Oecologia (2007) 153:699–711
DOI 10.1007/s00442-007-0761-8

Grasshopper (Orthoptera: Acrididae) communities respond to fire, bison grazing and weather in North American tallgrass prairie: a long-term study

Jayne L. Jonas · Anthony Joern

Received: 1 November 2006 / Accepted: 30 April 2007 / Published online: 2 June 2007
© Springer-Verlag 2007

Abstract Because both intrinsic and extrinsic factors influence insect population dynamics, operating at a range of temporal and spatial scales, it is difficult to assess their contributions. Long-term studies are ideal for assessing the relative contributions of multiple factors to abundance and community dynamics. Using data spanning 25 years, we investigate the contributions of weather at annual and decadal scales, fire return interval, and grazing by bison to understand the dynamics of abundance and community composition in grasshopper assemblages from North American continental grassland. Each of these three primary drivers of grassland ecosystem dynamics affects grasshopper population and community dynamics. Negative feedbacks in abundances, as expected for regulated populations, were observed for all feeding guilds of grasshoppers. Abundance of grasshoppers did not vary in response to frequency of prescribed burns at the site. Among watersheds that varied with respect to controlled spring burns and grazing by bison, species composition of grasshopper assemblages responded significantly to both after 25 years. However, after more than 20 years of fire and grazing treatments, the number of years since the last fire was more important than the managed long-term fire frequency per se. Yearly shifts in species composition (1983–2005), examined using non-metric multidimensional scaling and fourth-corner analysis, were best explained by local weather events occurring early in grasshopper life cycles. Large-scale patterns were represented by the Palmer Drought Severity Index and the North Atlantic Oscillation (NAO). The NAO was significantly correlated with annual mean frequencies of grasshoppers, especially for forb- and mixed-feeding species. Primary grassland drivers—fire, grazing and weather—contributing both intrinsic and extrinsic influences modulate long-term fluctuations in grasshopper abundances and community taxonomic composition.

Keywords Fire frequency · Konza Prairie · Long-Term Ecological Research Program · Weather · Insect populations

Introduction

Abundances and community structure of insects vary in response to both intrinsic and extrinsic factors, and understanding the relative roles of each in population and community processes is a long-standing problem in ecology (Andrewartha and Birch 1954; Barbosa and Schultz 1987; Berryman 1999; Dempster and McLean 1998; Denno and McClure 1983; Price 1995; Royama 1992; Turchin 2003). Intrinsic influences from biotic interactions can act through multiple density- and frequency-dependent feedbacks that alter patterns of species abundances and coexistence (Brook and Bradshaw 2006; Dennis and Taper 1994). Extrinsic factors, as exemplified by weather conditions, act independently from the state of an insect population or community, but can affect insect population and community dynamics in a fashion reflecting their variable timing and

---

Communicated by Oswald Schmitz.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-007-0761-8) contains supplementary material, which is available to authorized users.

J. L. Jonas (✉) · A. Joern
Division of Biology, Kansas State University,
Manhattan, KS 66506, USA
e-mail: jjonas@ksu.edu

A. Joern
e-mail: ajoern@ksu.edu

extent (Dempster and McLean 1998). Effects of weather can sometimes act directly on insects. For example, body temperature influences metabolic processes, which in turn affects demographic responses and species interactions (Gutierrez 1996; Logan and Powell 2001; Logan et al. 2006; Stamp 1993). Weather can also act indirectly by altering the availability of resources (White 1993), affecting habitat structure, or influencing the strength of species interactions (Ovadia and Schmitz 2004). In grasslands, for example, differences in vegetation characteristics (biomass, structure, identity and diversity of plant species) and associated heterogeneity of these attributes strongly affect insect abundance, species richness and taxonomic composition (Evans 1988a; Joern 2004, 2005; Meyer et al. 2002; Rambo and Faeth 1999). Variation in the action of both intrinsic and extrinsic factors, whatever the underlying mechanisms, influences observed patterns of insect population and community dynamics (Ovadia and Schmitz 2004). Because natural variability can have such effects on insect population and community dynamics, long-term studies greatly assist our ability to tease apart the nature of multiple combinations of key factors over time, facilitating the synthesis of the roles of external and internal drivers (Likens 1988; Magnuson 1990).

Grasshoppers are dominant insect herbivores in grasslands, naturally exhibiting much temporal variability in abundance and species composition (Belovsky and Slade 2000; Branson et al. 2006; Joern and Gaines 1990; Lockwood 1993; Lockwood 1997; Meyer et al. 2002). Although multiple processes account for such responses (Joern and Gaines 1990), few studies assess the relative contribution of these effects over long periods of time. Both external factors driven largely by weather (Capinera 1987; Capinera and Horton 1989; Fielding and Brusven 1990) and density-dependent feedbacks from biotic interactions (Belovsky and Joern 1995; Belovsky and Slade 1995; Chase and Belovsky 1994; Kemp and Dennis 1992; Schmitz 1997; Schmitz and Sokol-Hessner 2002) may account for variation in grasshopper abundances and community composition. The boundaries of variability seen in grasshopper populations and communities over long periods remain to be fully delineated, and the mechanisms underlying the observed variability are largely unknown (Evans 1984; Evans 1988a).

In this study, we analyze long-term grasshopper abundance data from Kansas Flint Hills tallgrass prairie to assess how fire frequency, bison grazing and weather—major drivers of tallgrass prairie structure and function (Knapp et al. 1998)—modulate grasshopper abundances and species composition. Multiple studies at this site have shown the importance of these drivers to primary production, vegetation structure and plant community composition (Knapp et al. 1998), but few studies have investigated the degree to which the same drivers affect consumers over the long term (Evans 1984, 1988a, b; Kaufman et al. 1998).

Fire frequency and bison grazing clearly alter vegetation and plant communities with consequent influences on consumers in our study system (Collins et al. 1998; Knapp et al. 1999). We hypothesized that the effects of periodic fire on plant community dynamics would indirectly affect grasshoppers based on their feeding modes: grass-feeding species would be most abundant in annually burned sites, and forb-feeding species would be most common on sites with a 4-year fire return interval (FRI), a view supported by short-term studies (Evans 1984, 1988b; Joern 2004; Meyer et al. 2002). Because they have a larger pool of potential host plants from which to select, we did not expect mixed-feeding species to be affected by FRI. We also expected that long-term grassland management practices would significantly shift the taxonomic composition of grasshopper communities as habitat characteristics changed (Joern 2004, 2005). Species composition among watersheds, which was similar prior to the application of fire and grazing treatments, was expected to diverge significantly in response to more than 20 years of alternate fire and grazing management activities.

As the third major grassland driver, weather has much potential to structure grasshopper communities at short-term and decadal time scales. Weather in North American continental grasslands is notoriously variable (Greenland et al. 2005) and may contribute to grasshopper population and community responses (Capinera 1987; Fielding and Brusven 1990). For example, grasshopper abundances and population growth rates from other North American sites have been significantly correlated with precipitation and temperature (e.g., heating degree days) (Capinera and Horton 1989; Fielding and Brusven 1990; Gage et al. 1976; Johnson and Worobec 1988; Mukerji and Gage 1978; Mukerji and Randell 1975). At decadal scales, regional climate drivers such as the North Atlantic Oscillation (NAO), Pacific Decadal Oscillation (PDO), or El Niño–Southern Oscillation (ENSO) (Hallett et al. 2004; Hurell et al. 2003; Mysterud et al. 2003; Stenseth et al. 2002) may independently contribute to predicting temporal changes in species abundances and community structure. Although decadal weather patterns influence responses by other organisms (Lima et al. 1999, 2002; Merritt et al. 2001; Stenseth et al. 2002), the impact on continental North American grassland insects is unknown. Long-term trends suggest that decadal weather patterns in association with other factors could play a significant role in grasshopper population and community responses (Branson et al. 2006).

As grasshopper abundances and community species composition are expected to differ according to responses by key resources to fire frequency, bison grazing and weather (Belovsky and Joern 1995; Belovsky and Slade

1995; Branson 2005; Evans 1984, 1988a, b; Joern 2004, 2005; Joern and Behmer 1998), we address the following primary goals using long-term abundance data: (1) evaluate the effects of fire frequency on temporal changes in grasshopper abundance; (2) determine the likelihood of negative feedbacks characteristic of population regulation as contrasted with highly variable fluctuations driven by external factors; (3) investigate the importance of fire frequency and bison grazing on grasshopper community composition; and (4) contrast decadal-scale weather influences on grasshopper communities with those based on short-term annual weather events. Finally, conclusions from analyses of long-term data will be compared with those of short-term studies to get a sense of the proper scale for understanding grasshopper dynamics in this continental grassland. Population abundances of three feeding guilds (grass feeders, mixed feeders and forb feeders), which range from oligophagous to polyphagous accordingly, are treated separately in our analyses.

Materials and methods

Konza Prairie long-term grasshopper data

Data used in these analyses were collected at Konza Prairie Biological Station (KPBS), Manhattan, Kansas as part of the US National Science Foundation Long-Term Ecological Research (LTER) Program and archived on the Konza LTER website, www.konza.ksu.edu (dataset cgr022). A replicated watershed-level experimental design at KPBS allows one to test the long-term effects of ungulate grazing and periodic fire on the tallgrass prairie ecosystem (Knapp and Seastedt 1998). Prescribed fire treatments were implemented between 1972 and 1977, and a bison (*Bos bison*) herd was introduced to a portion of KPBS in stages between 1987 and 1992.

Grasshoppers were sampled at all transects twice a year, during the mid-summer, from 1982 to 2005 on six to eight ungrazed watersheds and from 2002 to 2005 on six watersheds grazed by bison. Grasshoppers were sampled from two permanent upland transects in each watershed used. The abundance of each grasshopper species collected in each of ten sets of sweep-net samples along each transect is reported; each dataset records abundances of 20 sweeps for a total of 200 sweeps per transect. Data from 1992 to 1995 were unavailable because samples were damaged prior to identification. Detailed information on the sampling protocol is described in the cgr022 metadata file available on the Konza Prairie LTER website.

Frequency of each grasshopper species was calculated from these data as the proportion of the ten sets in which a species was collected at a given transect; all frequency values were arcsine–square root transformed prior to statistical analysis. Due to the sensitivity of sweep-net sample counts to sampling technique (Evans et al. 1983) and the inability to translate these count data directly to density (individuals/m^2), frequency was used as the most appropriate measure of abundance for comparisons among watersheds and years.

Statistical analyses

An unbalanced hierarchical repeated measures ANOVA was used to test the effects of fire, time and the interaction between fire and time on the mean frequency of species within each grasshopper feeding guild. Grasshopper species were classified as belonging to one of three feeding guilds: grass feeding, forb feeding, or mixed feeding (Campbell et al. 1974; Mulkern et al. 1969). Watersheds within treatments (1-year FRI, watersheds 1D and SpB; 4-year FRI, watersheds 4B and 4F; 20-year FRI, watershed 20B) and transects within watersheds were treated as random effects and time was a repeated measures factor. These watersheds range in size from 16.4 to 54.5 ha, with transects within each watershed located on upland fingers separated by 250–500 m. Grasshopper data from watersheds containing bison were not collected until 2002, therefore grazed treatments were not included in this analysis because the time series was too short.

Species composition was analyzed using non-metric multi-dimensional scaling (NMDS) and fourth-corner statistics (Dray and Legendre, in review; Legendre et al. 1997). NMDS ordination was based on Euclidean distance in PC-ORD (version 4) with each solution based on 40 runs of the data with the final solution compared against 50 Monte Carlo runs (McCune and Grace 2002). While we were able to non-parametrically and visually assess changes in species composition in relation to environmental variables with NMDS, fourth-corner statistics allowed us to assess the effects of environmental variables on communities based on behavioral, morphological, or life history characteristics of the species. The fourth-corner package (http://www.biomserv.univ-lyon1.fr/~dray/) was used in the R program version 2.4.1 (RDCT 2006) to conduct multivariate and univariate fourth-corner analyses. Permutation models 2 and 4 were run for all datasets (Dray and Legendre, in review). Permutation model 2 tests the hypothesis that species composition is linked to environmental variables (H_1), while model 4 tests the hypothesis that species composition is linked to species traits (H_2). To test the hypothesis that environmental variables influence composition based on species traits (H_3) at $\alpha_3 = \alpha_1 * \alpha_2 = 0.05$, we used $\alpha_1 = \alpha_2 = 0.2236$ for both models 2 and 4 (Dray and Legendre, in review). The species traits used were feeding guild, life history, flight ability, and size (S1). For the species at KPBS, species characteristics were independent of one another (χ^2, $P > 0.1$) except for feeding guild and flight ability which were marginally significant ($P = 0.062$).

The mean frequency of species in each watershed was used to analyze community structure in 1982 and 2005 in response to watershed-scale management practices. The environmental matrix for these analyses included bison grazing and FRI as categorical variables and the number of years since fire (YSF) as a quantitative variable. Fire-related data for KPBS were obtained from the burn history dataset available on the Konza LTER website.

To assess changes in grasshopper communities over time as influenced by larger-scale weather patterns, the mean frequency of each species at KPBS was calculated for each year. The environmental matrix included 12 local precipitation and temperature factors chosen a priori as those most likely to affect grasshoppers during different developmental stages, a state-level index of drought conditions (Palmer Drought Severity Index, PDI), and three large-scale atmospheric phenomena which can affect interior continental North America: the Southern Oscillation Index (SOI), the PDO index, and the NAO index (Table 1). Local weather variables for KPBS were collected near the headquarters area at KPBS and assembled from the awe01 dataset available on the Konza LTER website. PDI values for Kansas were downloaded from the National Climate Data Center climate monitoring website (http://www.ncdc.noaa.gov/oa/climate/research/monitoring.html). SOI and NAO values were downloaded from the National Center for Atmospheric Research, Climate Analysis Section website (http://www.cgd.ucar.edu/cas/). PDO values were downloaded from the University of Washington Joint Institute for the Study of the Atmosphere and Oceans website (http://www.jisao.washington.edu/pdo/).

Table 1 Local, regional and large-scale variables used for analyses of weather effects on annual species composition of grasshopper communities at Konza Prairie Biological Station (KPBS)

Local weather events
Growing season (April–August)[a]
Total precipitation (mm)
Coefficient of variation of precipitation
Heating degree days (>20°C)
Coefficient of variation of daily maximum temperature
Fall (September$_{t-1}$–November$_{t-1}$)
Average daily maximum temperature (°C)
Total precipitation (mm)
Winter (December$_{t-1}$–March$_{t}$)
Average daily maximum temperature (°C)
Total precipitation (mm)
Regional weather index
Palmer Drought Index
Decadal atmospheric phenomena
Southern Oscillation Index
North Atlantic Oscillation Index
Pacific Decadal Oscillation Index

[a] Analysis included growing season$_t$ and growing season$_{t-1}$ weather events, where t is time (year)

Results

Long-term trends in grasshopper abundance

The grass-feeding species, particularly *Phoetaliotes nebrascensis* and *Orphulella speciosa*, were the most abundant grasshoppers at KPBS; forb-feeding species, especially *Melanoplus keeleri*, *Melanoplus scudderi*, and *Hypochlora alba*, were not as common (S1). Mixed-feeding species, including *Melanoplus femurrubrum* and *Melanoplus bivittatus*, were the among least common grasshoppers at KPBS in these samples. Grass-feeding species frequencies displayed the greatest variability across years [coefficient of variation (CV) = 4.5], while mixed-feeding species were the least variable (CV = 1); the CV of frequency = 3.3 for forb-feeding species. Despite the variability in abundances, plotting frequency$_t$ versus frequency$_{t+1}$, where t is time (year), shows that all three feeding guilds vary through time around the line with a slope equal to 1 (no change in population size between years) (Fig. 1).

Effects of fire on grasshopper feeding guilds

Fire alone did not significantly impact the frequencies of any of the three feeding guilds, while all three did vary with time over the 24 years of this dataset (Table 2, Fig. 2). Only the mixed-feeding guild had a significant interaction between FRI and year (Fig. 2c), with abundance on 4- and 20-year FRI watersheds typically more similar to one another than on the annually burned watersheds, particularly from 1992 to 2005.

Effects of fire and grazing on grasshopper species composition

Grasshoppers were first sampled in 1982 after approximately 10 years of fire management, but prior to the reintroduction of bison at KPBS. NMDS ordination did not detect structure in the species composition on the watersheds in 1982. Fourth-corner analysis showed a significant effect of YSF on composition based on the flight ability and size of the species (Table 3). Poor fliers and medium-sized species were positively associated and strong fliers and large species were negatively associated with increased YSF (S2).

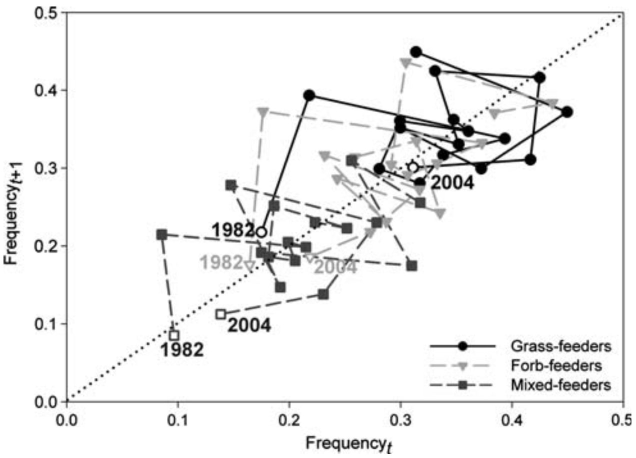

Fig. 1 Changes in annual mean frequencies of grass-feeding (*black circle*), forb-feeding (*black inverted triangle*), and mixed-feeding (*black square*) grasshopper species on ungrazed watersheds from 1982 to 2005 at Konza Prairie Biological Station (KPBS), Kansas with each year represented by one datapoint for each feeding guild. The *dotted line* represents no change in frequency from year (time *t*), to *t* + 1; points *above the line* indicate years of increasing, while those *below the line* represent years of decreasing frequency. For clarity, only the first (*t* = 1982) and most recent (*t* = 2004) data points for each feeding guild are labeled and appear as *open symbols*. There are no points for years *t* = 1991 up to and including *t* = 1995 because samples from 1992 to 1995 were damaged prior to identification

Table 2 Results of hierarchical repeated measures ANOVA tests on the effects of fire and time (year) on grass-feeding, forb-feeding, and mixed-feeding grasshopper species from 1982 to 2005 on watersheds at KPBS that were not grazed

Factor	*df*[a]	*df*[b]	*F*	*P*-values
Grass-feeding species				
Fire	2	2	4.04	0.1985
Year	19	133	6.54	<0.0001
Fire × Year	38	133	1.06	0.3953
Forb-feeding species				
Fire	2	2	1.06	0.4865
Year	19	133	8.96	<0.0001
Fire × Year	38	133	1.37	0.0978
Mixed-feeding species				
Fire	2	2	0.49	0.6699
Year	19	133	6.15	<0.0001
Fire × Year	38	133	1.50	0.0495

[a] Numerator *df*

[b] Denominator *df*

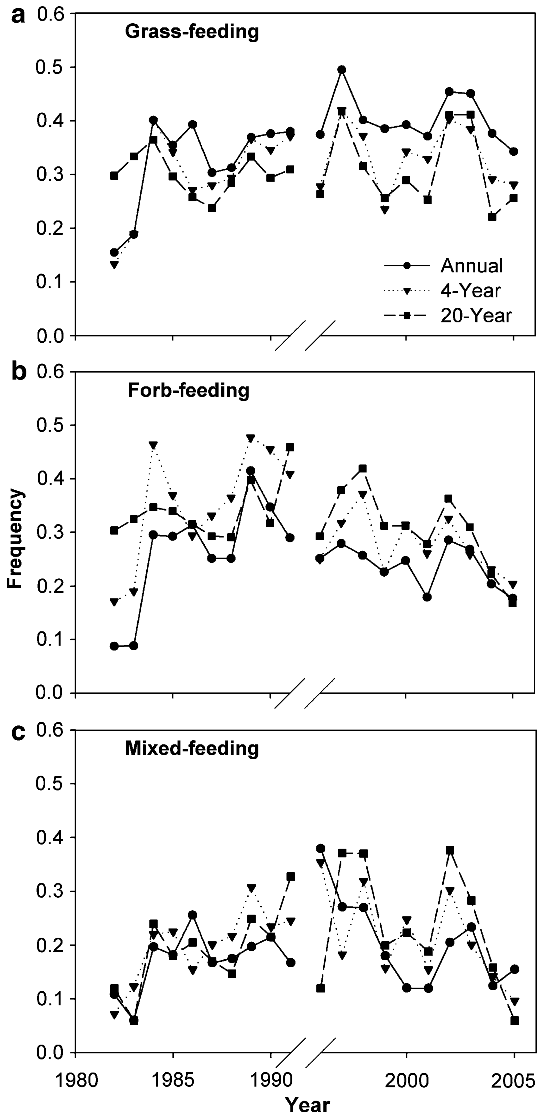

Fig. 2 Annual mean frequencies of **a** grass-feeding, **b** forb-feeding, and **c** mixed-feeding grasshopper species in watersheds with prescribed burns scheduled annually (*black circle*), every 4 years (*black inverted triangle*), and every 20 years (*black square*) at KPBS. Four-year transects were burned in 1983, 1987, 1991, 1998, 2000, 2003, and 20-year transects were only burned in 1991. There are no data for 1992 up to and including 1995 because samples from those years were damaged prior to identification

NMDS analysis of 2005 grasshopper species composition resulted in an ordination with a final stress of 3.03 and instability of 0.00001 after 91 iterations. The three-dimensional solution accounted for 98% of the variation in the data (axis 1, $r^2 = 0.35$; axis 2, $r^2 = 0.24$; axis 3, $r^2 = 0.39$). YSF was associated with axes 1 and 2 of the ordination, while there was no detectable relationship with FRI (Fig. 3a). There was also a significant effect of YSF on composition based on the flight ability of the species (Table 3) in fourth-corner analysis. Poor fliers were positively associated with increased YSF, while strong fliers were negatively affected by YSF (S2). NMDS ordination indicated that there was a large effect of bison grazing on grasshopper communities (Fig. 3), although fourth-corner results showed a strong effect of bison under model 2 only (Table 3).

Table 3 Multivariate fourth-corner analyses of the effects of land management in 1982 and 2005 and weather from 1982 to 2005 on grasshopper species composition based on species traits. Rejection of the null hypothesis (H_o: weather affects species composition based on the traits of the species) requires $P < 0.2236$ (results in *bold*) under both models 2 and 4 to maintain an overall $\alpha = 0.05$ (Dray and Legendre, in review). *GS* Growing season, *CV* coefficient of variation

Analysis	Environmental variable	Feeding guild			Flight ability			Size			Phenology		
		Eta^2	Model 2	Model 4	Eta^2	Model 2	Model 4	Eta^2	Model 2	Model 4	Eta^2	Model 2	Model 4
1982	Fire return interval	0.063	(0.760)	(0.359)	0.038	(0.742)	(0.429)	0.020	(0.846)	(0.725)	0.005	(0.903)	(0.941)
	Years since fire	0.125	(0.619)	(0.542)	**0.335**	**(0.191)**	**(0.184)**	**0.428**	**(0.012)**	**(0.082)**	0.044	(0.426)	(0.812)
2005	Fire return interval	0.200	(0.264)	(0.432)	0.318	(0.203)	(0.256)	0.164	(0.246)	(0.511)	0.125	(0.253)	(0.613)
	Years since fire	0.106	(0.507)	(0.612)	**0.402**	**(0.150)**	**(0.167)**	0.132	(0.328)	(0.542)	0.115	(0.280)	(0.591)
	Bison grazing	2.412	(0.001)	(0.226)	0.495	(0.105)	(0.456)	0.163	(0.524)	(0.913)	0.832	(0.017)	(0.624)
Weather	GS precipitation$_t$	0.002	(0.205)	(0.503)	**0.004**	**(0.130)**	**(0.083)**	0.003	(0.130)	(0.393)	0.001	(0.649)	(0.835)
	CV GS precipitation$_t$	**0.003**	**(0.080)**	**(0.079)**	**0.005**	**(0.108)**	**(0.009)**	0.001	(0.349)	(0.342)	**0.004**	**(0.049)**	**(0.080)**
	GS heating degree days$_t$	0.000	(0.758)	(0.602)	0.001	(0.612)	(0.209)	0.001	(0.329)	(0.127)	0.001	(0.392)	(0.188)
	CV GS temperature$_t$	0.000	(0.868)	(0.668)	0.000	(0.959)	(0.871)	0.000	(0.935)	(0.851)	0.000	(0.738)	(0.428)
	GS precipitation$_{t-1}$	**0.005**	**(0.037)**	**(0.066)**	**0.004**	**(0.151)**	**(0.030)**	0.000	(0.903)	(0.935)	0.001	(0.426)	(0.515)
	CV GS precipitation$_{t-1}$	0.001	(0.567)	(0.604)	0.003	(0.260)	(0.049)	**0.003**	**(0.102)**	**(0.083)**	**0.002**	**(0.124)**	**(0.175)**
	GS heating degree days$_{t-1}$	0.001	(0.532)	(0.454)	0.003	(0.254)	(0.028)	**0.003**	**(0.088)**	**(0.042)**	**0.003**	**(0.062)**	**(0.058)**
	CV GS temperature$_{t-1}$	0.000	(0.955)	(0.934)	0.000	(0.933)	(0.852)	0.000	(0.933)	(0.911)	0.001	(0.673)	(0.560)
	Fall precipitation	0.001	(0.600)	(0.457)	0.002	(0.329)	(0.019)	0.000	(0.890)	(0.849)	0.002	(0.276)	(0.143)
	Fall temperature	0.000	(0.840)	(0.842)	0.000	(0.843)	(0.709)	0.000	(0.705)	(0.722)	**0.004**	**(0.025)**	**(0.023)**
	Winter precipitation	0.001	(0.361)	(0.094)	0.002	(0.336)	(0.010)	0.000	(0.663)	(0.398)	0.001	(0.489)	(0.174)
	Winter temperature	0.002	(0.325)	(0.405)	**0.005**	**(0.109)**	**(0.016)**	0.001	(0.644)	(0.732)	0.001	(0.352)	(0.456)
	Palmer Drought Index	0.001	(0.557)	(0.525)	0.001	(0.442)	(0.136)	**0.003**	**(0.149)**	**(0.089)**	**0.004**	**(0.018)**	**(0.013)**
	Southern Oscillation Index	0.000	(0.935)	(0.844)	0.000	(0.890)	(0.663)	0.000	(0.955)	(0.891)	0.000	(0.862)	(0.655)
	North Atlantic Oscillation Index	**0.006**	**(0.011)**	**(0.053)**	**0.004**	**(0.161)**	**(0.058)**	0.001	(0.302)	(0.515)	0.002	(0.263)	(0.500)
	Pacific Decadal Oscillation Index	0.001	(0.563)	(0.403)	0.000	(0.685)	(0.357)	0.000	(0.988)	(0.985)	0.000	(0.693)	(0.563)

Eta^2 statistics with *P*-values (9,999 permutations) from models 2 and 4 *in parentheses* are given for all tests

Influence of weather on grasshopper communities

Ordination of annual mean frequencies of grasshopper species at KPBS had a final stress of 4.73 and instability of 0.00001 after 61 iterations (Fig. 4). The three-dimensional solution accounted for 96.6% of the variation in the data (axis 1, $r^2 = 0.40$; axis 2, $r^2 = 0.28$; axis 3, $r^2 = 0.29$). The ordination of annual mean frequencies revealed associations between grasshopper communities and growing season precipitation$_t$ and PDI along axis 2 and NAO along axis 3 (Fig. 4). Nine weather variables were significant in fourth-corner analysis (Table 3); of these, seven were local and two were larger-scale variables. Growing season precipitation at t and $t - 1$, CV of growing season precipitation$_t$, and winter temperature were associated with shifts in species composition related to feeding guilds and flight ability, as was NAO. The positive phase of the NAO was associated with increased abundance of forb feeders and poor fliers, while mixed feeders and strong fliers were more common during the negative phase of the NAO cycle (S3). Shifts in composition relating to size and phenology of the species were associated with growing season heating degree days$_{t-1}$, CV growing season precipitation at t and $t - 1$, fall temperature, and PDI (Table 3). Medium-bodied and late-hatching species were more common during years with high PDI values, while large-bodied and early-hatching species were more abundant during low PDI years (S3).

Discussion

Long-term records indicate that grasshopper population and community dynamics at Konza Prairie are highly responsive to both extrinsic and intrinsic factors. Extrinsic effects of weather influence grasshopper abundances and community composition. Bison grazing also affects community composition, although it is not yet known if feedbacks exist between grasshopper and bison grazing. There is also strong evidence for population regulation in the form of negative feedbacks for all feeding guilds (Fig. 1), an intrinsic response consistent with the action of density dependence (Brook and Bradshaw 2006; Royama 1992; Turchin

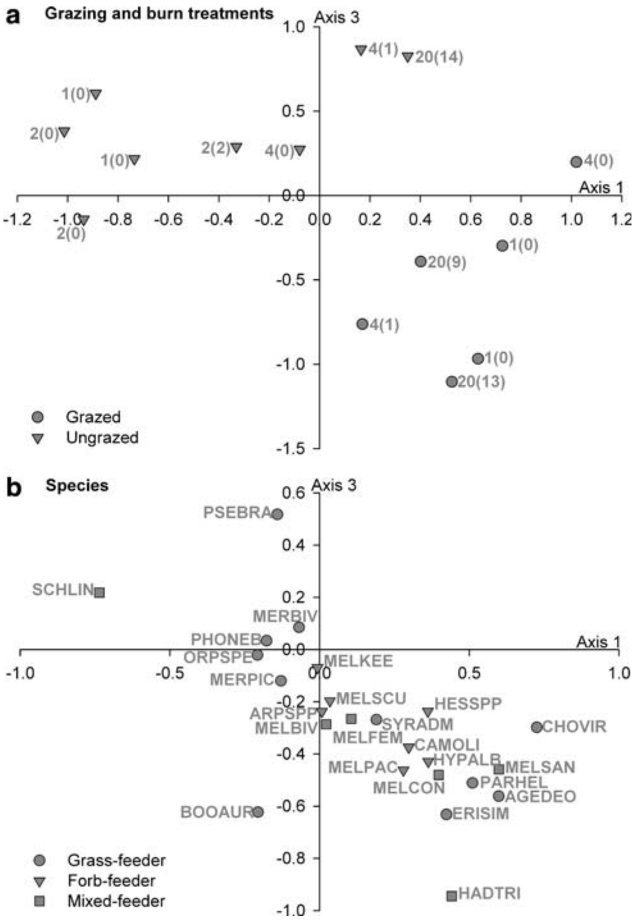

Fig. 3a, b Non-metric multidimensional scaling ordination of grasshopper species composition of watersheds sampled in 2005; axes 1 and 3 account for 74% of the variation in the data. **a** Each point represents the species composition of the grasshopper community in either grazed (*black circle*) or ungrazed (*black triangle*) watersheds. The fire return interval of each watershed (1, 4, or 20 years) is indicated next to the point corresponding to that watershed, with the number of years since the last fire indicated *in parentheses*. **b** Each point represents a species with symbols denoting the feeding guild (grass-feeding *black circle*, forb-feeding *black inverted triangle*, and mixed-feeding *black square*) to which each species belongs. See Electronic Supplementary Material for species' abbreviations

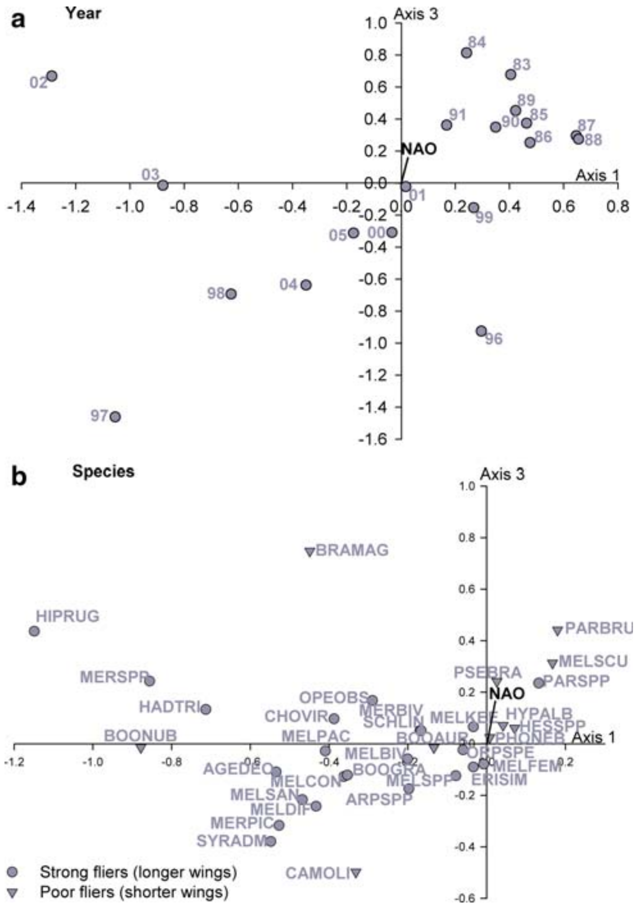

Fig. 4a, b Non-metric multidimensional scaling ordination of annual mean grasshopper species composition at KPBS from 1982 to 1991 and 1996–2005; axes 1 and 3 account for 69% of the variation in the data. **a** Each point represents the species composition at KPBS in a given year with the last two digits of the year indicated next to each point. There are no data for 1992 up to and including 1995 because samples from those years were damaged prior to identification. **b** Each point represents a species. Symbols denote strong fliers (longer wings, *black circle*) or weak fliers (short wings, *black inverted triangle*). See Electronic Supplementary Material for species' abbreviations. Community structure was correlated with the North Atlantic Oscillation index (*NAO*)

2003). These feedback patterns were also found for most of the individual species (data not shown) such that the pattern seen at the feeding guild level generally reflected that of the species within each guild. Our results extend the findings of Evans (1988a) and Collins (2000) who concluded that grasshopper communities at KPBS are regulated through biotic feedbacks. The general trend toward stability identified by Evans (1988a) using only 5 years of grasshopper data was supported by our analysis spanning 25 years of community data. The action of extrinsic drivers in this system interact with density-dependent processes, probably by altering resource availability or the ability of grasshopper consumers to utilize resources (Ovadia and Schmitz 2004). Understanding grasshopper responses in North American continental grasslands requires that we consider multiple influences that operate at a range of spatial and temporal scales.

We could not conduct a formal continuous time series analysis because of an unfortunate 4-year gap in the data (1992–1995). We dealt with this break in the data by comparing pre- and post-gap periods when assessing effects on community composition, or we relied on the time series segments that were available to assess regulation (Fig. 1). The gap in the record did prevent us from using some nonlinear analyses to evaluate population and community trends (Turchin 2003), but we do not feel that our general conclusions are compromised.

Effects of fire and bison on grasshopper feeding guilds

Fire had only a minor effect on fluctuations in grasshopper frequencies. After more than 25 years of fire management at KPBS, the mixed-feeding guild was the only one to show an interaction between fire frequency and year. Like fire management in most temperate North American grasslands, the majority of prescribed burning at KPBS is currently conducted during the spring. Although we did not detect strong or consistent effects of fire on grasshopper abundance, it is possible that fire during other seasons may lead to more pronounced responses. For example, late summer fires are more likely to negatively affect grasshopper abundance because it is a time when many grasshopper species mate and lay eggs (Dempster 1963; Hewitt 1985).

Spring fires have significant effects on habitat characteristics. Although they may accelerate grasshopper phenology by removing litter and warming the upper soil layers (Evans 1984; Meyer et al. 2002), we expected that spring fires would have a stronger effect on grasshoppers due to changes in plant community composition and structure. Annual burning shifts plant communities toward warm-season C_4 grass dominance and decreases in cool-season C_3 grass and forb abundance (Collins 2000; Hartnett and Fay 1998). Although the warm-season grasses do not decrease, infrequent fires are typically associated with increased abundances of cool-season grasses, forbs and woody species than found on frequently burned sites (Hartnett and Fay 1998).

Grass-feeding species were somewhat but not significantly more common in annually burned than infrequently burned sites (Fig. 2a), as expected given the positive effects of annual spring fires on warm-season grasses. Two previous, short-term studies conducted at KPBS using different measures of abundance found grass-feeding species were most common on annually burned watersheds (Evans 1988b; Meyer et al. 2002); a third short-term study showed a similar but not significant trend for increased densities on annually burned watersheds (Joern 2004). Four of the 7 years in which the short-term studies were conducted are coincident with those used in the long-term dataset here and also showed grass-feeding species to be more abundant on annually burned watersheds. However, grass-feeding species were found to be equally or more abundant on watersheds experiencing less frequent fire in several other years. Cool-season grasses, which are generally more common on infrequently burned watersheds, also tend to account for a large portion of the diets of many grass-feeding species (Mulkern et al. 1969), although most grass feeders also readily consume warm-season grasses (Barbehenn et al. 2004; Heidorn and Joern 1984; Pinder and Jackson 1988; Pinder and Kroh 1987). These unexpected patterns not only demonstrate the utility of long-term data for capturing nuances in temporal dynamics, but also our incomplete understanding of the mechanisms driving this ubiquitous group of consumers. This is of particular importance given that multiple short-term studies conducted at the same study site did not fully capture the relationship between fire and annual variability in grass-feeding species.

Although Evans (1984, 1988b) found that forb-feeding species were most common on watersheds with a 4-year FRI in short-term studies, our long-term results show that forb-feeder frequencies were not significantly affected by FRI. Forb-feeding species tended to be most abundant and diverse on the infrequently burned sites (Collins and Steinauer 1998), however, and it is possible that they were tracking changes in the composition or structure of plant communities. Since at least 1996, forb-feeder frequencies have shown an overall decline. Unfortunately, it appears that this decline began sometime between 1992 and 1995, the years for which grasshopper data are unavailable. Long-term shifts in plant communities (Collins 2000), especially in infrequently burned watersheds, may be negatively affecting forb-feeding species through decreased availability of suitable host plants or habitat structure.

Little is known about the ecology of mixed-feeding grasshopper species. Because they tend to occur in low abundances in native grasslands and typically prefer forbs (Campbell et al. 1974; Mulkern et al. 1969), mixed-feeding species have often been pooled with forb-feeding species (Evans 1984, 1988a, b). We did not expect mixed-feeding species to be affected by spring fire given our view that spring fire would most likely affect grasshoppers indirectly by altering plant community composition and that mixed feeders have a wider diet breadth (both grasses and forbs). The mixed-feeding guild, however, was the only one to show a significant interaction between FRI and year (Fig. 2c) although the pattern remains unclear.

The results of our analyses on the effects of both fire and bison grazing on species composition provide further support for our conclusion that spring fire alone is not a primary driver of grasshopper dynamics. The first set of grasshopper samples at KPBS, collected in 1982, were taken 5–10 years following initiation of fire treatments, but prior to the reintroduction of bison. Although NMDS ordination found no differences in communities at the sites sampled in 1982, fourth-corner analysis showed an effect of YSF associated with the flight ability of species in both 1982 and 2005. These results strongly suggest that species with well-developed flight abilities responded to recently burned areas more quickly than those that are poor fliers.

After more than 25 years of fire and nearly 15 years of bison grazing, however, the contributions and interactions of these ecosystem drivers on grasshopper community dynamics appear to be complex. The ordination identified bison grazing as having a strong influence on species assemblages in 2005 (Fig. 3a), with a general increase in the abundance of forb- and mixed-feeding species on grazed sites (S2). Ungrazed sites were characterized by two dominant tallgrass prairie grasshoppers, *P. nebrascensis* and *O. speciosa*, both of which are grass-feeding species (Fig. 3b). Grazed watersheds were more likely to contain a diversity of species from all three feeding guilds, including several species which are generally uncommon (frequency <0.10), including *Pardalophora haldemanii*, *Chortophaga viridifasciata*, and *Melanoplus sanguinipes* (Fig. 3b). In fourth-corner analyses, there were significant effects of bison grazing under model 2 only, which indicates that the relationship between grazing and grasshopper species composition is complex and we were not able to capture in our analysis the dynamics of the relationship with the actual species traits.

Grazed watersheds are characteristically more complex floristically than ungrazed sites with regard to plant communities (Collins and Smith 2006; Towne et al. 2005). Not only does grazing influence the identity of plant species present (including increased plant species diversity and increased cover of forbs) (Collins et al. 1998), but it also leads to greater variability in the horizontal and vertical structure of vegetation (Joern 2005; Towne et al. 2005). Areas of dense vegetation potentially provide refuge from predators (Schmitz 2006), while areas of bare ground facilitate thermoregulation and oviposition activities (Dempster 1963; Hewitt 1985; Joern 2005). In assessing the relationship between grasshopper species richness and several plant community characteristics, Joern (2005) found species richness to be most strongly associated with variability in plant canopy height, accounting for 45% of the variation in grasshopper species richness. Plant species richness showed a significant effect on grasshopper species richness (Joern 2005).

Both NMDS ordination and fourth-corner analysis also revealed a relationship between species composition and fire along axis 2. However, it was the number of years since the last fire, rather than overall fire frequency, that influenced species composition; communities on watersheds burned less than a year prior to sampling (YSF ≤ 1) were different than those that had not been burned for many years (YSF ≥ 9), regardless of grazing treatment. A similar result was reported by Joern (2004) with regard to overall grasshopper density. There were no significant effects of FRI on grasshopper density, while there was a significant correlation between density and the time since fire with the highest densities occurring in sites with YSF ≤ 1. Bison tend to selectively graze recently burned areas (YSF < 2) (Biondini et al. 1999). At KPBS the grazing treatment is not implemented on individually fenced watersheds; there is one large grazing enclosure encompassing 12 watersheds that receive the full suite of fire treatments. Therefore, long-term unburned watersheds in grazed areas may not be heavily influenced by bison during the growing season and essentially function as ungrazed sites from the perspective of grasshoppers.

These data also suggest that complex interactions between these two groups of consumers may operate. Based on consumption estimates and feeding characteristics (Meyer et al. 2002; Pfadt 1994), grasshoppers may potentially remove up to 20% annual net primary production (ANPP) in grasslands. Considering that current stocking rates of bison at KPBS result in the removal of 20–25% ANPP, it is reasonable to expect that interactions between invertebrate and ungulate grazers are important. For instance, bison feed primarily on grasses and tend to select warm-season over cool-season grasses disproportionate to their abundance during the growing season (Plumb and Dodd 1993). Most of the grasshoppers strongly associated with ungrazed watersheds were the grass-feeding species that also tend to consume warm-season over cool-season grass species (Mulkern et al. 1969) (Fig. 3b).

Influence of weather on grasshopper communities

Of the three primary grassland ecosystem drivers, climate-associated weather patterns are the most unpredictable. Unlike fire and grazing treatments at KPBS, which are managed at the watershed level, weather patterns operate at a larger spatial scale and are similar for all of the watersheds in any given year. Growing season precipitation was the only local weather factor correlated with species composition in NMDS ordination (axis 2) and also the only one in which fourth-corner analysis revealed shifts in composition to be associated with feeding guilds (Table 3, S3). Precipitation and temperature factors are the abiotic factors most often associated with grasshopper population dynamics (Capinera and Horton 1989; Dempster 1963; Gage and Mukerji 1977; Hewitt 1985). Sensitivity of grasshopper populations to precipitation is likely associated with trade-offs between host plant quality, quantity, and susceptibility to predators, pathogens and parasites (Belovsky and Slade 1995; Dempster 1963; Hewitt 1985; Joern and Behmer 1998; Joern and Gaines 1990; Joern and Mole 2005). Temperature can affect insects both directly by influencing developmental rates (Mukerji et al. 1977; Mukerji and Randell 1975), and indirectly through changes in plant community structure and host quality (Richardson et al. 2002). We included PDI in our analysis as a measure of the combined effects of precipitation and temperature on grasshopper communities, although the index integrates these factors over a larger spatial extent than just KPBS. We found that PDI was important in both NMDS and fourth-corner analyses. Fourth-corner analysis shows that PDI reflects the combined effects of the four local weather variables associated shifts in grasshopper species composition based on size and phenology (Table 3). The weak positive relationship between NMDS axis 2 and both PDI and growing season precipitation, and the negative effect of PDI on early hatching species (S3), suggests that interactions between temperature and precipitation may be most important in influencing development of grasshoppers during embryonic and early nymphal stages.

There was also a strong signal between the decadal level influence of NAO and grasshopper species composition (Fig. 4, Table 3). To our knowledge, this is the first study to document a link between the NAO and terrestrial insects in North America, although it has been correlated with the population dynamics of spittlebugs in Finland (Halkka et al. 2006) and other taxa, including plants, amphibians, birds, and mammals, in both North America and Europe (Mysterud et al. 2003). A distinct shift in grasshopper communities between the positive and negative phases of the NAO is clear (Figs. 4, 5). Although NAO may affect precipitation patterns, its primary effect on continental North America appears to be associated with increased wintertime temperatures (Hurell et al. 2003). The combined effects of three precipitation-related variables and winter temperatures on grasshopper species composition based on feeding guild and flight ability appear to be integrated by the NAO index (Table 3). The NMDS ordination shows that following winters in which NAO was in its positive phase, many of the common grasshopper species, including *Hypochlora alba*, *Hesperotettix* spp., *Phoetaliotes nebrascensis*, *M. scudderi*, *M. keeleri*, and *Pseudopomala brachyptera*, were most abundant (Fig. 4b). Less common grasshopper species, including *Campylacantha olivacea*, *Melanoplus sanguinipes*, *Mermiria picta*, *Melanoplus packardii*, and *Boopedon gracile*, appeared to be more abundant during the negative phase of the NAO cycle. These shifts in species composition were associated with negative responses by mixed-feeding species and positive responses by species that are poor fliers (S3). Detailed studies are required to uncover mechanisms for these responses.

The strong and consistent relationship between weather and shifts in composition related to flight ability of the species (Table 3, S3) was unexpected because most individuals are collected as nymphs with undeveloped wings. Previous growing season and winter weather, as well as NAO (which mainly affects winter weather) accounted for three of the five factors associated with grasshopper flight ability, which may indicate lagged effects of parental dispersal ability on grasshopper responses to weather.

Conclusion

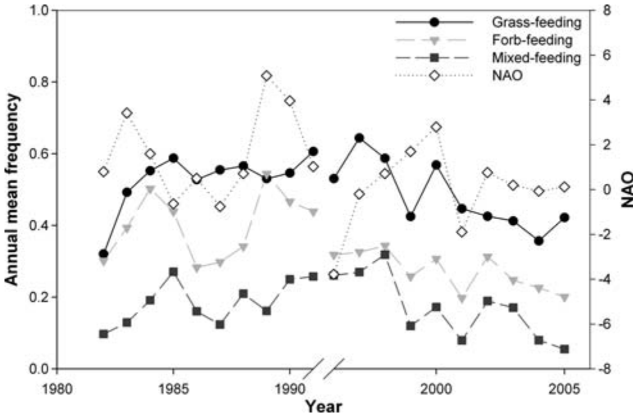

Fig. 5 Annual mean frequencies of grass-feeding (*black circle*), forb-feeding (*black inverted triangle*), and mixed-feeding (*black square*) grasshopper species from 1982 to 2005 overlaid with the NAO (*open diamond*) index values for the same years. Points represent mean grasshopper frequencies on ungrazed watersheds during each year at KPBS

Each of the three primary grassland ecosystem drivers influences grasshopper population and community dynamics. Despite significant effects of fire on plant communities, fire alone does not account for fluctuations of grasshopper abundances or species composition. However, the interaction between the length of time after fire and bison grazing significantly impacts grasshopper populations and communities at KPBS although the functional mechanisms underlying these responses are not well understood. Understanding the potential interactions between these two groups of grazers with otherwise vastly different habits will require future research. The relationship between NAO and grasshopper composition provides insights into a potential driver for periodic changes in overall grasshopper abundances at decadal time scales (Branson et al. 2006), and suggests ways in which the roles of annual precipitation and temperature patterns can be expanded to a longer time scale. Finally, comparing our results based on a 25-year LTER dataset to those of short-term studies illustrates the contributions of long-term studies to new insights as well as the reasonably high success of shorter studies to understanding mechanisms underlying grasshopper population dynamics. Although underlying mechanisms remain unclear, we revealed grasshopper community responses to both grassland management and weather patterns that were not captured by short-term studies.

Our results indicate that the population and community dynamics of grasshoppers, a major group of grassland consumers, are driven by complex interactions including both intrinsic and extrinsic factors. Negative feedbacks among all three feeding guilds suggested that density dependence is likely to play an important role in the regulation of these species. Factors extrinsic to grasshopper populations operating at different spatial and temporal scales also strongly influenced community-level dynamics. Grazing by bison had a much larger impact on these insect herbivores than did spring fire, and large-scale weather patterns were also shown to be important drivers of community dynamics. Additionally, this is one of the first studies to document that NAO, operating at decadal scales, can influence terrestrial insect consumers. Given this result, it will be particularly interesting to explore the role of atmospheric oscillations (e.g., NAO, ENSO, PDO) on long-term consumer dynamics in different ecosystems. As research on ecological responses to climate change progresses, understanding the influence of these large-scale oscillations on consumers may lead to important insights into ecosystem dynamics.

Acknowledgements Konza Prairie is partly owned by the Nature Conservancy and managed by the Division of Biology at Kansas State University (KSU) though the KPBS. Many individuals contributed to the development and maintenance of the Konza Prairie grasshopper database over the 25 years of its existence, especially E. W. Evans, B. Danner, and A. Kuhl. We also are indebted to A. Kula and G. Towne for early discussions of the Konza LTER database. S. Dray (University of Lyon, France) and J. Higgins (KSU Department of Statistics) assisted with statistical analyses. S. Dray, J. Apple, S. Parsons and two anonymous reviewers provided helpful comments on previous drafts of the manuscript. Research was supported by the NSF LTER Program at KPBS, NSF DEB0456522, and NSF EPS0553722 (Ecological Forecasting). This is publication 07–247-J from the Kansas Agricultural Experiment Station. This research was conducted in accordance with the laws of Riley County, Kansas.

References

Andrewartha HG, Birch LC (1954) The distribution and abundance of animals. University of Chicago Press, Chicago, Ill.

Barbehenn RV, Chen Z, Karowe DN, Spickard A (2004) C_3 grasses have higher nutritional quality than C_4 grasses under ambient and elevated atmospheric CO_2. Global Change Biol 10:1565–1575

Barbosa P, Schultz JC (eds) (1987) Insect outbreaks. Academic Press, New York

Belovsky GE, Joern A (1995) Regulation of grassland grasshoppers: differing dominant mechanisms in time and space. In: Cappucino N, Price PW (eds) Novel approaches for the study of population dynamics: examples from insect herbivores. Academic Press, New York, pp 359–386

Belovsky GE, Slade JB (1995) Dynamics of two Montana grasshopper populations: relationships among weather, food abundance and intraspecific competition. Oecologia 101:383–396

Belovsky GE, Slade JB (2000) Insect herbivory accelerates nutrient cycling and increases plant production. Proc Natl Acad Sci USA 97:14412–14417

Berryman AA (1999) Principles of population dynamics. Thornes, Cheltenham

Biondini ME, Steuter AA, Hamilton RG (1999) Bison use of fire-managed remnant prairies. J Range Manage 52:454–461

Branson DH (2005) Effects of fire on grasshopper assemblages in a northern mixed-grass prairie. Environ Entomol 34:1109–1113

Branson DH, Joern A, Sword GA (2006) Sustainable management of insect herbivores in grassland ecosystems: new perspectives in grasshopper control. BioScience 56:743–755

Brook BW, Bradshaw CJA (2006) Strength of evidence for density dependence in abundance time series of 1198 species. Ecology 87:1445–1451

Campbell JB, Arnett WH, Lambley JD, Jantz OK, Knutson H (1974) Grasshoppers (Acrididae) of the Flint Hills native tallgrass prairie in Kansas. In: Station AR (ed) vol. 19. Kansas State University, Manhattan, Kans.

Capinera JC (1987) Population ecology of rangeland grasshoppers. In: Capinera JC (ed) Integrated pest management on rangeland: a shortgrass perspective. Westview Press, Boulder, Colo., pp 162–182

Capinera JC, Horton DR (1989) Geographic variation in effects of weather on grasshopper infestation. Environ Entomol 18:8–14

Chase J, Belovsky GE (1994) Experimental evidence for the included niche. Am Nat 143:514–527

Collins SL (2000) Disturbance frequency and community stability in native tallgrass prairie. Am Nat 155:311–325

Collins SL, Knapp AK, Briggs JM, Blair JM, Steinauer EM (1998) Modulation of diversity by grazing and mowing in native tallgrass prairie. Science 280:745–747

Collins SL, Smith MD (2006) Scale-dependent interaction of fire and grazing on community heterogeneity in tallgrass prairie. Ecology 87:2058–2067

Collins SL, Steinauer EM (1998) Disturbance, diversity, and species interactions in tallgrass prairie. In: Knapp AK, Briggs JM, Hartnett DC, Collins SL (eds) Grassland dynamics: long-term ecological research in tallgrass prairie. Oxford University Press, New York, pp 140–156

Dempster JP (1963) The population dynamics of grasshoppers and locusts. Biol Rev 38:490–529

Dempster JP, McLean IFG (eds) (1998) Insect populations: in theory and practice. Kluwer, Dordrecht

Dennis B, Taper M (1994) Density dependence in time series observations of natural populations: estimation and testing. Ecol Monogr 64:205–224

Denno RF, McClure MS (eds) (1983) Variable plants and herbivores in natural and managed systems. Academic Press, New York

Dray S, Legendre P (in review) Linking species traits to environmental characteristics: the fourth-corner problem revisted. Ecology

Evans EW (1984) Fire as a natural disturbance to grasshopper assemblages of tallgrass prairie. Oikos 43:9–16

Evans EW (1988a) Community dynamics of prairie grasshoppers subjected to periodic fire: predictable trajectories or random walks in time? Oikos 52:283–292

Evans EW (1988b) Grasshopper (Insecta:Orthoptera:Acrididae) assemblages of tallgrass prairie: influences of fire frequency, topography and vegetation. Can J Zool 66:1495–1501

Evans EW, Rogers RA, Opfermann DJ (1983) Sampling grasshoppers (Orthoptera: Acridide) on burned and unburned tallgrass prairie: night trapping vs. sweeping. Environ Entomol 12:1449–1454

Fielding DJ, Brusven MA (1990) Historical analysis of grasshopper (Orthoptera: Acrididae) population responses to climate in southern Idaho, 1950–1980. Environ Entomol 19:1786–1791

Gage SH, Mukerji MK (1977) A perspective of grasshopper population distribution in Saskatchewan and interrelationship with weather. Environ Entomol 6:469–479

Gage SH, Mukerji MK, Randell RI (1976) A predictive model for seasonal occurence of three grasshopper species in Saskatchewan (Orthoptera: Acrididiae). Can Entomol 108:245–253

Greenland D, Goodin D, Smith RC (eds) (2005) Climate variability and ecosystem response at LTER sites. Oxford University Press, New York

Gutierrez AP (1996) Applied population ecology. Wiley, New York

Halkka A, Halkka L, Halkka O, Roukka K, Pokki J (2006) Lagged effects of North Atlantic Oscillation on spittlebug *Philaenus spumarius* (Homoptera) abundance and survival. Global Change Biol 12:2250–2262

Hallett TB, Coulson EA, Clutton-Brock TH, Pemberton JM, Grenfell B (2004) Why large-scale climate indices seem to predict ecological processes better than local weather. Nature 430:71–75

Hartnett DC, Fay PA (1998) Plant populations: patterns and processes. In: Knapp AK, Briggs JM, Hartnett DC, Collins SL (eds) Grassland dynamics: long-term ecological research in tallgrass prairie. Oxford University Press, New York, pp 81–100

Heidorn TJ, Joern A (1984) Differential herbivory on C_3 versus C_4 grasses by the grasshopper *Ageneotettix deorum* (Orthoptera: Acrididae). Oecologia 65:19–25

Hewitt GB (1985) Review of factors affecting fecundity, oviposition, and egg survival of grasshoppers in North America. In. U.S. Department of Agriculture, Agricultural Research Service, p 35

Hurell JW, Kushnir Y, Otterson G, Visbeck M (2003) An overview of the North Atlantic Oscillation. In: The North Atlantic Oscillation: climatic significance and environmental impact. Geophysical Monograph 134. American Geophysical Union, pp 1–35

Joern A (2004) Variation in grasshopper (Acrididae) densities in response to fire frequency and bison grazing in tallgrass prairie. Environ Entomol 33:1617–1625

Joern A (2005) Disturbance by fire frequency and bison grazing modulate grasshoper assemblages in tallgrass prairie. Ecology 86:861–873

Joern A, Behmer ST (1998) Impact of diet quality on demographic attributes in adult grasshoppers and the nitrogen limitation hypothesis. Ecol Entomol 23:174–184

Joern A, Gaines SB (1990) Population dynamics and regulation in grasshoppers. In: Chapman RF, Joern A (eds) Biology of grasshoppers. Wiley, New York, pp 415–482

Joern A, Mole S (2005) The plant stress hypothesis and variable responses by blue grama grass (*Bouteloua gracilis*) to water, mineral nitrogen, and insect herbivory. J Chem Ecol 31:2069–2090

Johnson DL, Worobec A (1988) Spatial and temporal computer analysis of insects and weather: grasshoppers and rainfall in Alberta. Mem Entomol Soc Can 146:33–46

Kaufman DW, Kaufman GA, Fay PA, Zimmerman JL, Evans EW (1998) Animal populations and communities. In: Knapp AK, Briggs JM, Hartnett DC, Collins SL (eds) Grassland dynamics. Oxford University Press, New York, pp 113–139

Kemp WP, Dennis B (1992) Density dependence in rangeland grasshoppers. Oecologia 96:1–8

Knapp AK, Blair JM, Briggs JM, Collins SL, Hartnett DC, Johnson LC, Towne EG (1999) he keystone role of bison in North American tallgrass prairie. BioScience 49:39–50

Knapp AK, Briggs JM, Hartnett DC, Collins SL (eds) (1998) Grassland dynamics: long-term ecological research in tallgrass prairie. Oxford University Press, New York

Knapp AK, Seastedt TR (1998) Introduction: grasslands, Konza Prairie, and long-term ecological research. In: Knapp AK, Briggs JM, Hartnett DC, Collins SL (eds) Grassland dynamics: long-term ecological research in tallgrass prairie. Oxford University Press, New York, pp 3–15

Legendre P, Galzin R, Harmelin-Vivien ML (1997) Relating behavior to habitat: solutions to the fourth-corner problem. Ecology 78:547–562

Likens GE (ed) (1988) Long-term studies in ecology: approaches and alternatives. Springer, New York

Lima M, Keymeyer JE, Jaksic FM (1999) ENSO-driven rainfall variability and delayed density dependence cause rodent outbreaks in western South America: linking demography and population dynamics. Am Nat 153:476–491

Lima M, Merritt JF, Bozinovic F (2002) Numerical fluctuations in the northern short-tailed shrew: evidence of nonlinear feedback signatures on population dynamics and demography. J Anim Ecol 71:159–172

Lockwood JA (1993) Environmental issues involved in biological control of rangeland grasshoppers (Orthopter: Acrdididae) with exotic agents. Environ Entomol 22:503–518

Lockwood JA (1997) Grasshopper population dynamics: a prairie perspective. In: Gangwere SK, Muralirangan MC, Muralirangan M (eds) The bionomics of grasshoppers, katydids and their kin. CAB International, New York, pp 103–128

Logan JA, Powell JA (2001) Ghost forests, global warming, and the mountain pine beetle. Am Entomol 47:160–172

Logan JD, Wolesensky W, Joern A (2006) Temperature-dependent phenology and predation in arthropod systems. Ecol Model 196:471–482

Magnuson JJ (1990) Long term ecological research and the invisible present. BioScience 40:495–501

McCune B, Grace JB (2002) Analysis of ecological communities. MJM Software Design, Gleneden Beach

Merritt JF, Lima M, Bozinivic F (2001) Seasonal regulation in fluctuating small mammal populations: feedback structure and climate. Oikos 505–514

Meyer CK, Whiles MR, Charleton RE (2002) Life history, secondary production, and ecosystem significance of acridid grasshoppers in annually burned and unburned tallgrass prairie. Am Entomol 48:40–49

Mukerji MK, Gage SH (1978) A model for estimating hatch and mortality of grasshopper egg populations based on soil moisture and heat. Ann Entomol Soc Am 71:183–190

Mukerji MK, Gage SH, Randell RL (1977) Influence of embryonic development and heat on population trend of three grasshopper species (Orthoptera: Acrididae) in Saskatchewan. Can Entomol 109:229–236

Mukerji MK, Randell RL (1975) Estimation of embryonic development in populations of *Melanoplus sanguinipes* (Fabr.) (Orthoptera: Acrididae) in the fall. Acrida 4:9–18

Mulkern GB, Pruess KP, Knutson H, Hagen AF, Campbell JB, Lambley JD (1969) Food habits and preferences of grassland grasshoppers of the north central Great Plains. Agricultural Experiment Station, North Dakota State University, Fargo, p 32

Mysterud A, Stenseth NC, Yoccoz NG, Ottersen G, Langvatn R (2003) The response of terrestrial ecosystems to climate variability associated with the North Atlantic Oscillation. In: Hurrell JW, Kushnir Y, Ottersen G, Visbeck M (eds) The North Atlantic oscillation: climatic significance and environmental impact, vol 134. American Geophysical Union, Washington, D.C., pp 235–262

Ovadia O, Schmitz OJ (2004) Weather variation and trophic interaction strength: sorting the signal from the noise. Oecologia 140:398–406

Pfadt RE (1994) Field Guide to Common Western Grasshoppers. University of Wyoming, Agricultural Experiment Station

Pinder JE III, Jackson PR (1988) Plant photosynthetic pathways and grazing by phytophagous Orthopterans. Am Midl Nat 120:201–211

Pinder JE III, Kroh GC (1987) Insect herbivory and photosynthetic pathways in old-field ecosystems. Ecology 68:254–259

Plumb GE, Dodd JL (1993) Foraging ecology of bison and cattle on a mixed prairie: implications for natural area management. Ecol Appl 3:631 - 643

Price PWaMDH (1995) Novelty and synthesis in the development of population dynamics. In: Price NCaPW (ed) Population dynamics: new approaches and synthesis. Academic Press, San Diego, Calif., pp 389–412

Rambo JL, Faeth SH (1999) Effect of vertebrate grazing on plant and insect community structure. Conserv Biol 13:1047–1054

[RDCT] R Development Core Team (2006) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org

Richardson SJ, Press MC, Parsons AN, Hartley SE (2002) How do nutrients and warming impact on plant communities and their insect herbivores? A 9-year study from a sub-Arctic heath. J Ecol 90:544–556

Royama T (1992) Analytical population dynamics. Chapman & Hall, London

Schmitz OJ (1997) Press perturbations and the predictability of ecological interaction in a food web. Ecology 78:55–69

Schmitz OJ (2006) Predators have large effects on ecosystem properties by changing plant diversity, not plant biomass. Ecology 87:1432–1437

Schmitz OJ, Sokol-Hessner L (2002) Linearity in the aggregate effects of multiple predators in a food web. Ecol Lett 5:168–172

Stamp NE (1993) A temperate region view of the interaction of temperature, food quality and predators in caterpillar foraging. In: Stamp NE, Casey TM (eds) Caterpillars: ecological and evolutionary constraints on foraging. Chapman & Hall, New York

Stenseth NC, Mysterud A, Ottersen G, Hurrell JW, Chan KS, Lima M (2002) Ecological effects of climate fluctuations. Science 297:1292–1296

Towne EG, Hartnett DC, Cochran RC (2005) Vegetation trends in tallgrass prairie from bison and cattle grazing. Ecol Appl 15:1550–1559

Turchin P (2003) Complex population dynamics: a theoretical/empirical synthesis. Princeton University Press, Princeton, N.J.

White TCR (1993) The inadequate environment: nitrogen and the abundance of animals. Springer, Berlin