

A Spatial, Markovian Model of Rangeland Grasshopper (Orthoptera: Acrididae) Population Dynamics: Do Long-Term Benefits Justify Suppression of Infestations?

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Environ. Entomol. 33(2): 257–266 (2004)

ABSTRACT Using 49 yr of rangeland grasshopper (Orthoptera: Acrididae) survey data for Wyoming digitized into a spatially explicit format, we constructed a two-state (infested or uninfested) Markov chain model to evaluate the probabilities of population changes between states at the scale of 1 km². Our analyses revealed that only very limited areas of Wyoming are likely to support multiyear infestations of rangeland grasshoppers. Across the state, 91% of the land has a >50% probability of a transition from infested to uninfested conditions from one year to the next. Considering only the land that has ever been infested by grasshoppers, 55% of this area was found to have a >90% probability of becoming uninfested in the year after an infestation. The life expectancy of a grasshopper infestation in Wyoming is generally <2 yr, and large portions of the state can expect infestations to persist for <1 yr. Although rangeland grasshopper infestations are unlikely to persist for >1–2 yr, uninfested conditions are also unlikely to last. Of the land that has ever been infested, uninfested conditions are expected to persist for ≤10 yr on 36% of the area. Thus, rangeland grasshopper outbreaks are highly erratic events, with either infested or uninfested conditions lasting for short periods. Contrary to previous analyses at much coarser spatial scales, the probability of rangeland grasshopper infestations persisting for multiple years appears to be quite low. As such, for most of Wyoming there is little basis for prorating the benefits of control beyond the year of treatment.

KEY WORDS Markov chain, forecasting, pest management, geographic information system, spatial processes

THROUGHOUT THE WORLD, grasshoppers and locusts compete with humans and their livestock for crops and native forage. Hewitt and Onsager (1983) estimated that 25% of the available rangeland forage in the United States is eaten by grasshoppers, at an inflation-adjusted cost of \$600 million per year. Until recently, such losses were largely addressed by a government-subsidized program of insecticidal control. In 1996, the United States Department of Agriculture's (USDA) Animal and Plant Health Inspection Service (APHIS) terminated its cost-share program, which had paid 100% of the costs of grasshopper control on federal land, 50% of the costs on state land, and 33% of the costs on private land. As such, grasshopper control costs for ranchers have increased by 2- to 3-fold since the last major outbreak in 1986–88, while the price of cattle is virtually unchanged. In addition to their economic cost, large-scale insecticidal programs that "blanket" entire infestations may cause significant damage to the environment (USDA APHIS 2002) and may actually aggravate grasshopper outbreaks over

the long-term (Lockwood et al. 1988). Given that the control costs alone during the last outbreak were \$75 million, and the program involved blanketing >8 million ha with some 5 million liters of broad-spectrum insecticides (National Grasshopper Management Board 1995), there is an urgent need to develop ecologically sound, economically viable tools for rangeland grasshopper management.

With shrinking resources to treat grasshoppers, it is important for the landowner/manager to make informed decisions on how to deal with grasshopper outbreaks. Some entomologists believe economic benefits often extend beyond the year of treatment, based on the reproductive potential of grasshopper populations on rangeland (Pfadt 1977, Pfadt and Hardy 1987). However, others disagree (Blickenstaff et al. 1974). The answer to the question: "How long will an infestation persist?" is the single most important parameter in economic models of grasshopper control programs (Torell et al. 1987, Davis et al. 1992, Skold et al. 1995, Branting et al. 1997). This question can be phrased in various ways (e.g., Given that there is an infestation this year, what are the chances of an infestation next year? If a treatment is applied, will there be multiyear benefits? How long will an infestation last?), all of

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which are critical to sound pest management decisions. Considering the spatial variability in both range-land productivity and grasshopper population dynamics (Kemp et al. 1989, Schell and Lockwood 1997a, b), the answers to these questions must be developed and phrased in the appropriate spatiotemporal context. Given the spatial element of the problem and the nature of the available data (i.e., surveys that categorize land using nominal data, either infested or uninfested), the most appropriate analytical tools appear to be a combination of Geographic Information Systems (GIS) with two-state Markov chains. The integration of these methods allows a spatially explicit representation of the transition probabilities, duration, and multiyear dynamics of grasshopper infestations in Wyoming.

A GIS is an organized collection of data, managed via computer hardware and software to allow efficient storage, updating, manipulation, analysis, and display of geographically referenced information (Chou 1997, Chrisman 1997). These systems have been developed and implemented for a range of applications in agriculture, including pest management (Zesheng and Ling 1997, Swetnam 1998) and resource decision-support (Abbors et al. 1997, Mangold 1998). This technology has been used to analyze grasshopper and locust infestations in a wide range of settings. In Australia, Bryceson (1989) used satellite imagery to locate possible egg beds of the Australian plague locust, *Chortiocetes terminifera* (Walker). In Africa, a similar process was used to map areas where desert locusts, *Schistocerca gregaria* (Forsk.) are likely to breed, hatch, and develop (Tappan et al. 1991). Fielding and Brusven (1993) used a GIS to analyze relationships between grasshopper population densities and ecological conditions. In New Mexico and Montana, a GIS has been used to create maps of grasshopper populations to identify problem spots and aid in making management decisions (Kemp et al. 1989, Burckley 1995, Cigliano et al. 1992).

Schell and Lockwood (1997a, b) used a GIS to analyze 31 yr of grasshopper survey data to determine which areas in Wyoming are predisposed to infestations. The study produced a map showing the frequency (number of years) with which areas were infested. The frequency map produced from the 31-yr analysis was overlaid on maps showing vegetation, precipitation, elevation, evapotranspiration, landform, and soil associations to investigate how ecological factors affect grasshopper outbreaks. This GIS formed the basis for this current investigation of population dynamics.

Despite the wide-ranging applications of GIS for grasshopper management, this technology has not been used to make mathematical predictions of grasshopper populations. In principle, geographically referenced historical data in the form of electronic maps can be used to model and forecast population dynamics. Stander et al. (1989) defined a "process" as a series of events and a "stochastic process" as one that is not determined by its initial state. A stochastic process that has a discrete parameter and state space is called a

Markov chain (Bhat 1984). Based on a given series of events or states, a Markov chain predicts the probability of being in a state at a specific time and the time taken until a state is first reached (Stewart 1994).

Markov chain analysis has been used in several applications. In addition to sociological (Stander et al. 1989, Montgomery et al. 1994) and economic processes (Kim et al. 1991), this approach has been effective in modeling epidemiological events (Carpenter 1988, Berentsen et al. 1992). Two-state (conditions defined as being either infested or uninfested) Markov chain analyses have been applied to grasshopper population dynamics in Saskatchewan, Montana, and Wyoming (Kemp 1987, Lockwood and Kemp 1987, Mukerji and Hayhoe 1988). This approach was chosen as the means for modeling population dynamics because: 1) the resulting models are conceptually straightforward, 2) the results of the analysis are relevant to management (e.g., transitional probabilities between states), 3) the necessary sequences of states are available and extensive (annual records of grasshopper infestations), and 4) the results of the analysis are adaptable to graphical representation (Jeffers 1978).

Although Markov chain analyses have allowed estimations of probability, stability, and duration of grasshopper outbreaks, the spatial scale has been extremely coarse (e.g., entire counties or districts; Kemp 1987, Lockwood and Kemp 1987). With more accurate spatial analyses, the quality of information, the ecological interpretability, and the value to pest management of these dynamic models could be dramatically enhanced. Thus, the goal of this research was to integrate Markovian models with a GIS to produce fine-scale analyses of grasshopper population dynamics that could be used to assess whether multiyear benefits should be included in economic evaluations of grasshopper management programs.

Materials and Methods

Data Acquisition. We based our analyses on yearly grasshopper survey maps from state (Wyoming Department of Agriculture [WDA]) and federal (United States Department of Agriculture, Animal and Plant Health Inspection Service [USDA APHIS]) agencies. These maps were compiled and digitized, as described by Schell and Lockwood (1997a). The USDA conducted an annual grasshopper survey at 25–50 locations in each of the counties. At each location, 18 visualized square-foot counts for grasshopper population density estimation were taken. Surveys for grasshoppers were conducted most intensively in the eastern part of Wyoming, where outbreaks most commonly occurred. From these point data, hand-drawn maps were then created using a subjective interpolation of the survey point data. The survey method of WDA was similar to that of the federal agency. The USDA supplied the data for the maps after 1985, and WDA supplied the data used in the USDA maps before 1985. Only maps from 1944 to 1980 and 1985 to 1996 could be used, as no surveys were conducted from

1981 to 1984. Although this gap precludes five transitions just before the time of a major outbreak, the analysis or balance of the data does include the largest absolute increase in infested area (1986–1987) and several other outbreaks of similar scale (e.g., 1962–1963 and 1973–1974) (Schell 1994).

Based on these maps, each location in Wyoming was determined to be in one of two different states: uninfested or infested. A location was considered infested if there were ≥ 9.6 grasshoppers/m² (8 grasshoppers/yard²). This was the only population density recorded on all maps throughout the entire period of survey. A density of ≥ 9.6 grasshoppers/m² was considered to be an “action” threshold for the consideration of treatment. This density was sometimes considered an economic injury level, although there was little empirical support for this assertion and such a fixed criterion did not take into consideration rangeland productivity, forage and livestock prices, grasshopper species composition, or other essential factors (Davis et al. 1992, Branting et al. 1997). Although the economic interpretation of this population density varies greatly, this value has ecological meaning in that it approximates the statistical carrying capacity of much western rangeland (Kemp and Dennis 1993).

The information from the hand-drawn maps was digitized into a raster GIS (ERDAS 1991), and the maps were stored in Lambert Conformal Conic projection (Schell 1994). Data for each year were represented as a separate grid. A grid cell size of 1 km² was used for the analyses. Each cell was coded as 0 if it was uninfested or 1 if the cell was infested (using the criterion of ≥ 9.6 grasshoppers/m²). The data were then exported from ERDAS into ArcView using the raster extension, Spatial Analyst (ESRI, Redlands, CA).

Data Analysis. The data represented a discrete parameter space set $t = (0, 1, 2, 3, \dots)$ where time 0 = 1944, 1 = 1945, and so on. As such, this data set was a discrete (time) parameter stochastic process or Markov chain. At any time t , the cells of the maps were in either the 0 (uninfested) or 1 (infested) state. Therefore, the state space was (0, 1) and the system was modeled using a two-state Markov chain.

Three sets of parameters were derived. First, we determined the probability of transition (the chance of grasshopper population in each cell switching from one state to another or remaining in the original state within a fixed increment of time). In this context, there were four possible transitions: uninfested \rightarrow uninfested (0 \rightarrow 0), uninfested \rightarrow infested (0 \rightarrow 1), infested \rightarrow uninfested (1 \rightarrow 0), and infested \rightarrow infested (1 \rightarrow 1). The probabilities of each of these transitions were determined according to formulae developed by Bhat (1972). Second, using the methods of Kemp (1987), we determined the duration of states. That is, by dividing elements within the appropriate rows of the transition matrix, we calculated the number of years that a particular state was expected to persist for a given cell. Third, we determined the stability of states. This parameter was calculated as the number of years that a cell could be expected to be

infested or uninfested given that it was currently in one or the other of these states.

The two-state Markov chain model was developed in ArcView using the software extension, Spatial Analyst. The full, operational system can be accessed at <http://www.sdvc.uwyo.edu/grasshopper/kzthesis/thesis.htm>. ArcView was used because it supports GIS operations and its functionality can be extended and altered using scripts written in Avenue, the object-oriented development language of ArcView (ESRI). The Markov extension provided spatial depiction and analysis of the fundamental measures for each cell pertaining to rangeland grasshopper ecology and management, including the three aforementioned parameters, as well as transition probabilities from 2 to 5 yr.

To assess possible origins or causes of the spatial pattern of population dynamics, we overlaid the Markov probability maps onto vegetation cover maps of Wyoming (adapted from Ostresh et al. 1990) to detect ecological associations between these two thematic layers. The analyses were performed using ArcView GIS 3.2 and ERDAS Imagine 8.6 software. The vegetation map was digitized and imported into ERDAS Imagine as a raster file. The Markov transition shapefiles were imported in ERDAS Imagine, converted into raster format, and reprojected into the same projection that was used for the vegetation map. The GIS analyses (ERDAS Imagine procedure, Summary) were performed by overlaying the thematic layers of vegetation with the transitions of greatest management relevance (uninfested \rightarrow infested and infested \rightarrow infested).

Results

When the Markov chain analysis was applied to rangeland grasshopper data from 1944 to 1996, it was apparent that only very limited areas of Wyoming were likely to support multiyear infestations (Table 1; Fig. 1). The highest probabilities of a transition from infested to infested conditions were seen in the eastern plains, surrounding a large, relatively uninfested area—a pattern that matched the one described by Schell and Lockwood (1997a) in their study of the grasshopper outbreaks. The ecotopographic regions surrounding the “hole” in the spatial distribution of grasshopper outbreaks were characterized by Schell and Lockwood (1997a) as: Black Hills (the frequently infested region in the extreme northeast), Platte-Goshen-Niobrara complex (the region within the three most frequently infested counties in the southeastern part of the state), Laramie Mountains (the infested region appearing as a northwesterly extension from the previous region), Southern Big Horn Mountains (the central region as the western limit of the eastern plains), and Northern Powder River Basin (the frequently infested region directly north of the previous region). The only disjunct region with a high probability of transition from infested to infested conditions (i.e., >50%) occurred in the northwestern area of the Big Horn basin.

Table 1. Amount of land in Wyoming associated with 1 yr transition probabilities of rangeland grasshopper populations derived from Markov chain analysis

Transition	Probability of transition	Percentage of land	Area of land (km ²)
Uninfested→uninfested	0.00-0.10	0	0
	0.11-0.20	0.0	0
	0.21-0.30	0.0	0
	0.31-0.40	0.0	0
	0.41-0.50	0.0	0
	0.51-0.60	0.0	0
	0.61-0.70	0.3	761
	0.71-0.80	2.1	5,325
	0.81-0.90	10.9	27,640
	0.91-1.00	86.7	219,852
Infested→uninfested	0.00-0.10	0.0	0
	0.11-0.20	0.0	0
	0.21-0.30	0.1	254
	0.31-0.40	0.5	1,268
	0.41-0.50	3.9	9,890
	0.51-0.60	1.6	4,057
	0.61-0.70	7.5	19,018
	0.71-0.80	4.9	12,425
	0.81-0.90	4.5	11,411
	0.91-1.00	27.8	70,495
	NA*	49.2	124,760

* Refers to areas of land in which no grasshopper infestations have been documented, so transition probabilities cannot be calculated.

Although some areas clearly had higher probabilities of continuing infestations, the areas with even moderately high probabilities of such transitions (i.e., 40–60%) were highly constrained. Indeed, 91% of the land in Wyoming had a >50% probability of a transi-

tion from infested to uninfested conditions from one year to the next. Of the entire state, 87% of the land had a >90% chance of staying uninfested in the subsequent year, if currently uninfested. Considering only the land in the state that had ever been infested by grasshoppers (i.e., potential outbreak habitat), more than half (55%) of this area was found to have a >90% probability of becoming uninfested in the year after an infestation.

The life expectancy of a grasshopper infestation in Wyoming was generally <2 yr, and large portions of the state supported infestations expected to persist for <1 yr (Fig. 2). Consistent with the previous findings, the areas with the longest expected durations of infestations overlapped considerably, with those having the highest probability of a transition from infested to infested conditions (Fig. 1). Slightly more than half (51%) of the state (128,818 km², approximately the size of the state of Mississippi) had ever reported a rangeland grasshopper infestation (Table 2). Of the area that had been infested at any time since 1944, 97% of the land had an expected duration of infestation of ≤1 yr, and 99% of the area had an expected duration of ≤2 yr (Fig. 3).

Although rangeland grasshopper infestations do not appear likely to persist for >1–2 yr, uninfested conditions are also unlikely to last for a prolonged period of time. A substantial area (46,659 km² or 36% of the land that has ever been infested) can expect uninfested conditions to persist for ≤10 yr (Table 2; Fig. 4). Thus, an area equivalent to that of Vermont and New

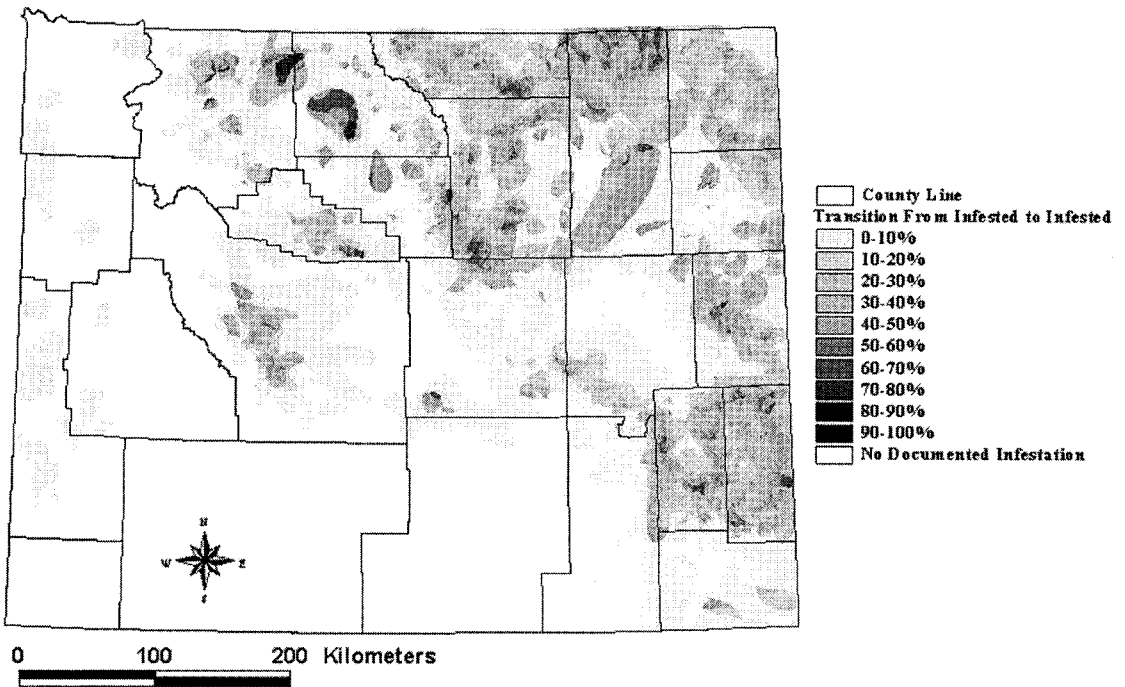


Fig. 1. Probabilities of a 1-yr transition from infested to infested conditions (based on ≥ 9.6 grasshoppers/m²) for rangeland grasshopper populations in Wyoming, based on two-state Markov chain analysis of 49 yr of survey data.

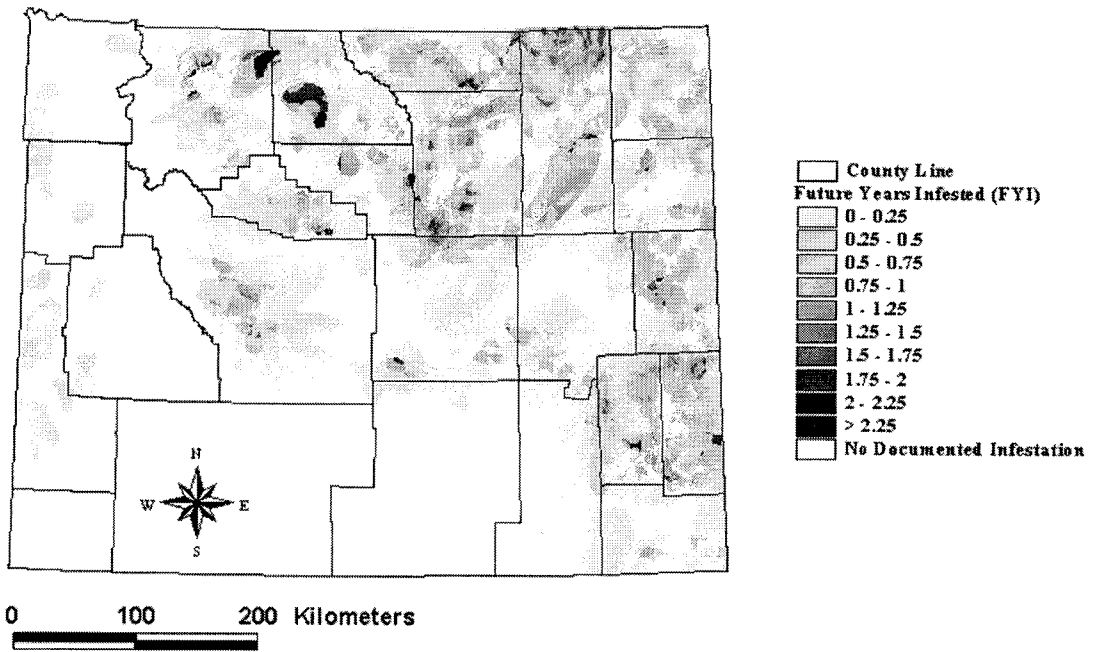


Fig. 2. Expected duration of rangeland grasshopper infestations (based on ≥ 9.6 grasshoppers/m²) in Wyoming, based on two-state Markov chain analysis of 49 yr of survey data.

Hampshire combined is likely to experience a grasshopper outbreak every decade. And a smaller, yet substantial area comprising 10% of the land that has ever been infested (13,440 km², an area equal to that of Connecticut) is expected to become infested every 5 yr or less.

The overlay of transition probability classes with vegetation classes revealed that the ecosystems with the highest probability of becoming infested are not necessarily the lands in which infestations persist

Table 2. Areas of land in Wyoming associated with expected durations of existing states of rangeland grasshopper populations derived from Markov chain analysis

Future state	Time in state (yr)	Percentage of land	Area of land (km ²)	
Uninfested	0-5	5.3	13,440	
	6-10	13.1	33,219	
	11-15	7.5	19,018	
	16-20	0.1	254	
	21-25	9.9	25,104	
	26-30	0.0	0	
	31-35	0.0	0	
	36-40	0.0	0	
	41-45	1.7	4,311	
	46-50	13.2	33,472	
	NA*	49.2	124,760	
Infested	0.0-1.0	49.3	125,014	
	1.1-2.0	1.3	3,297	
	2.1-3.0	0.2	507	
	3.1-4.0	0.0	0	
	4.1-5.0	0.0	0	
		NA*	49.2	124,760

* Refers to areas of land in which no grasshopper infestations have been documented, so transition probabilities cannot be calculated.

(Tables 3 and 4). With respect to uninfested→infested transitions, mixed-grass prairie constituted 22% of the state, but this ecosystem accounted for 29–100% of the highest classes (35–50% probability). Similarly, ponderosa pine woodlands was over-represented in the high, transition classes (25–45% probability). Lodgepole pine forest was under-represented in all transition classes except 40–45%, in which its frequency (34%) was more than 3 times greater than its occurrence in the state (10%).

With respect to infested→infested transitions, juniper woodlands constituted just 2% of the state, but this ecosystem accounted for 10–83% of the highest classes (80–100% probability). The two vegetation classes that dominated the highest probability classes of uninfested→infested transitions (mixed-grass prairie and ponderosa pine woodlands) occurred in $\leq 4\%$ of the high infested→infested transition classes (70–100%). Douglas fir forests and woodlands were under-represented in all transition classes except 80–90%, in which its frequency (14%) was more than 4 times greater than its occurrence in the state (3%).

Discussion

The ecological and management implications of this study of the population dynamics of rangeland grasshoppers are constrained by several factors related to the quality of data, the effects of treatment, and the scale of analysis. Interpretations of our findings must be developed in context of these three limitations.

With respect to the quality of the data, it should be recognized that the records omit major outbreak pe-

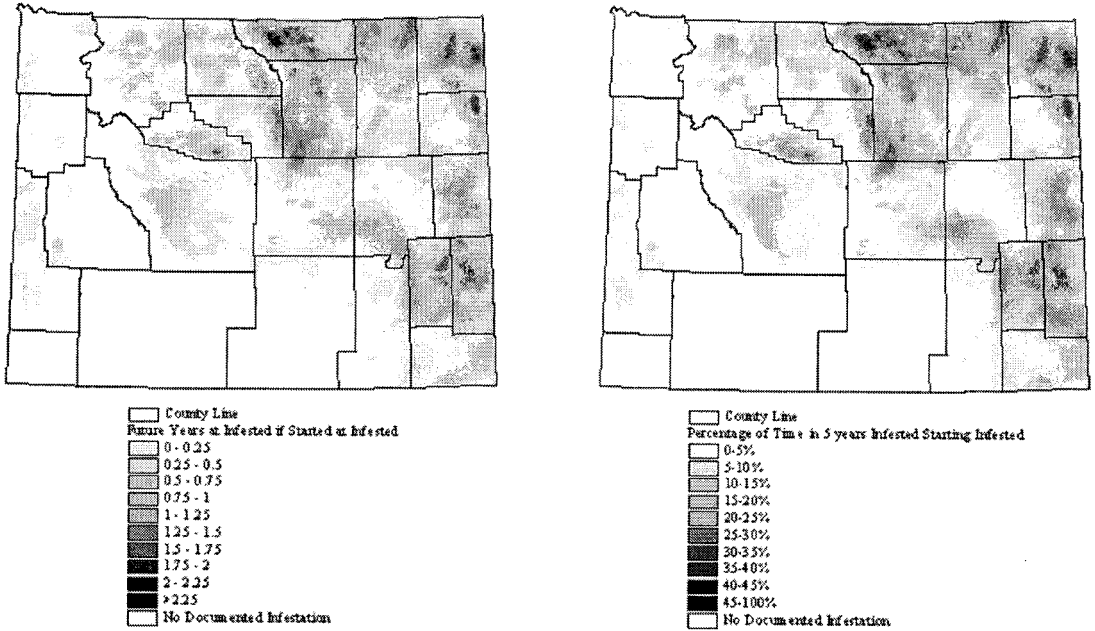


Fig. 3. Number of years and percentage of time (in the next 5 yr) that infested conditions (based on ≥ 9.6 grasshoppers/ m^2) are expected to persist, given that there is currently an infestation of rangeland grasshoppers in Wyoming, based on two-state Markov chain analysis of 49 yr of survey data.

riods in the 1930s and 1950s (Pfadt and Hardy 1987). Although our data include the outbreak that occurred in the 1980s, we cannot assume that the same dynamics for all periods are necessarily represented in the time

series used in our study. We further note that the APHIS survey data are a pooling of all species of grasshoppers. Although the majority of grasshoppers (>80%) in high density infestations are usually pest

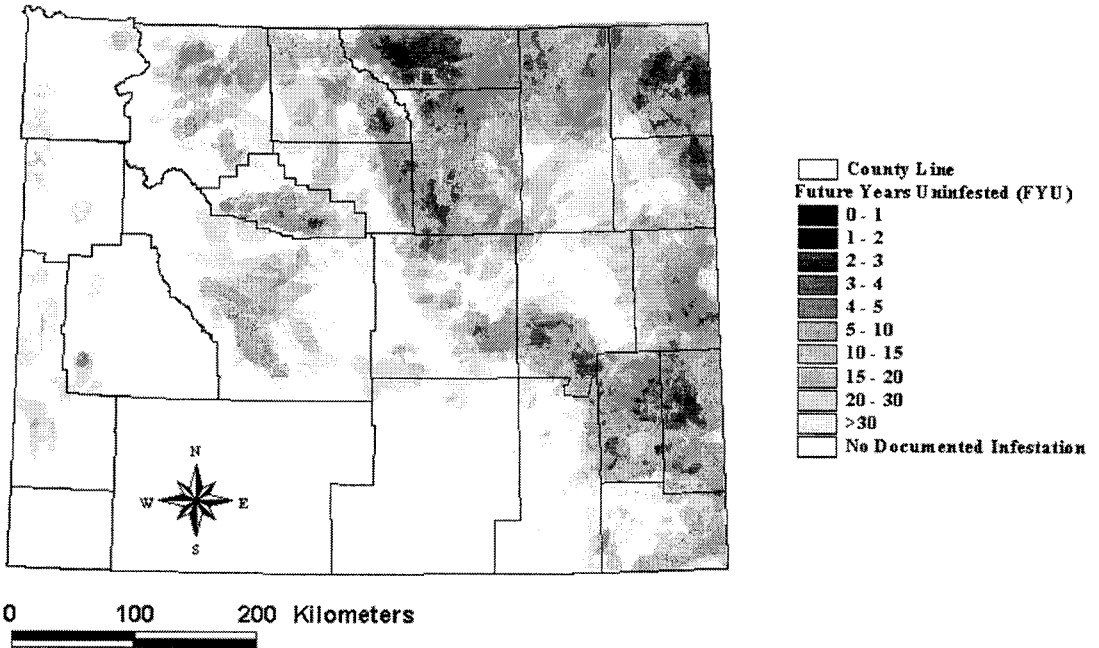


Fig. 4. Expected duration of uninfested conditions (based on ≥ 9.6 grasshoppers/ m^2) in Wyoming, based on two-state Markov chain analysis of 49 yr of survey data.

Table 3. Percentage of Wyoming occupied by major vegetation types and their association with uninfested→infested transition probability classes as determined by Markov chain analysis

Vegetation community	Area (% of state)	Uninfested→infested transition probability (% of class)						
		15–20	20–25	25–30	30–35	35–40	40–45	45–50
Alpine tundra	1.3	0.1	0	0	0	0	0	0
Sand dunes	0.2	0	0	0	0	0	0	0
Sage brush steppe	45.6	24.2	14.0	9.7	23.9	17.7	9.9	0
Desert shrubland	4.4	0	0	0	0	0	0	0
Mixed-grass prairie	22.2	35.8	51.9	24.7	21.3	29.2	31.7	100
Juniper woodland	2.4	6.7	4.2	1.6	0	0	0	0
Oak woodland	0.2	0.6	0.1	5.9	5.2	1.8	0	0
Ponderosa pine woodland	5.5	26.4	19.2	50.9	39.7	29.2	24.2	0
Spruce fir forest	4.8	0.8	1.7	0.3	0	0	0	0
Douglas fir forest	3.2	1.0	3.1	2.4	3.5	14.5	0	0
Lodgepole pine forest	10.0	4.6	5.9	4.7	6.4	7.5	34.2	0
Aspen forest	0.2	0.1	0	0	0	0	0	0

species (Kemp 1992), there are often nontarget and beneficial acridids in the assemblage. Furthermore, the different species in an infestation may have different population dynamics, such that a pooling of grasshoppers during the surveys generates a biologically complex synthesis of diverse processes. Finally, the data were available only in a categorical format (e.g., 0–3, 4–7, 8–15, and >15 grasshoppers/yr²) so that analyses such as ours will tend to emphasize short-term shifts in responses across the boundaries of these categories.

In terms of treatment effects (i.e., pest control programs), there are no consistent or reliable spatial data on the areas of Wyoming that have been involved in such efforts. An approximation of the total areas involved was gleaned for five frequently treated counties based on records from particular years in which the areas (if not precise locations) of treatments were available (Lockwood et al. 1988). These records indicated that from 1964 to 1986, a period for which there were treatment records in 12 of the years, the average area treated was 8.8% (0.1–23.2%) of the total area. These were probably overestimates of the actual proportion of the land subjected to control, as years with little treatment rarely generated reports. As such, the direct, overall effect of insecticidal suppression on the course of grasshopper population dynamics was probably rather limited, although the longer-term ef-

fects of eliminating natural enemies with broad-spectrum insecticides may have been considerable (Lockwood et al. 1988). Even so, to the extent that pest management practices have altered the population dynamics of grasshoppers, it is possible that the maps and analyses generated via the Markov chain procedure could misrepresent normal processes. Relative to natural dynamics, our analyses may overestimate the probability of transitions from infested to uninfested conditions (if control programs were effective in suppressing outbreaks) or overestimate the transitions from uninfested to infested conditions (if control programs made outbreaks more frequent by virtue of creating “enemy-free” space [Lockwood et al. 1988]). Of course, the reliable application of our model to future infestations depends on the fundamental elements and processes of the system being similar to the conditions under which the historical data were collected. This assumption appears reasonable, as there are no profound or acute alterations in the ecology or management of rangelands currently underway or expected in the foreseeable future.

With regard to the scale of analysis, it is possible that a different resolution (greater or less than 1-km² grid cells) could have yielded other results. The probability of a rangeland grasshopper infestation persisting, expanding, or collapsing appears to be a function of its size, with larger areas being more likely to be sustained

Table 4. Percentage of Wyoming occupied by major vegetation types and their association with infested→infested transition probability classes as determined by Markov chain analysis

Vegetation community	Area (% of state)	Infested→infested transition probability (% of class)						
		30–40	40–50	50–60	60–70	70–80	80–90	90–100
Alpine tundra	1.3	0.4	0.1	0.3	0.5	0	0	0
Sand dunes	0.2	0	0	0	0	0	0	0
Sagebrush steppe	45.6	26.2	28.8	36.4	23.0	10.5	4.8	16.7
Desert shrubland	4.4	1.9	3.8	0	33.0	81.4	61.9	0
Mixed-grass prairie	22.2	48.0	46.2	41.3	24.7	4.0	0	0
Juniper woodland	2.4	3.3	1.4	3.8	1.7	3.3	9.5	83.3
Oak woodland	0.2	0.3	0.1	0	0	0	0	0
Ponderosa pine woodland	5.5	13.7	15.2	14.3	14.5	0.8	0	0
Spruce fir forest	4.8	1.1	0.6	1.3	0.9	0	9.5	0
Douglas fir forest	3.2	2.3	2.6	1.1	1.4	0	14.3	0
Lodgepole pine forest	10.0	2.8	1.2	1.5	0.3	0	0	0
Aspen forest	0.2	0	0	0	0	0	0	0

both within and between years (Lockwood and Schell 1995). However, once an infestation reaches 1,000 ha (10 km^2), the probability of persistence or expansion generally stabilizes. Thus, the grid-cell size in the current study encompasses the spatial scale that appears to provide the greatest sensitivity to ecological processes. In addition, this resolution is a reasonable approximation of the geographic accuracy of the survey data (Schell and Lockwood 1997a). Finally, the spatial scale used in our study is particularly relevant to pest managers and ranchers, as it approximates the size of typical ownership and management units (i.e., many producers fence and manage pastures along section lines, with a common unit being a "section," equal to $\approx 2.5 \text{ km}^2$).

With these considerations in mind, several important findings emerge from the current study with regard to grasshopper ecology and pest management (including both survey and treatment programs). In ecological terms, the spatiotemporal pattern of rangeland grasshopper outbreaks suggests that these events are perhaps more localized and short-term than previously thought (USDA APHIS 1987, Kemp et al. 1989, Liebhold et al. 1993, Lockwood and Lockwood 1997). Earlier studies using Markovian analyses (Lockwood and Kemp 1987, Lockwood et al. 1988) reported much higher 1-yr transition probabilities from infested to infested conditions than the current work (mean = 0.703, median = 0.800, range = 0.333–0.960). These previous investigations lacked the refined spatial analysis of the present work, and considered a county to be infested if there was any area with ≥ 9.6 grasshoppers/ m^2 . As such, the transition probabilities were grossly overestimated with respect to absolute values and practical spatial units of pest management (although for the purposes of revealing relative frequencies of infestations and making ecological comparisons among counties, the method was defensible). Our current study shows that the northern tier of counties has extremely few areas with an infested \rightarrow infested transition probability > 0.50 , and the modal probability is 0.0–0.1.

Rather than the classical view that grasshopper outbreaks are infrequent, large-scale processes, it may be the case that they are relatively common, small-scale events. The appearance of regional outbreaks covering hundreds of thousands of hectares could be the result of a relatively coarse perceptual scale and the bias arising from management programs that operated on very large units of land (APHIS considered 4,000 ha as the smallest area that could qualify for a federally supported/subsidized grasshopper control program). The findings of relatively frequent, localized infestations as characterizing rangeland grasshopper population dynamics also accord with earlier work showing that high-density infestations were most often between 100 and 1,000 ha; two-thirds of grasshopper infestations in an intensive 5-yr study fell within this range of sizes (Lockwood and Schell 1995).

Strong associations between areas with high probabilities of becoming or staying infested and vegetation types provide insight as to the ecology of grass-

hopper infestations. Schell and Lockwood (1997a, b) reported that mixed-grass prairie and ponderosa pine woodlands had the highest frequencies of grasshopper infestations in Wyoming. The current study substantiates this earlier finding with respect to the ecosystems having the highest uninfested \rightarrow infested transition probabilities. The seemingly anomalous case of a high probability in lodgepole pine forest may reflect grasshopper outbreaks in montane meadows within this larger ecosystem (Pfadt 1996).

Although the probability of a landscape becoming infested reflected previous work on infestation frequencies, the analysis of infestation persistence (highest infested \rightarrow infested transition probabilities) revealed a markedly different set of ecological associations. That is, juniper woodlands were most commonly associated with continuing grasshopper infestations. Although this ecosystem rarely became infested, once an infestation began it had an abnormally high probability of persisting. Conversely, the mixed-grass prairies and, to a lesser extent, the ponderosa pine woodlands had unusually frequent transitions to infested conditions, but these populations were likely to revert to lower densities in the following year. The ponderosa pine woodlands represent an ecotone between grasslands and mountains in the eastern half of Wyoming, while the juniper woodlands are an analogous ecotone in the western half of the state. Thus, it may be the case that these transitional lands include the ecological factors that support grasshopper outbreaks, being not as dry and hot as the grasslands, but not as wet and cool as the mountains, a phenomenon that has been noted in the biogeography of grasshoppers in Russia (Lockwood and Sergeev 2000).

In terms of rangeland grasshopper surveys as a basis for predictive models, experience has demonstrated that the dynamics of rangeland grasshopper populations are difficult to forecast (Watts et al. 1982, Lockwood and Lockwood 1991, 1997). However, in an ongoing effort to predict grasshopper outbreaks, APHIS produces maps showing the results of the annual adult grasshopper population surveys conducted in the western United States. The premise of this method is that if an area supports high densities of grasshoppers one year, it will probably do so the following year. However, this method has not had much success in predicting grasshopper outbreaks (Edwards 1962, Watts et al. 1982, Davis et al. 1992).

In our experience, low-density grasshopper populations (4–8 grasshoppers/ m^2) have the potential of rapidly reaching very high levels (≥ 30 grasshoppers/ m^2), if certain species are present (J.A.L., unpublished observations). In a study conducted in southeastern Wyoming, areas up to 7,400 ha changed from very low grasshopper densities (< 3 grasshoppers/ m^2) to potentially damaging levels (10–15 grasshoppers/ m^2) in 1 yr (Lockwood and Schell 1995). At a larger scale, the current study also tends to refute the notion that a high or low population density in one year is a good predictor of similar conditions in the next year. Hence, the fundamental assumption of the current forecasting method may be called into question. Surveys for adult

grasshoppers in mid to late summer may have limited value in terms of making future management decisions, particularly at the scale of individual agricultural enterprises.

The population dynamics revealed in the current study have at least two implications for rangeland grasshopper control practices. First, the evidence strongly suggests that the vast majority of the landowners/managers do not receive multiyear benefits from treatments. Hence, in most cases, the economic returns on a control program must be justified with regard to the value of the current savings in forage. This represents a potentially significant departure from common assumptions (Skold and Davis 2000), and it suggests that efforts to further reduce the economic costs of control programs are paramount to creating viable treatment options (Lockwood and Schell, 1997; Lockwood et al. 2000a, 2002b).

Second, in Wyoming and perhaps several other western states, it appears that significantly smaller scale grasshopper management programs are taking place (often a few hundred or thousand hectares are treated, rather than tens of thousands of hectares), as APHIS continues to withdraw its support from treatment activities. These reductions in the scale of treatment also reflect a growing interest in the adoption of preventive efforts via so-called "hot spot" treatments that target localized, high density infestations with the potential to expand into more serious outbreaks (Huddleston et al. 2000, Lockwood et al. 2000b). Because such irruptive loci most often collapse on their own (Lockwood and Schell 1995), understanding the conditions in which these hot spots persist or expand is vital to improving the efficiency of this preventive strategy.

The current study is the first to examine the dynamics of rangeland grasshoppers over a large-scale region using a fine resolution (100 ha or 1 km²). With this approach, it was possible to provide both the fine resolution and the spatial coverage necessary for making sound pest management decisions under the conditions of contemporary range management. Although we do not know, in mechanistic terms, why particular areas are prone to persistent or frequent infestations (i.e., a high probability of an infested→infested transition or a high probability of an uninfested→infested transition), we have identified areas with these propensities. As such, it is possible to manage the pests in context of this knowledge and to begin to explore the ecological factors that may underlie these processes.

Acknowledgments

We thank H. Bauer, R. Gantenbein, and S. Schell for their assistance in the development and implementation of this work.

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Received for publication 7 October 2002; accepted 11 December 2003.