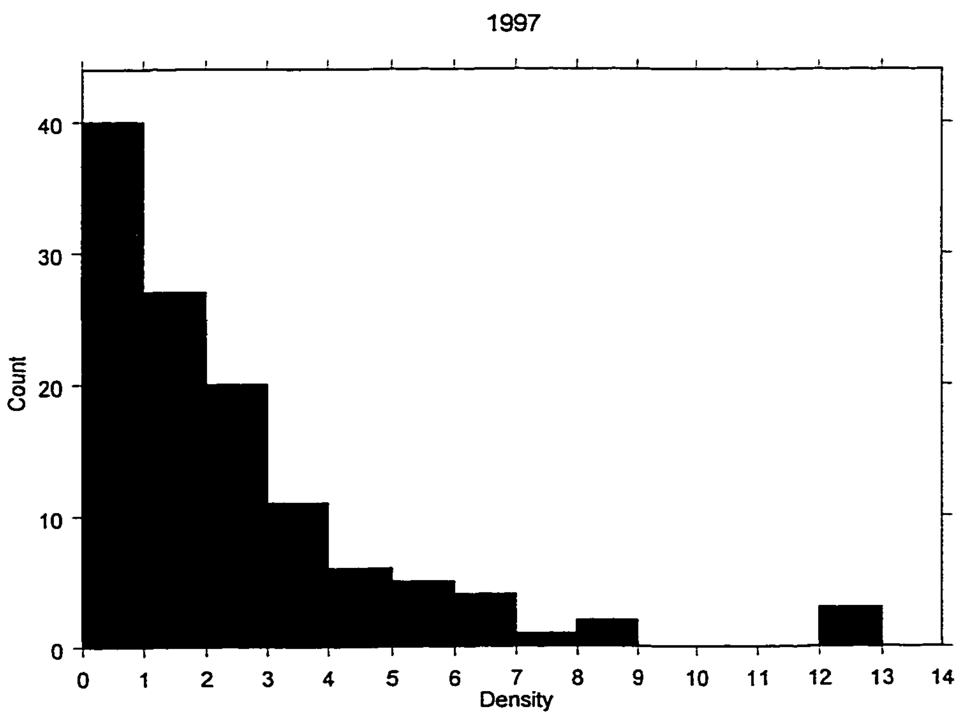



Figure A.3. Posted grasshopper densities for 1993. Some sites have been moved or omitted for legibility.

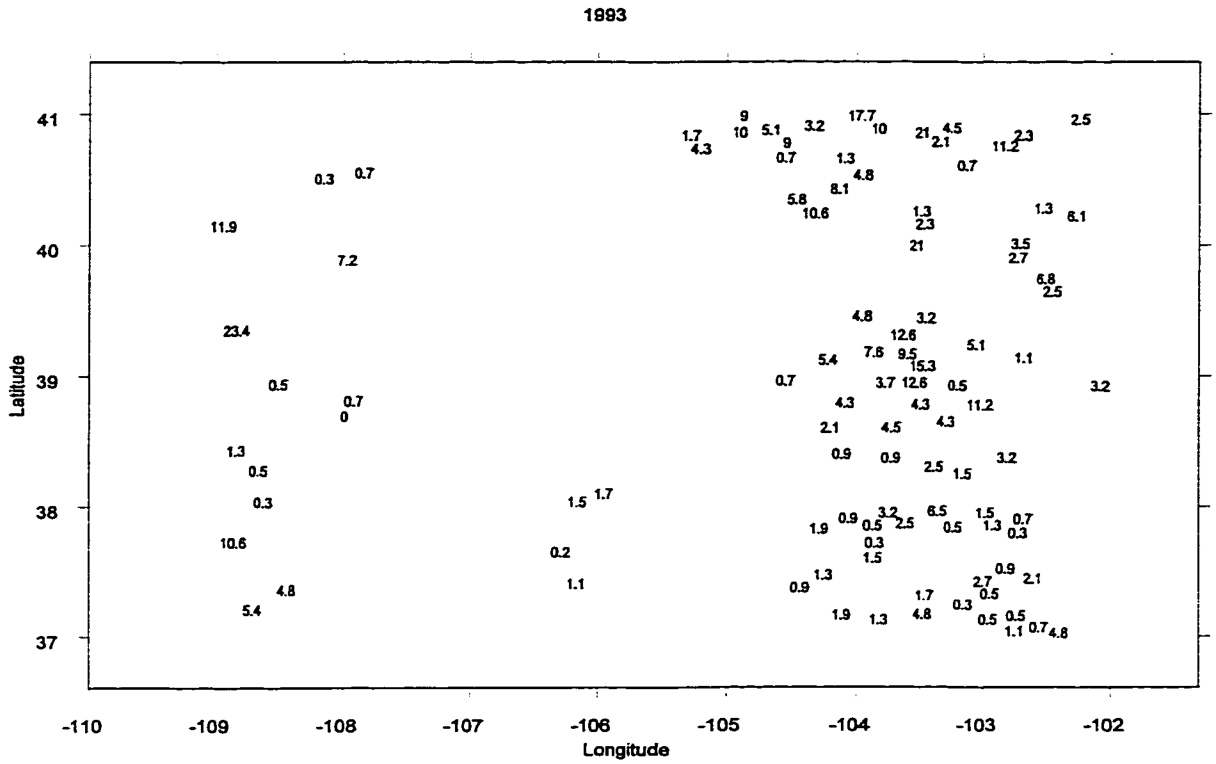


Figure A.4. Posted grasshopper densities for 1994. Some sites have been moved or omitted for legibility.

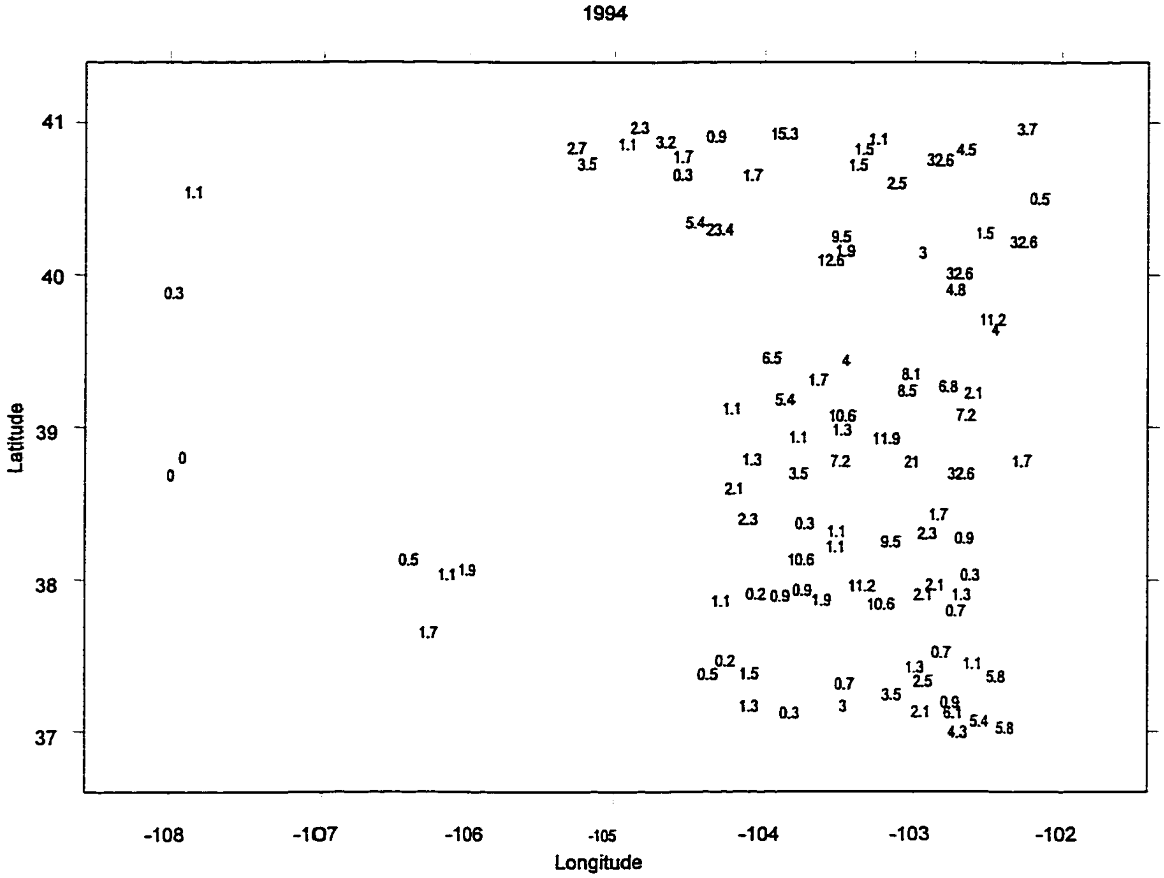


Figure A.5. Posted grasshopper densities for 1995. Some sites have been moved for legibility.

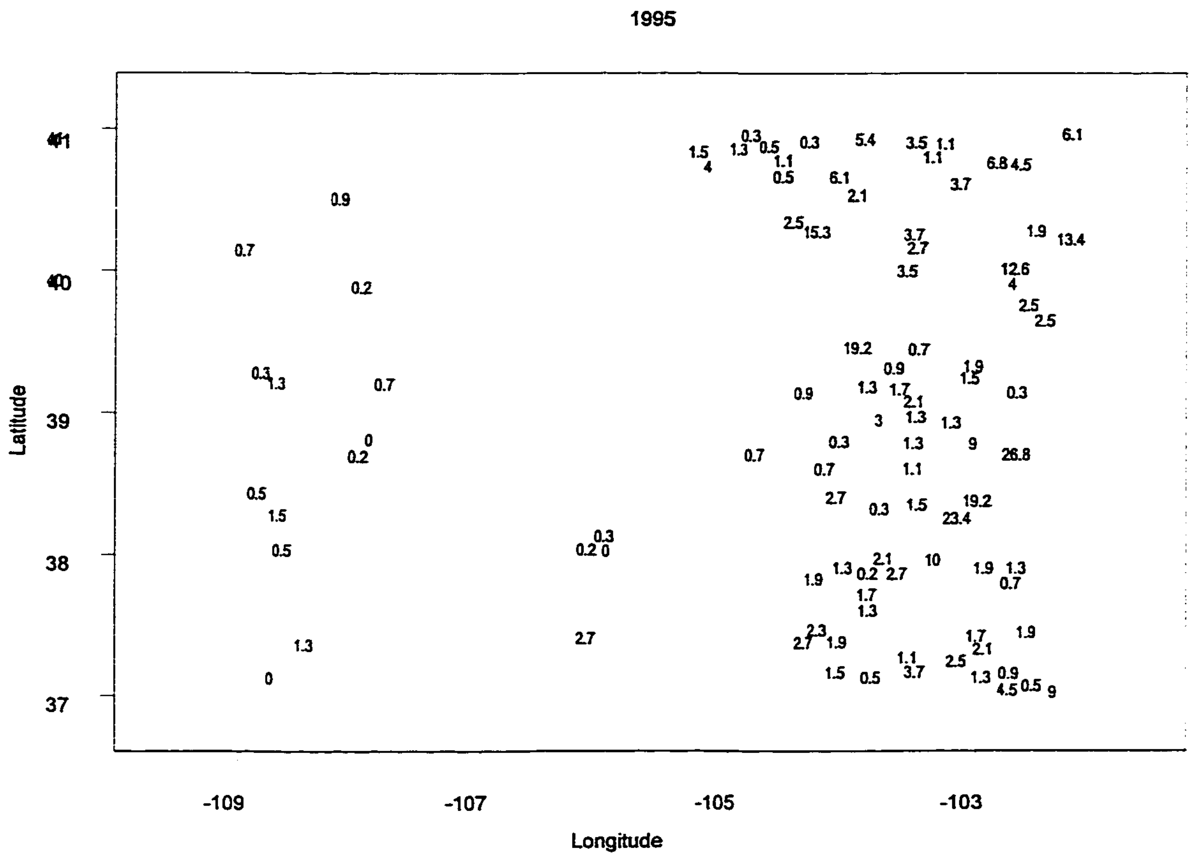


Figure A.6. Posted grasshopper densities for 1997. Some sites have been moved for legibility.

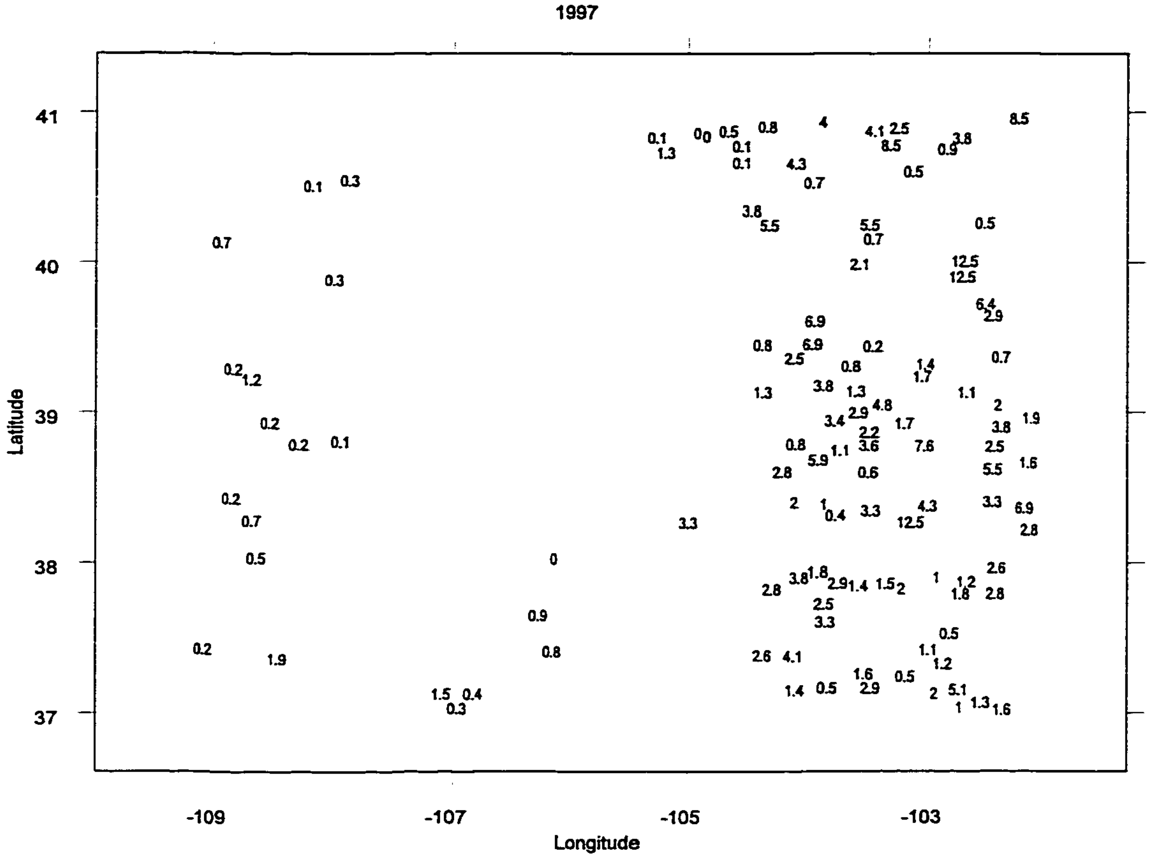
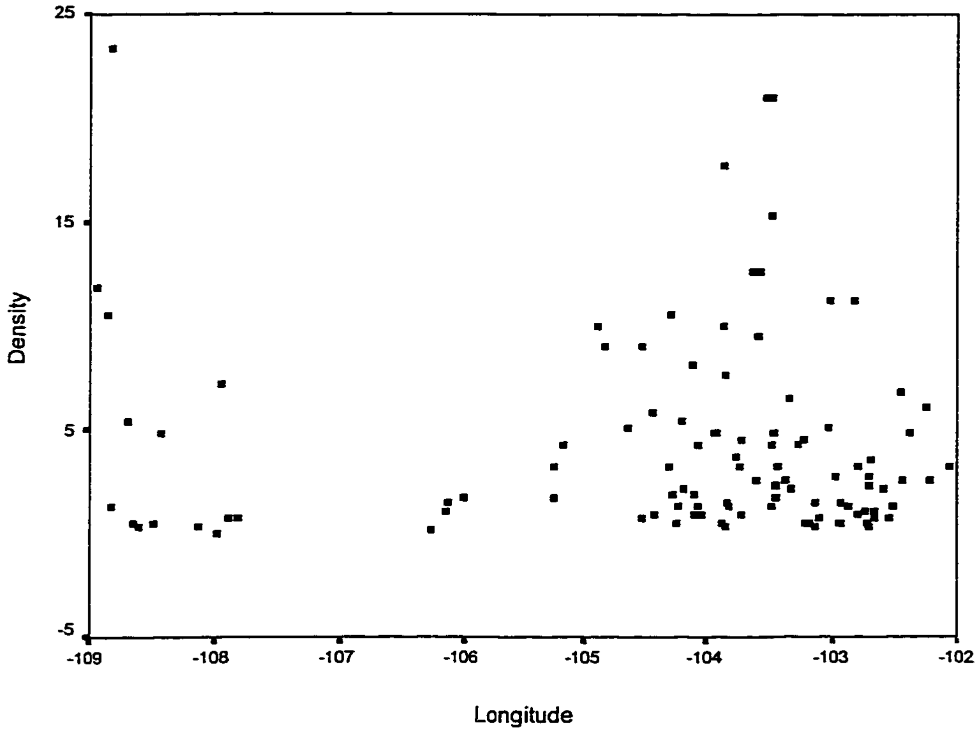


Figure A.7. Bivariate scatterplots (density vs. location) for 1993. Grasshopper density is given in number of individuals per $m^2$.



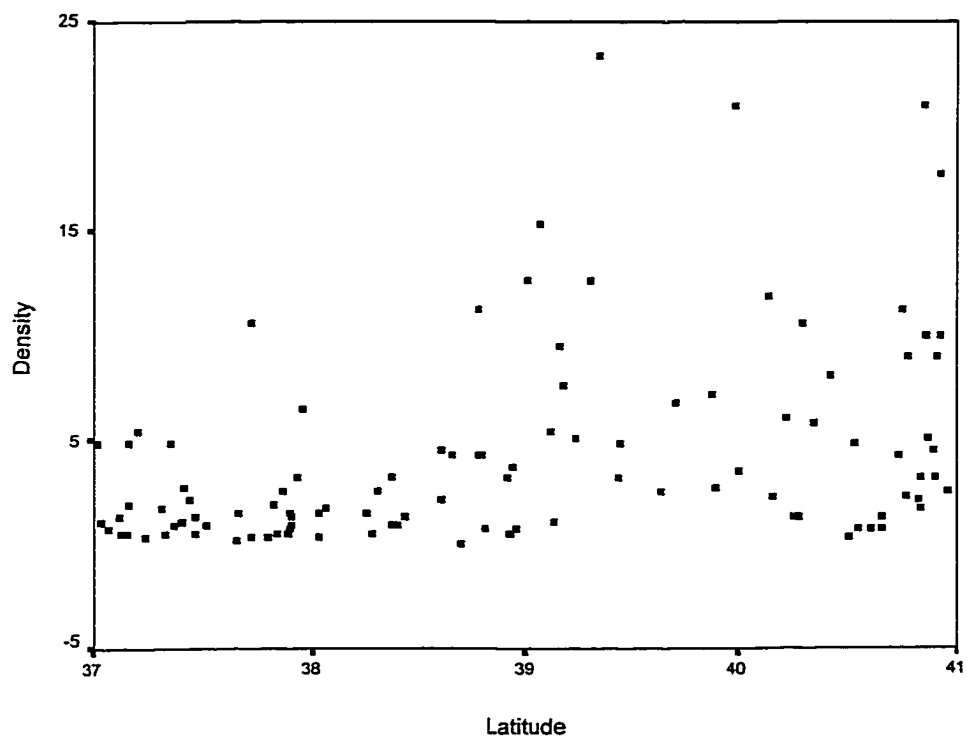
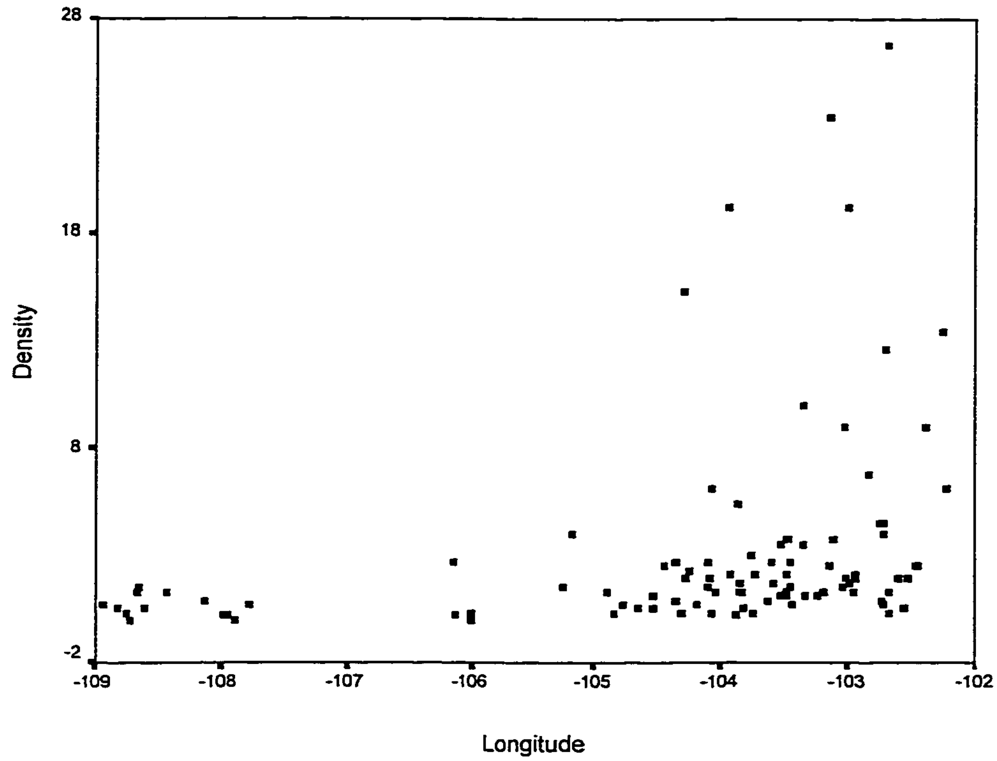



Figure A.8. Bivariate scatterplots (density vs. location) for 1995. Grasshopper density is given in number of individuals per m$^2$.



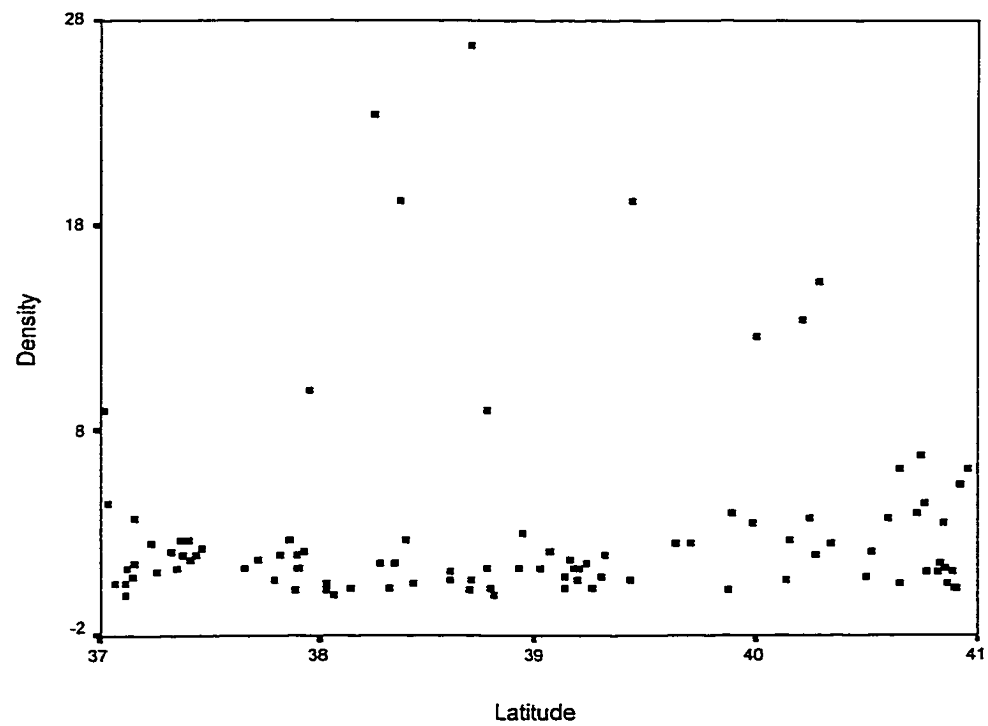
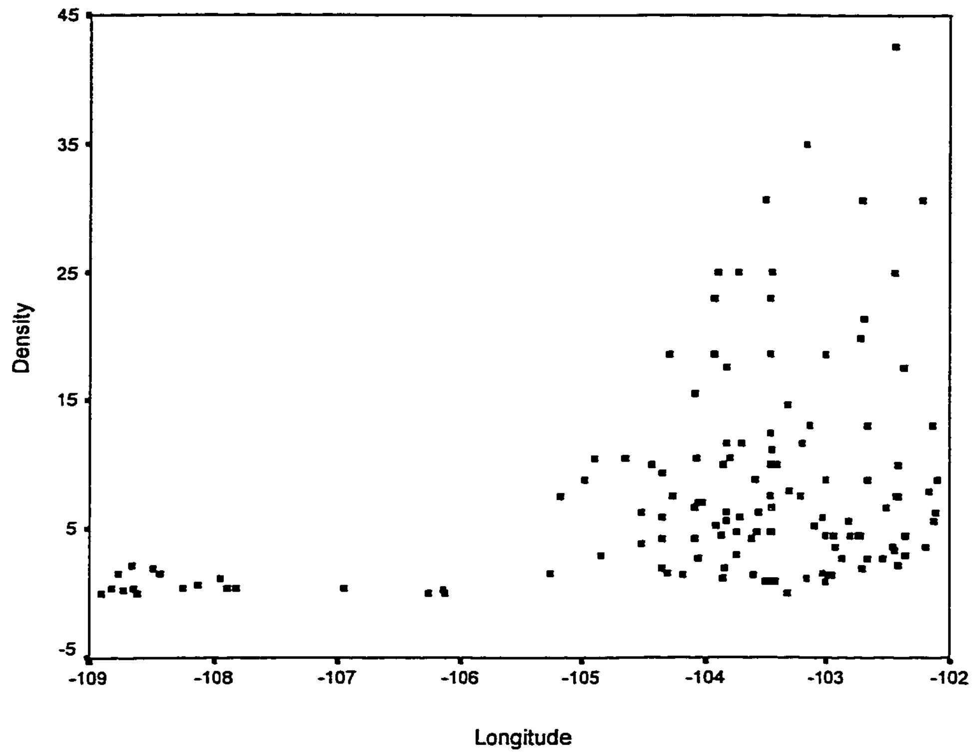



Figure A.9. Bivariate scatterplots (density vs. location) for 1996. Grasshopper density is given in number of individuals per $m^2$.



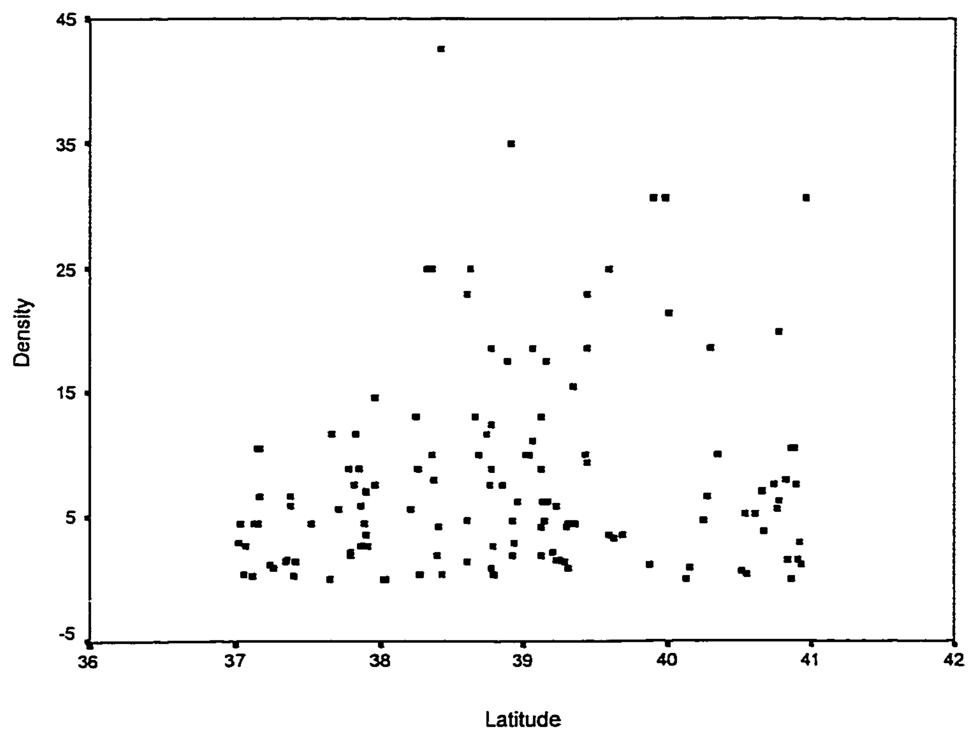
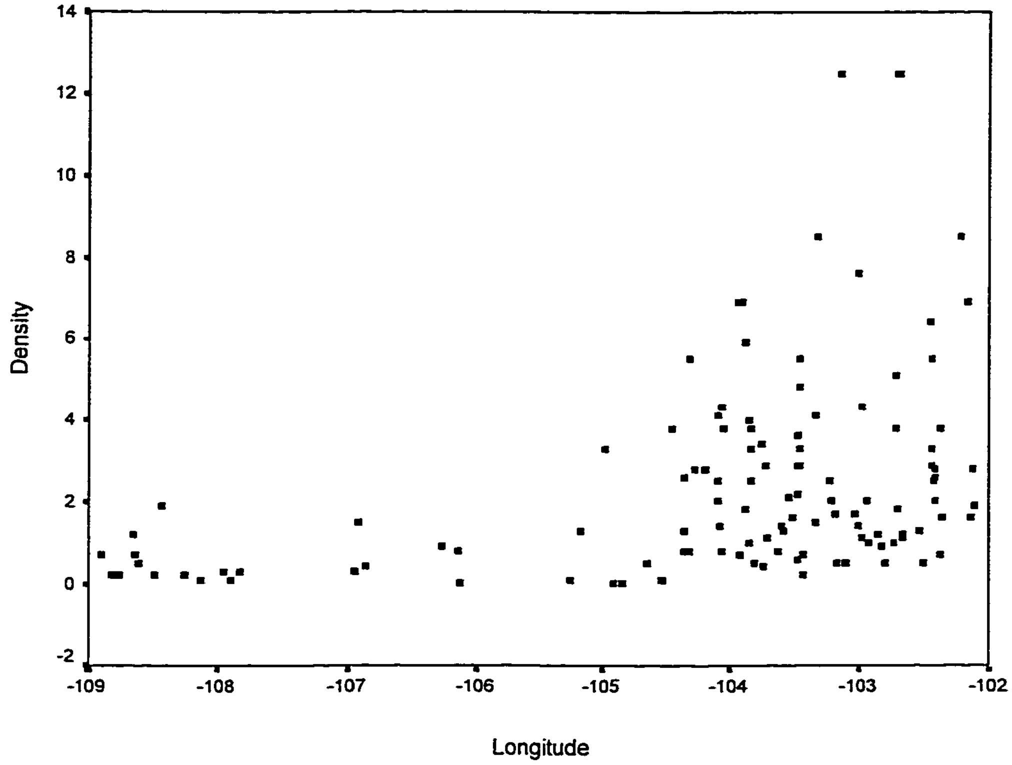



Figure A.10. Bivariate scatterplots (density vs. location) for 1997. Grasshopper density is given in number of individuals per $m^2$.



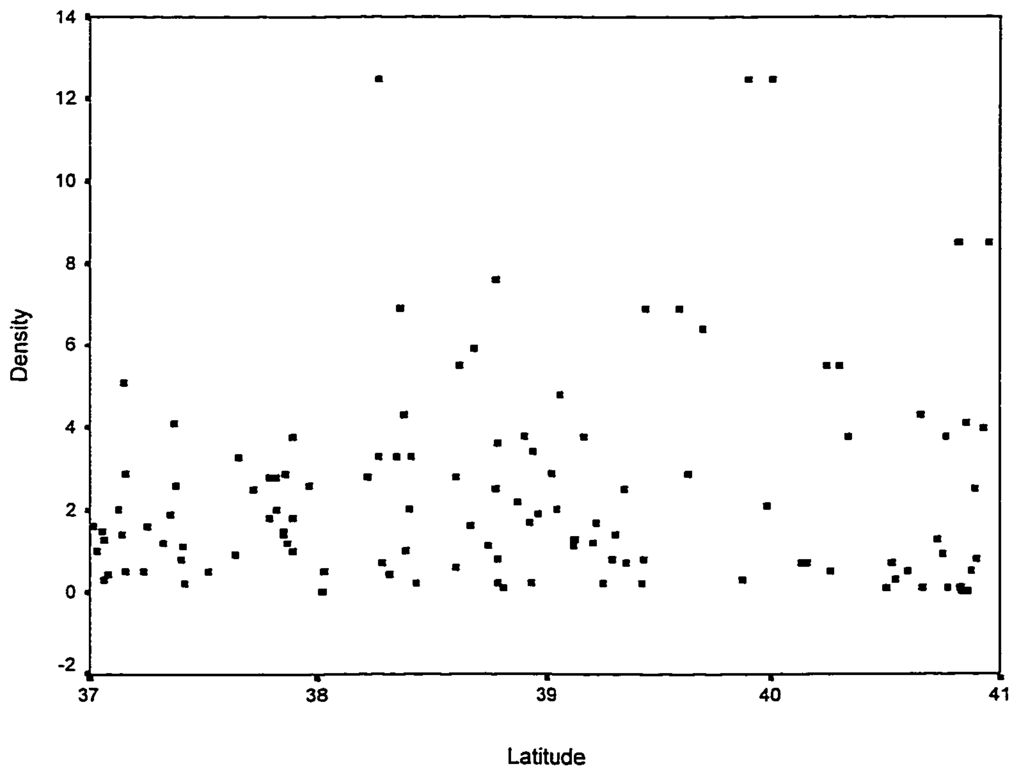
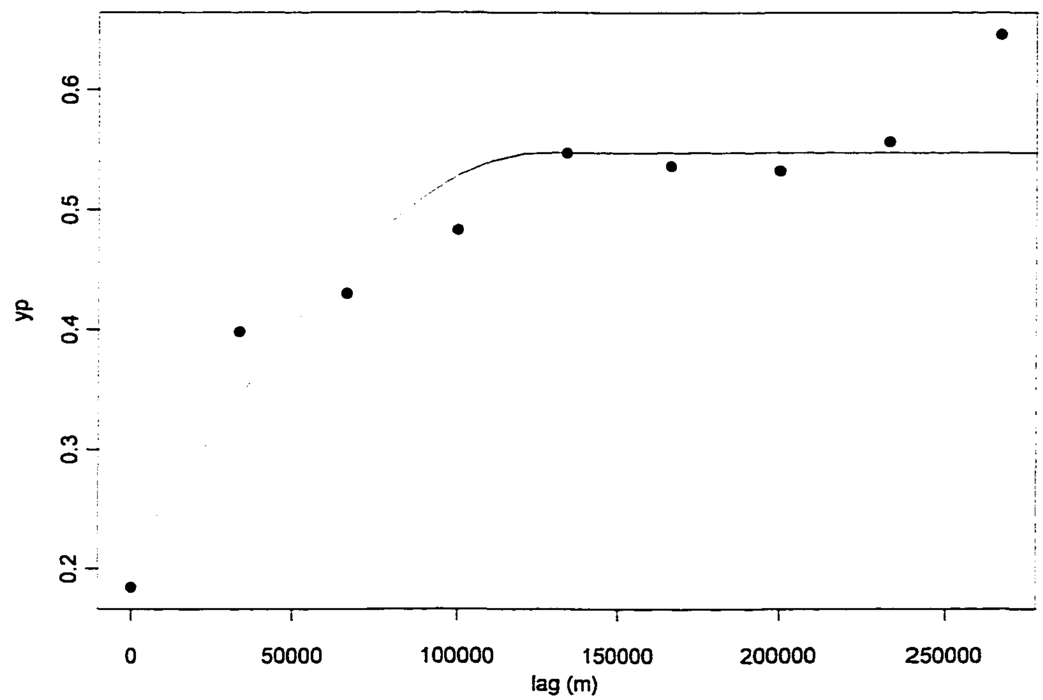



Figure A.11. A. Variogram for 1993 grasshopper densities, all sites. B. Variogram for 1993 grasshopper densities, eastern Colorado sites only.

A




B

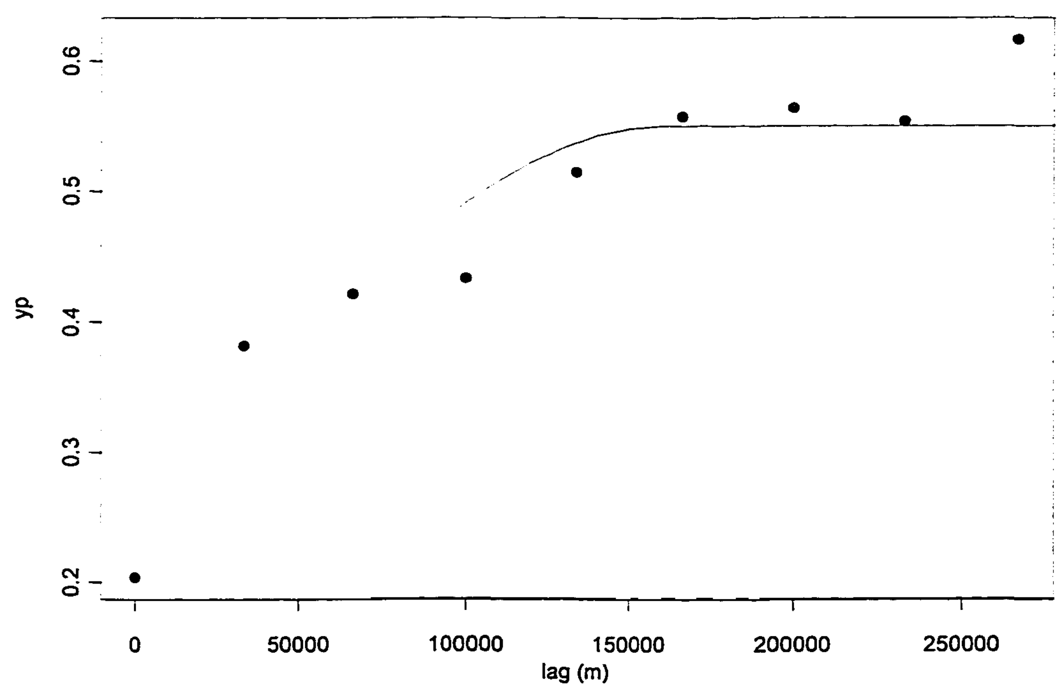
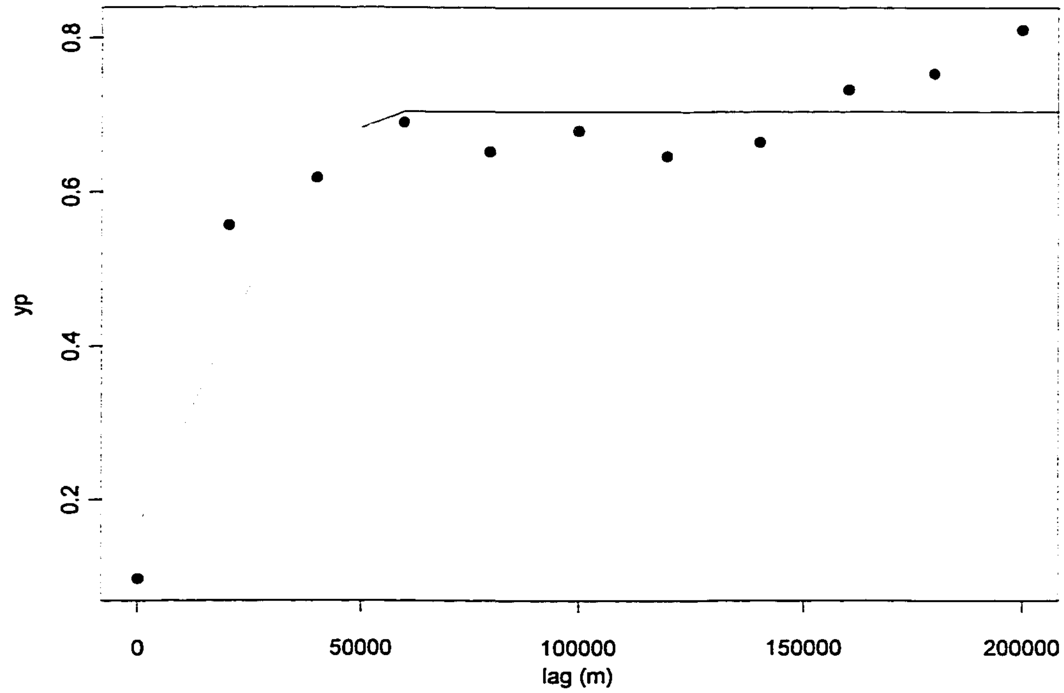


Figure A.12. A. Variogram for 1994 grasshopper densities, all sites. B. Variogram for 1994 grasshopper densities, eastern Colorado sites only.

A




B

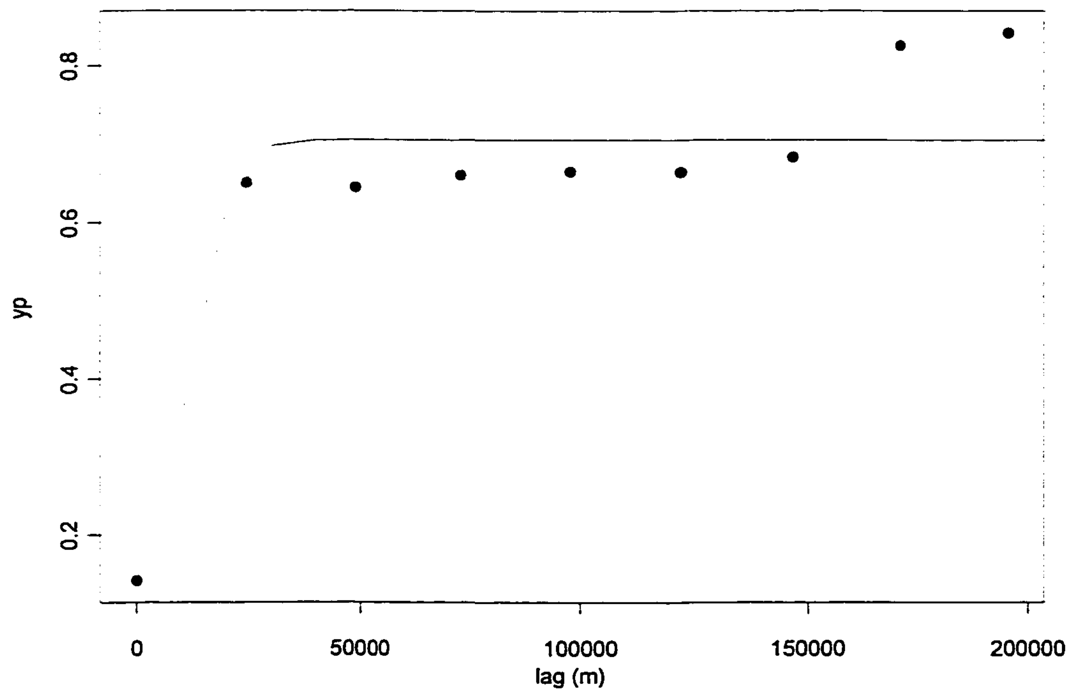
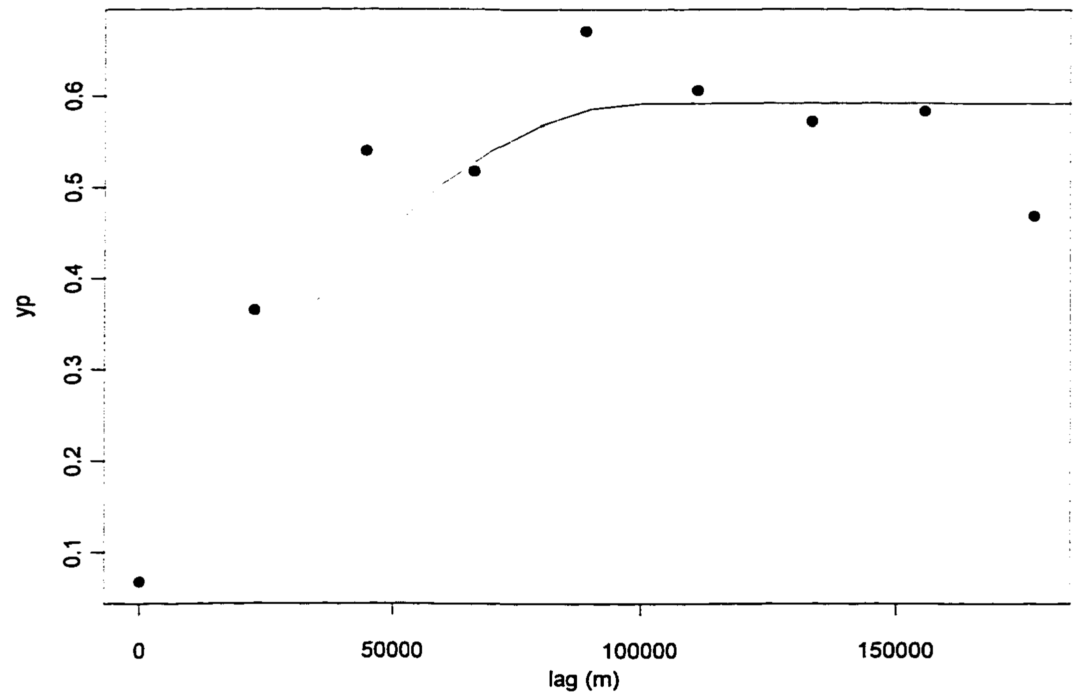


Figure A.13. A. Variogram for 1995 grasshopper densities, all sites. B. Variogram for 1995 grasshopper densities, eastern Colorado sites only.

A




B

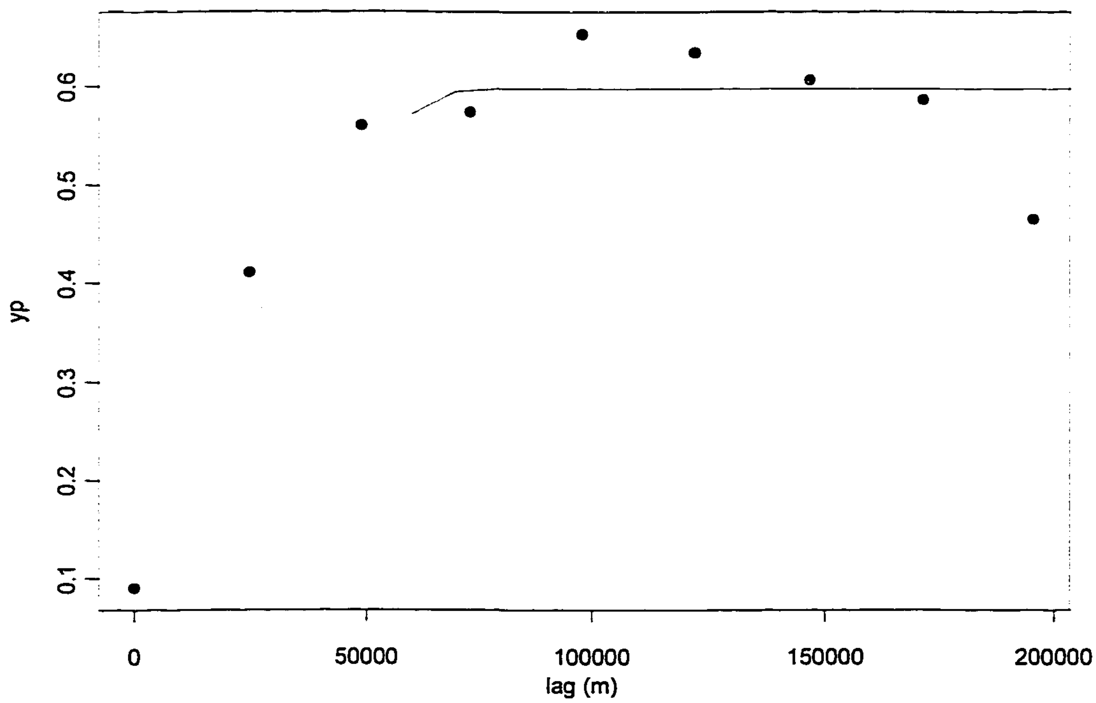
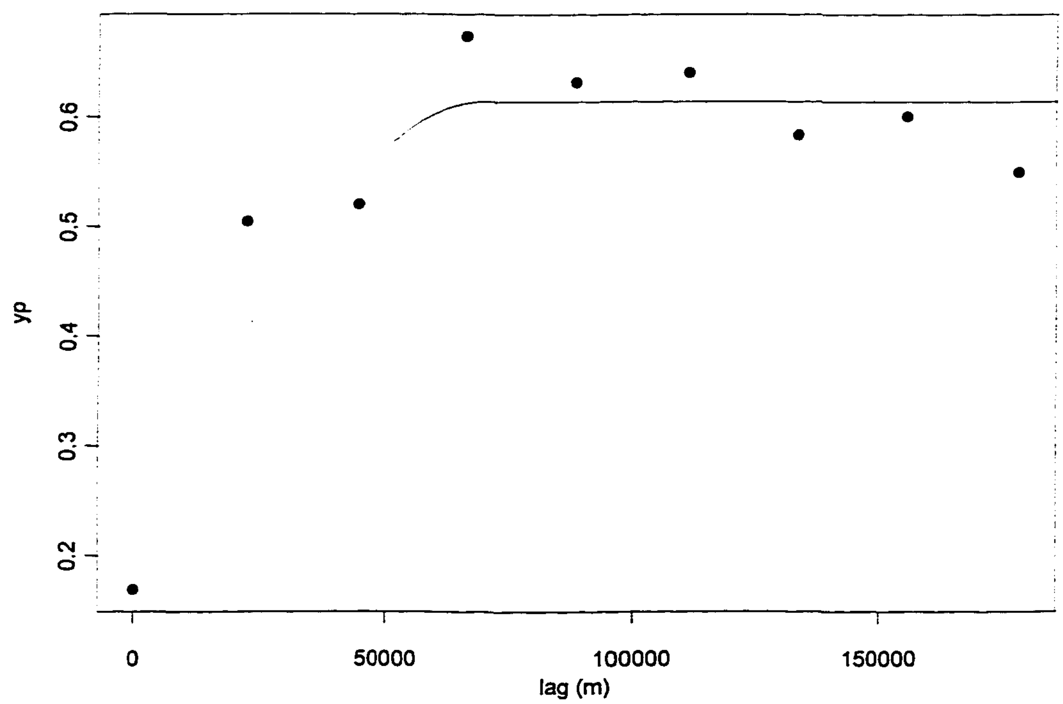


Figure A.14. A. Variogram for 1996 grasshopper densities, all sites. B. Variogram for 1996 grasshopper densities, eastern Colorado sites only.

A




B

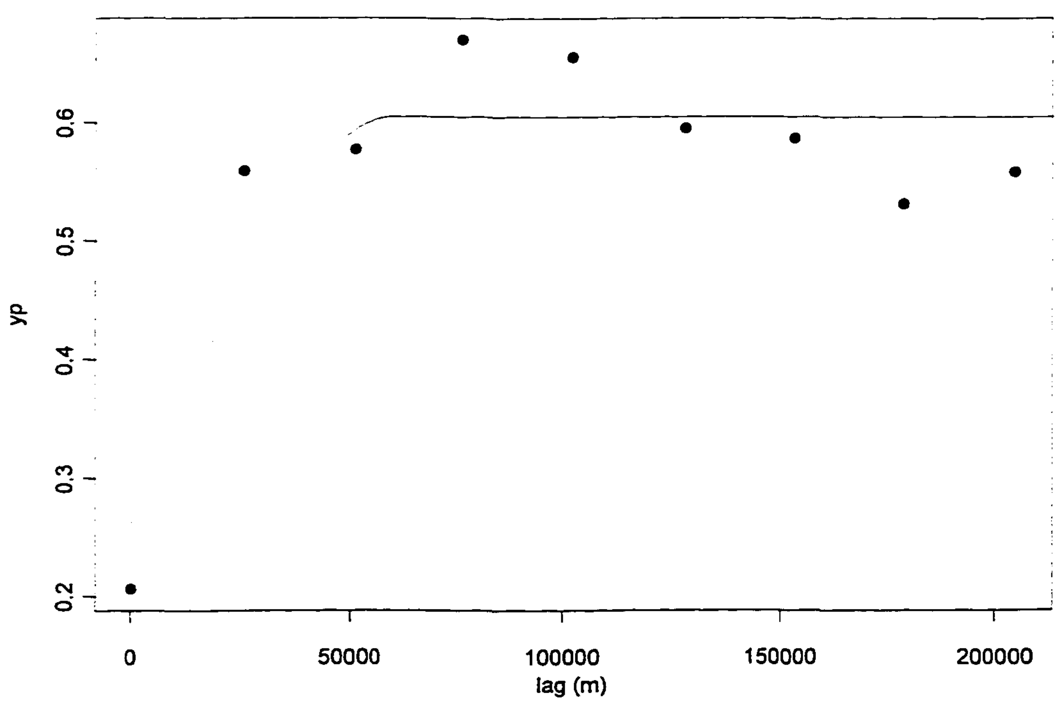
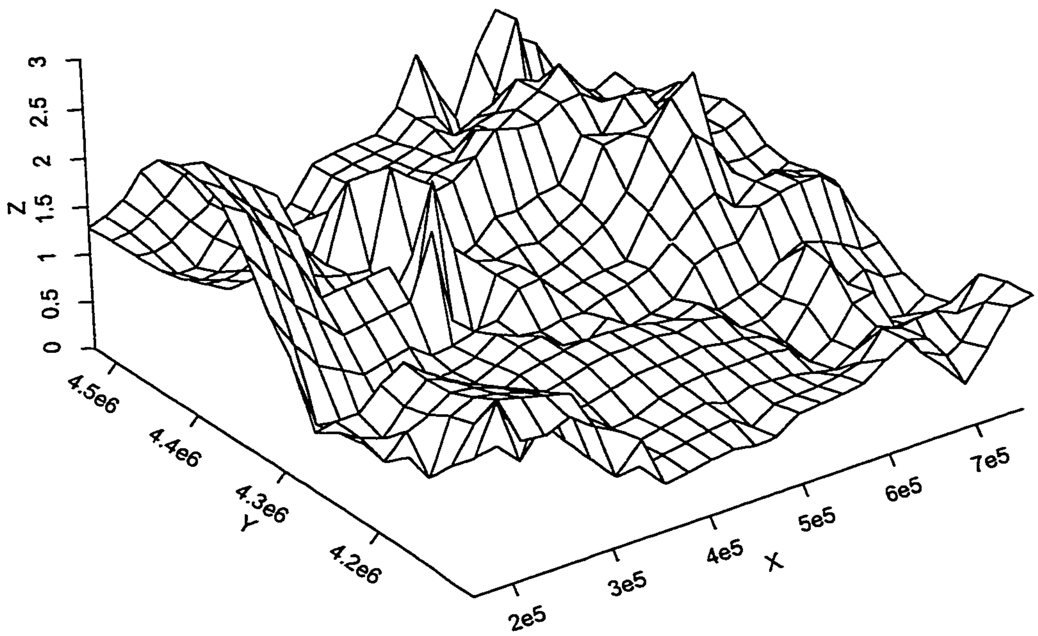


Figure A.15. Kriging results for all Colorado sites. A. Kriged surface for 1993 grasshopper densities. B. Standard error surface for 1993 grasshopper densities.

A




B

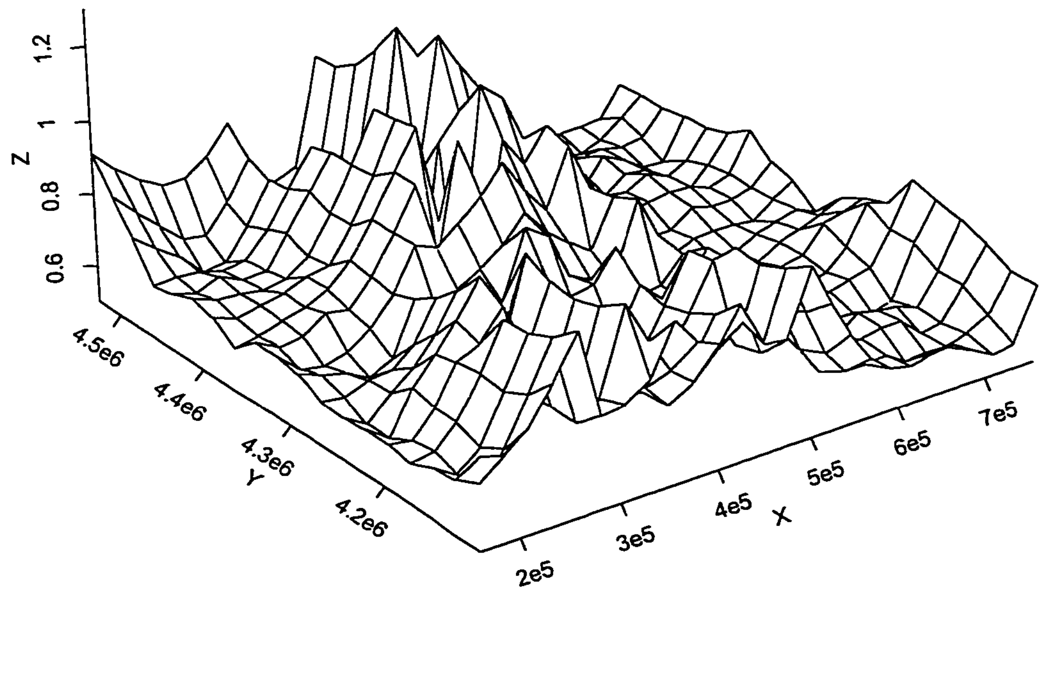
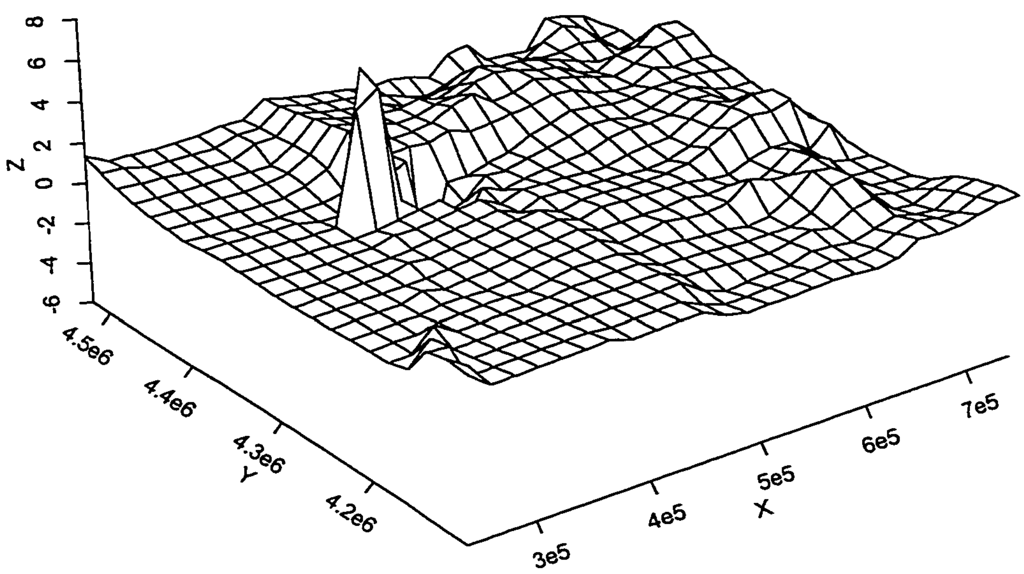


Figure A.16. Kriging results for all Colorado sites. A. Kriged surface for 1994 grasshopper densities. B. Standard error surface for 1994 grasshopper densities.

A




B

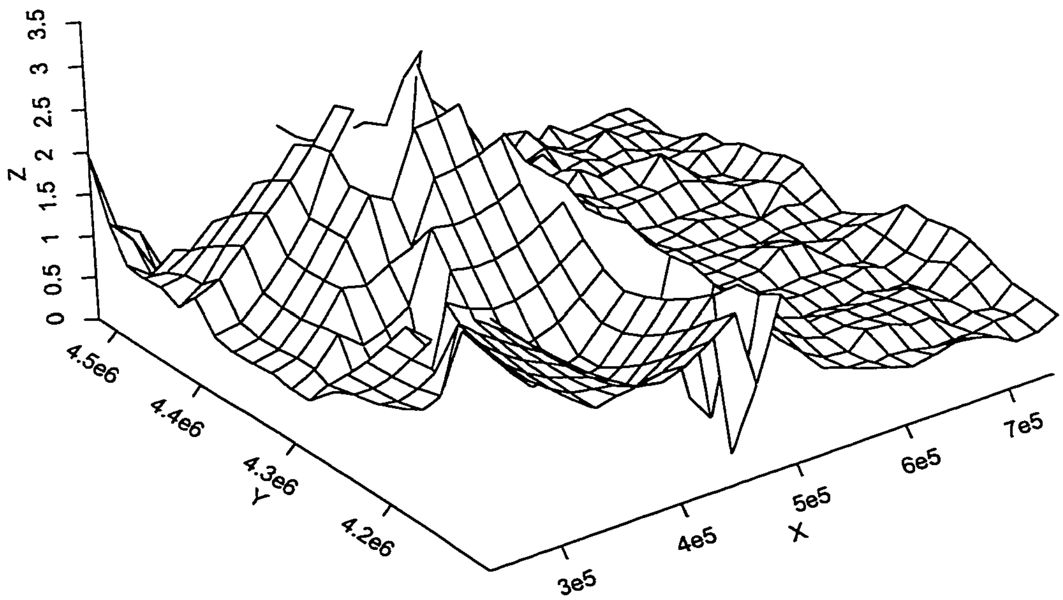
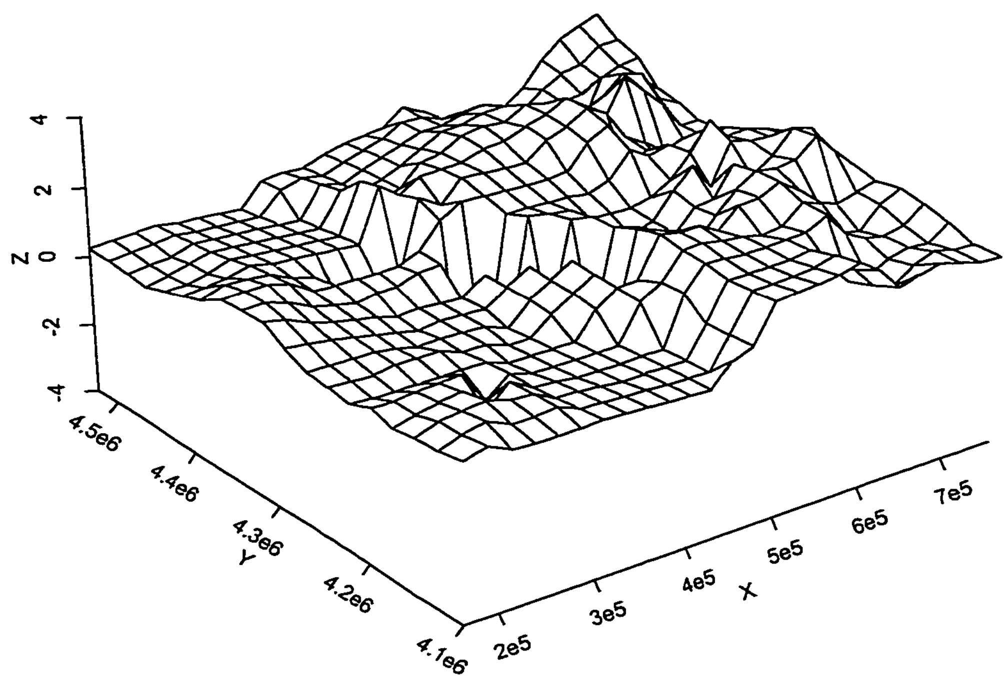


Figure A.17. Kriging results for all Colorado sites. A. Kriged surface for 1996 grasshopper densities. B. Standard error surface for 1996 grasshopper densities.

A




B

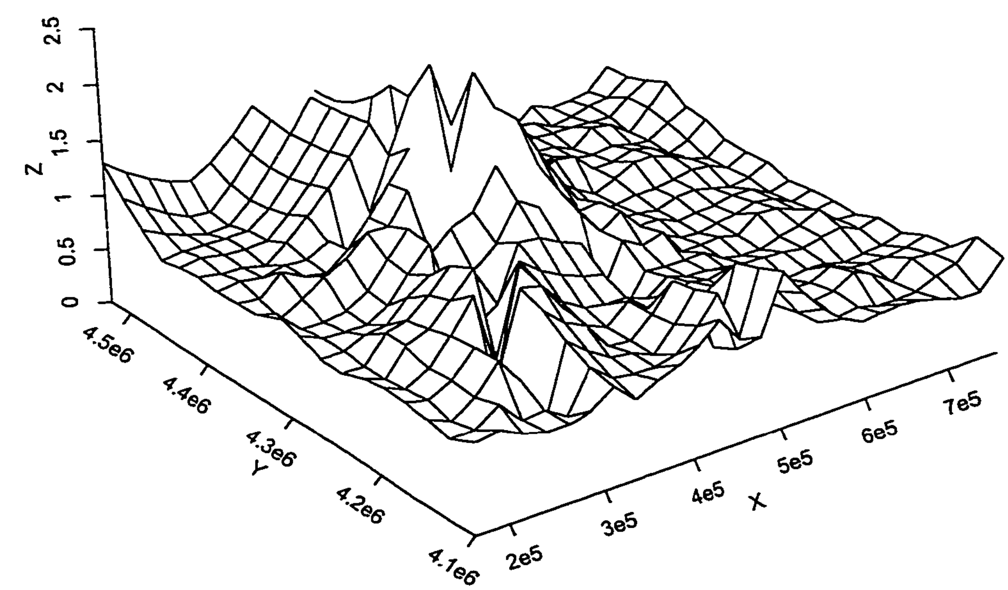
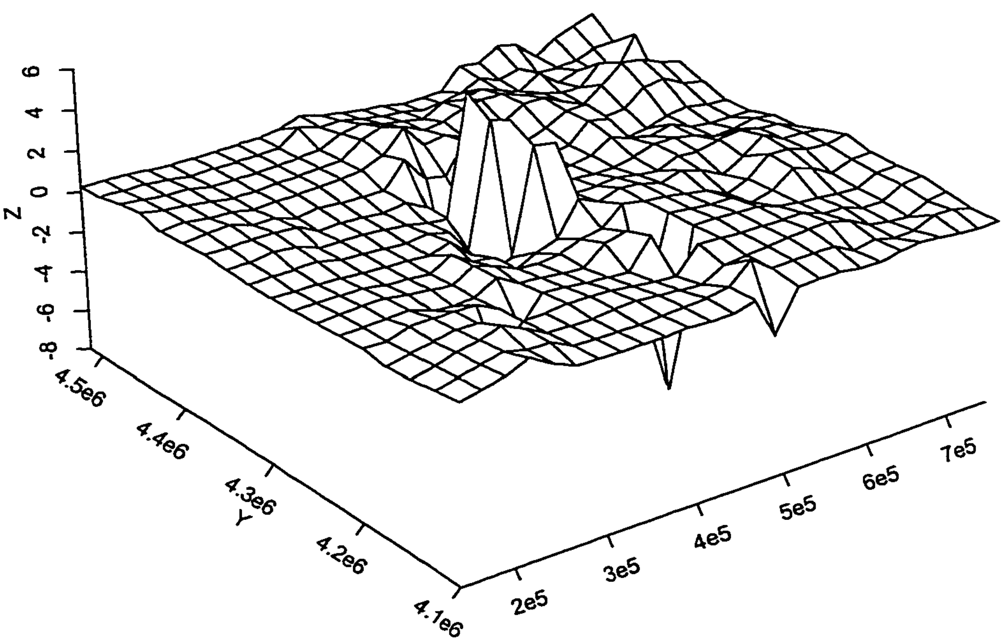


Figure A.18. Kriging results for all Colorado sites. A. Kriged surface for 1997 grasshopper densities. B. Standard error surface for 1997 grasshopper densities.

A




B