

LONG-TERM VARIATION IN ABUNDANCE OF ELLIOT'S SHORT-TAILED SHREW (*BLARINA HYLOPHAGA*) IN TALLGRASS PRAIRIE

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Elliot's short-tailed shrews (*Blarina hylophaga*) were studied in tallgrass prairie at Konza Prairie Biological Station, Kansas. Based on sampling of 14 permanent traplines from autumn 1981 to spring 1999, relative abundance was high in autumn ($\bar{X} = 2.5 \pm 0.4 SE$ shrews/trapline) but very low in spring (<0.1 shrews/trapline). Interannual variability in abundance in autumn was large with a range 0.1–7.0 shrews/trapline. Relative abundance of shrews in autumn was correlated positively with precipitation, soil moisture, and depth of plant litter and correlated negatively with proportion of area burned and maximum temperature. Two variables, precipitation, and amount of litter, accounted for 87% of variation in abundance of shrews in autumn. Ambient moisture and a well-developed litter layer that ameliorates microclimatic extremes appear to be the most important factors influencing abundance of shrews in tallgrass prairie.

Key words: abiotic factors, *Blarina hylophaga*, Elliot's short-tailed shrew, Kansas, long-term study, population dynamics, tallgrass prairie

Ecological studies of variation in abundances of small mammals are typically 1–5 years in duration. Although short-term studies may document variability in abundances, they often cannot examine possible factors influencing interannual patterns of variation in abundance. Long-term studies (≥ 10 years in duration) offer an opportunity to describe temporal variability and to assess possible influences of environmental factors on abundances by using correlative approaches. Long-term studies are also more likely to include extreme highs and lows of abundances as well as extreme environmental conditions such as droughts.

Variation in abundance of small mammals often has been explained by examining relationships between variation in numbers of individuals and variation in abiotic and biotic factors such as precipitation and

food availability (Churchfield et al. 1995; Getz 1994; Heske et al. 1997; Sheftel 1989; Smith et al. 1974). These studies detected numerous relationships between abundance of small mammals and variation in abiotic and biotic variables, but relationships generally have been weak. Lack of strong patterns may be because of numerous factors, including multiple limiting factors (Kaufman et al. 1998), population regulation by internal factors, adaptations to extreme abiotic conditions, or relatively invariant abiotic conditions. For example, it is extremely difficult to elucidate abiotic factors that influence abundance when no extreme weather conditions occur to alter survival and reproduction.

Shrews are especially susceptible to extremes of temperature or precipitation because of their small size, high metabolic rates (Pearson 1947; Taylor 1998), large demand for water (Chew 1951), and lack of

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fat reserves (Churchfield 1990). Owing to these physiological characteristics, abundance of shrews should be influenced negatively by low precipitation and high temperature (i.e., drought conditions). For shrews in central United States, weather conditions should have especially important influences on abundance because this region is characterized by large variation in weather patterns which include frequent very hot, dry summers (Borchert 1950).

We examined the relationship between abundance of Elliot's short-tailed shrews (*Blarina hylophaga*) in tallgrass prairie and the magnitude of abiotic and biotic factors over an 18-year period. We generated a series of predictions regarding influences of precipitation, temperature, soil moisture, amount of area burned, annual net primary production (ANPP), and amount of plant litter on abundance of short-tailed shrews. We expected shrew abundance to be affected positively by increased precipitation and soil moisture because of availability of free water for drinking and access to and abundance of invertebrate prey (Chew 1951; Churchfield 1990; Genoways and Choate 1998). Shrews were expected to respond negatively to both extremely low temperatures in winter and extremely high temperatures in summer because of metabolic stress caused by these conditions (Churchfield 1990). A moderate to well-developed litter layer should provide suitable foraging sites and act to moderate extremes of temperature and low humidity (Choate and Fleharty 1975; Churchfield 1990; Kaufman et al. 1989; Knapp et al. 1998; Merritt 1986, 1995). We expected shrews to respond positively to increasing amounts of litter and negatively to burning because fire removes litter. Increases in ANPP lead to increased canopy cover, which ameliorates microclimates (Waterhouse 1955), and likely favors increased abundances of shrews.

MATERIALS AND METHODS

Study area.—Our study was conducted at the Konza Prairie Biological Station, a 3,487-ha tall-

grass prairie located in Riley and Geary counties in Flint Hills region of northeastern Kansas (39°05'N, 96°35'W—Marzolf 1988). More than 90% of Konza Prairie is native tallgrass prairie and is dominated by C₄ grasses such as big bluestem (*Andropogon gerardii*), Indian grass (*Sorghastrum nutans*), and switch grass (*Panicum virgatum*—Freeman 1998). All sampling for this study was conducted in unplowed, native tallgrass prairie.

Konza Prairie is divided into >50 experimental fire-grazer treatments. Treatments consist of a combination of controlled burning (periodicities ranging from 1 to 20 years) and grazing (grazed by bison, *Bos bison*, and ungrazed) regimes. Sampling of shrews was conducted in 4 ungrazed treatments with prescribed fire periodicities of 20, 4, and 1 years between fires, and in 3 grazed treatments with prescribed fire periodicities of 20, 4, and 1 years between fires. Treatments were large with an average area of 67.8 ha (range: 16.4–133.4 ha). Long-term prescribed burning regime was initiated in 1972, whereas bison were not introduced into grazed study sites until 1992 after small mammals were sampled in spring.

Trapping.—Small mammals were sampled in autumn and spring, from autumn 1981 to spring 1999 in two permanent sites in each of the 7 treatments. Trapping in spring was initiated in March. Trapping in autumn began in October for 16 years and in early November for 2 years. In each of the 14 sites, trapping was conducted for 4 consecutive nights in each season. Small mammals at each of the sites were sampled using a 20-station trapline with stations spaced 15 m apart. Two large Sherman live traps (7.6 by 8.9 by 22.9 cm), baited with peanut butter and rolled oats, were placed at each station. We visited the traps each morning to record information and release captured animals. We collected data on sex, reproductive status, and body mass of each captured animal. We marked shrews by shaving a patch of hair so we could later identify previously captured individuals. Relative abundance (number of unique individuals/trapline) of shrews was used in all analyses. We conformed to guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998) to capture, handle, and take care of mammals.

Independent variables.—Precipitation and monthly temperatures for the 18-year period

were obtained from a weather station located in Manhattan, Kansas, 11.5 km north of the study site. We defined season-long precipitation as total precipitation from January through September of each year. Season-long maximum and minimum temperatures were defined as average maximum and minimum monthly temperatures for January through September of each year. Precipitation during summer was total precipitation for July through September. Maximum and minimum temperatures during summer were average maximum and minimum monthly temperatures for July through September of each year. These 2 periods were selected to examine temporal scale at which these variables might be most important for shrews. We assume that abundance of shrews would respond to general conditions during growing season (i.e., wet, dry, hot, or cold conditions). We also assumed that conditions during January–September would index conditions experienced by shrews before autumn sampling. January was selected as the start date for abiotic factors because conditions in late winter and early spring may influence factors (e.g., soil moisture or prey abundance) to which shrews respond. Summer period was selected to index extreme conditions (e.g., hot and dry conditions) during mid to late growing season, which may be a critical period for shrews.

Records maintained as a part of the Konza Prairie Long-Term Ecological Research Program provided data for soil moisture from 1983 to 1997, fire history from 1981 to 1998, amount of litter from 1984 to 1996, and ANPP from 1984 to 1996. Soil moisture, litter, and ANPP were measured by other investigators in a number of treatments each year. Averages of these values were used as indices of soil moisture, ANPP, and litter in our study sites. Soil moisture 25 cm below the surface was measured by using a neutron probe. Data were obtained every 2 weeks from 1 April through 1 November of each year. From November through March, monthly readings were taken when temperature was greater than -6°C and no snow cover was present (Briggs and Knapp 1995). We used soil moisture values for both season-long (January–September) and summer precipitations (July–September) to examine the relationship between abundance of shrews and soil moisture. ANPP and litter were measured by quadrat sampling (twenty 0.1 m^2 quadrats/treatment) in either August or September (estimated time of peak aboveground

biomass) of each year. We calculated proportion of study area burned each year (total area = 763 ha) to examine influence of fire on short-tailed shrews. The influence of grazers on short-tailed shrews was not examined because grazing intensity was light, and a low proportion (13%) of all stations showed signs of being grazed by bison during 1993–1998.

Statistical analysis.—We examined relationships between abundance of short-tailed shrews in autumn and precipitation, temperature, soil moisture, fire history, ANPP, and litter by conducting a series of regression analyses. Relative abundances of short-tailed shrews in spring were extremely low (<0.1 shrew/trapline) and, therefore, were not examined. One-tailed tests were used because direction of response of shrews, either positive or negative, to variation in abiotic and biotic factors was predicted a priori. We used condition–number method (Philippi 1993) to examine colinearity of independent variables before conducting multiple regression analyses. We found that colinearity was not a problem. All multiple regressions were conducted by using stepwise selection. Summary values for abundance and various abiotic and biotic factors are reported as $\bar{X} \pm 1\text{ SE}$. The magnitude of temporal variability was assessed by using percentage coefficient of variation (CV) for autumn abundance of shrews and abiotic and biotic environmental variables. Temporal variability in abundance was also characterized by using the standard deviation (SD) of logarithm (base 10) of relative abundance (Ostfeld 1988).

RESULTS

Relative abundance of shrews averaged 2.5 ± 0.4 shrews/trapline during 18 autumns from 1981 through 1998. Interannual variability of relative abundance in autumn was high. A peak of 7.0 shrews/trapline occurred in autumn 1993 and a low of 0.1 shrews/trapline was found just 1 year later (Fig. 1a). The CV for interannual variability in relative abundance during autumn was 78% and SD was 0.51. Abundances of shrews in spring averaged <0.1 shrews/trapline with a range of 0.0–0.2 shrews/trapline over 18 years; abundance of shrews in spring will not be considered further.

Environmental conditions.—Season-long

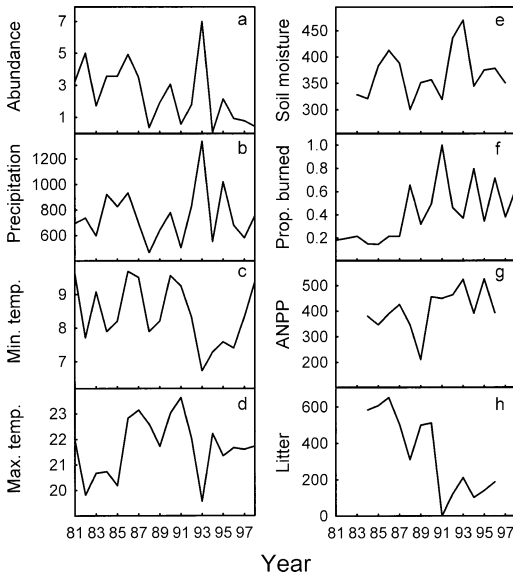


FIG. 1.—Interannual variability in abundance of Elliot's short-tailed shrews (*Blarina hylophaga*) and magnitude of environmental variables on Konza Prairie: a) mean abundance of shrews (number of individual shrews/trapline) in autumn; b) total precipitation (mm; January–September); c) mean minimum temperature (°C; January–September); d) mean maximum temperature (°C; January–September); e) mean soil moisture (kg/m³; January–September); f) proportion of the study area burned; g) mean above-ground net primary production (g/m²); and h) mean plant litter (g/m²).

precipitation averaged 755 ± 49 mm and varied 2.8-fold during 18 years ($CV = 28\%$, range: 468–1,339 mm; Fig. 1b). The greatest precipitation occurred in 1993 and the least in 1988. Precipitation in summer averaged 308 ± 34 mm and varied 7.4-fold during 18 years ($CV = 47\%$, range: 95–700 mm). Amounts of season-long precipitation and precipitation during summer were correlated positively ($r = 0.75$, $d.f. = 16$, $P < 0.001$). During 18 years, average season-long minimum temperature was $8.4 \pm 0.2^\circ\text{C}$ ($CV = 11\%$, range: 6.7–9.7°C; Fig. 1c) and average season-long maximum temperature was $21.7 \pm 0.3^\circ\text{C}$ ($CV = 5\%$, range: 19.6–23.6°C; Fig. 1d). Average maximum temperature in summer was $30.8 \pm$

0.3°C ($CV = 4\%$, range: 29.2–33.9°C). Season-long maximum temperatures and maximum temperatures in summer were not correlated ($r = 0.32$, $d.f. = 16$, $P > 0.05$). However, season-long precipitation and season-long maximum temperature were correlated negatively ($r = -0.68$, $d.f. = 16$, $P = 0.01$) as were summer values ($r = -0.60$, $d.f. = 16$, $P < 0.01$).

During 1983–1997, average season-long soil moisture was 408 ± 8 kg/m³ ($CV = 8\%$, range: 351–470 kg/m³; Fig. 1e). Soil moisture during summers of 1983–1997 averaged 368 ± 12 kg/m³ ($CV = 12\%$, range: 300–470 kg/m³). Amounts of season-long soil moisture and soil moisture in summer were highly correlated ($r = 0.90$, $d.f. = 13$, $P = 0.0001$). Season-long soil moisture was correlated positively with season-long precipitation ($r = 0.77$, $d.f. = 13$, $P < 0.01$).

The proportion of area burned varied depending on the amount of area burned by prescribed fires and occurrence of wildfires. On an average, 42% of our study area was burned each year; range was 14.5–100% ($CV = 61\%$; Fig. 1f). An increase in amount of area burned has occurred through time owing to changes in Konza Prairie management plan and a wildfire in 1991. Before 1988, <22% of site was burned each year (range: 14.5–21.4%), whereas 32% was the least burned each year during 1988–1998 (range: 32.0–100%).

Annual net primary production averaged 408 ± 23 g/m²; a high of 526 g/m² was found in 1995 and a low of 210 g/m² occurred in 1989 ($CV = 20\%$; Fig. 1g). Amount of litter varied greatly from the average of 341 ± 63 g/m² ($CV = 66\%$, range: 0–652 g/m²; Fig. 1h). In 1991, litter was not present because prescribed fires and a large wildfire removed vegetation and litter from all trapping sites.

Abundance versus environmental conditions.—Abundance of shrews in autumn was correlated positively to both season-long precipitation and precipitation during summer (season-long: $R^2 = 0.59$, $d.f. = 16$,

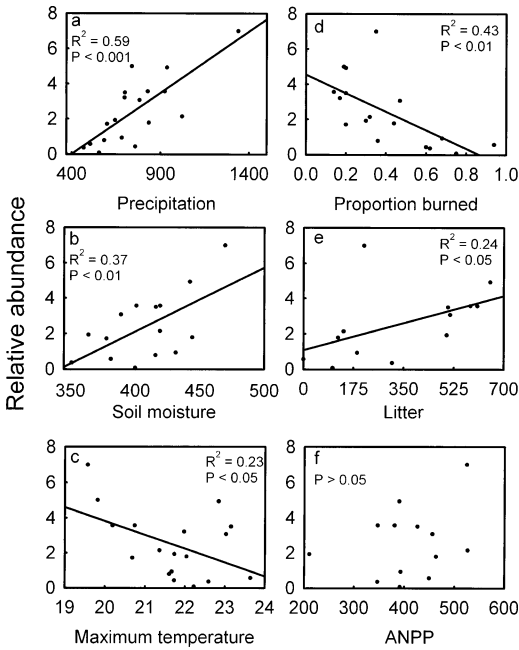


FIG. 2.—Relationship between relative abundance (number of individual shrews/trapline) of Elliot's short-tailed shrew (*Blarina hylophaga*) in autumn and a) total precipitation (mm; January–September); b) mean soil moisture (kg/m³; January–September); c) mean maximum temperature (°C; January–September); d) proportion of area burned; e) mean litter (g/m²); and f) mean above-ground annual net primary production (ANPP; g/m²).

$P < 0.001$; Fig. 2a; summer: $R^2 = 0.32$, $d.f. = 16$, $P < 0.01$; Fig. 3a). Abundance in autumn was also related positively to season-long soil moisture and soil moisture during summer (season-long: $R^2 = 0.37$, $d.f. = 13$, $P < 0.01$; Fig. 2b; summer: $R^2 = 0.47$, $d.f. = 13$, $P < 0.01$; Fig. 3b). The greatest abundance of shrews was recorded in autumn 1993 (7.0 shrews/trapline), the same year that highest precipitation and soil moisture were recorded. To examine the influence that the year 1993 had on the relationship between abundance of shrews and precipitation, we examined relationship for all possible consecutive 10-year periods. Significant positive relationships were found between abundance of shrews and precipitation for all 10-year periods (Table

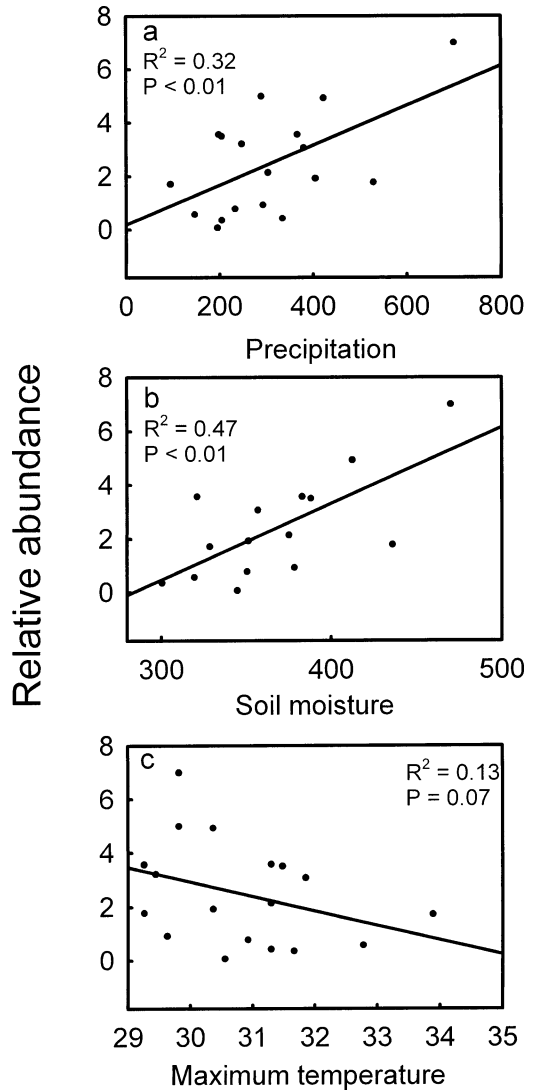


FIG. 3.—Relationship between relative abundance (number of individual shrews/trapline) of Elliot's short-tailed shrew (*Blarina hylophaga*) in autumn and a) precipitation (mm); b) mean soil moisture (kg/m³); and c) mean maximum temperature (°C) in summer (July–September).

1). Additionally, positive relationship between autumn abundance of shrews and precipitation was significant with the year 1993 removed from analysis ($R^2 = 0.38$, $d.f. = 15$, $P < 0.01$).

Abundance of shrews was correlated negatively with average season-long maxi-

TABLE 1.—Relationships between relative abundance (number of individuals/trapline) of Elliot's short-tailed shrews (*Blarina hylophaga*) and precipitation (January–September) for all possible consecutive 10-year periods on Konza Prairie, Kansas.

Years	R^2	F	P	$d.f.$
1981–1990	0.66	15.835	0.0041	8
1982–1991	0.74	22.654	0.0014	8
1983–1992	0.74	23.319	0.0013	8
1984–1993	0.86	50.714	0.0001	8
1985–1994	0.86	51.017	0.0001	8
1986–1995	0.74	22.567	0.0014	8
1987–1996	0.74	22.840	0.0014	8
1988–1997	0.83	37.733	0.0003	8
1989–1998	0.77	27.338	0.0008	8

imum temperature, but negative relationship between abundance of shrews and average maximum temperature in summer was weak (season-long: $R^2 = 0.23$, $d.f. = 16$, $P < 0.05$; Fig. 2c; summer: $R^2 = 0.13$, $d.f. = 16$, $P = 0.07$; Fig. 3c). Average minimum temperature had no detectable influence on abundance of shrews ($P = 0.74$).

Abundance of shrews in autumn was related negatively to proportion of area burned ($R^2 = 0.43$, $d.f. = 16$, $P < 0.01$; Fig. 2d) and positively to depth of plant litter ($R^2 = 0.24$, $d.f. = 11$, $P < 0.05$; Fig. 2e). These relationships were even stronger when data from extremely wet year, 1993, were removed from analyses (proportion of area burned: $R^2 = 0.61$, $d.f. = 15$, $P < 0.001$; depth of plant litter: $R^2 = 0.70$, $d.f. = 10$, $P < 0.001$). ANPP had no significant effect on abundance of shrews (current year: $P = 0.10$; Fig. 2f; previous year: $P = 0.14$).

The relationship of autumn abundance of shrews to environmental factors (season-long precipitation, soil moisture and maximum temperature, amount of litter, proportion of area burned, and ANPP) was examined further by using a multiple regression with stepwise selection. This analysis produced a model that contained only precipitation and amount of litter ($R^2 = 0.87$, $d.f. = 11$, $P < 0.01$). The same procedure

was used to examine relationships between abundance of shrews in autumn and amount of litter, proportion of area burned, ANPP, and summer measurements of precipitation, soil moisture, and maximum temperature. In contrast, this analysis produced a model that contained precipitation during summer but also included proportion of area burned and maximum temperature during summer ($R^2 = 0.77$, $d.f. = 11$, $P < 0.01$), but did not include amount of litter, ANPP, or soil moisture.

DISCUSSION

Variation in abundance of short-tailed shrews during autumn on Konza Prairie was high: a difference of >80-fold existed between the lowest and highest abundances recorded during the 18 years of our study. However, statistical magnitude of variation in abundance was moderate relative to other species of small mammals captured on Konza Prairie during 1981–1994 (Kaufman et al. 1998).

Our analyses indicated that abundance of short-tailed shrews in tallgrass prairie was strongly and positively related to precipitation. Consistent with this pattern, peak abundances of northern short-tailed shrews (*B. brevicauda*) were correlated positively with precipitation during January–August in bluegrass habitats in Illinois (Getz 1994). These shrews also failed to reach peak densities and declined to very low levels in July–August (typical time of peak abundance) during a year of record low precipitation. Similarly, abundances of southern short-tailed shrew (*B. carolinensis*) were correlated positively with precipitation during summer in South Carolina (Smith et al. 1974). Further, proportion of shrews included in diet of barn owls (*Tyto alba*) increased with increasing precipitation (Clark and Bunck 1991). This relationship was especially evident in northern and western areas of North America.

Abundance of Elliot's short-tailed shrews was also positively related to soil moisture. Because short-tailed shrews are semifosso-

rial, they may be responsive to sudden changes in soil moisture (Barbehenn 1958). In agreement with our observation, northern short-tailed shrews were more abundant in mesic than in xeric environments (Churchfield 1990; Getz 1961).

Relatively moist environmental conditions likely influence shrew abundance in 2 ways: availability of prey and reduced water intake. Xeric conditions reduce densities of invertebrates (Baker 1998; Churchfield 1990; Curry 1998), the major prey of short-tailed shrews (Bee et al. 1981; George et al. 1986). Densities of invertebrates are known to influence distribution and abundance of other species of shrews (Butterfield et al. 1981; Ivanter and Makarov 1994; Kaikusalo and Hanski 1985). Additionally, dry upper soil conditions force some invertebrates (e.g., earthworms) deeper into the soil (Gerard 1967) making them physically less available to shrews (Churchfield 1982). Increased availability of primary food resources in upper levels of soil and on soil surface accompanying high precipitation was associated with increased breeding success of common shrews (*Sorex araneus*—Pankakoski 1985). Further, shrews likely experience direct mortality caused by low water intake owing to a lack of either free water for drinking, or wet prey, or both. Northern short-tailed shrews experienced a 32% decrease in survival during a drought in Illinois (Getz 1994), consistent with the effect of reduced environmental moisture on abundance.

Abundance of short-tailed shrews was correlated negatively with average maximum temperature during January through September (Fig. 2c). This relationship likely was because of high temperatures encountered during warm months of year. Nine coolest years (summer temperature: $29.8 \pm 0.2^\circ\text{C}$) had an average abundance of 3.2 ± 0.7 shrews/trapline, whereas 9 warmest years (summer temperature: $31.8 \pm 0.3^\circ\text{C}$) had an average abundance of only 1.8 ± 0.4 shrews/trapline. Shrews of temperate zone have difficulty dealing with

high temperatures because of their high metabolic rate and small size (Churchfield 1990). Upper lethal ambient temperature for northern short-tailed shrews is 35°C . At this temperature, evaporative water loss cannot reverse hyperthermia (George et al. 1986). In northern short-tailed shrews, the rate of water loss increased 350% as temperature increased from 18 to 28°C (Chew 1951).

During 1981–1998, abundances of shrews in autumn were correlated negatively with proportion of area burned. This pattern was consistent with earlier studies of short-tailed shrews conducted in tallgrass prairie (Clark and Kaufman 1990; Clark et al. 1995; Kaufman et al. 1989; McMillan et al. 1995). Negative response of abundance of short-tailed shrew to fire likely resulted from removal of litter layer (Choate and Fleharty 1975; Kaufman et al. 1989). The positive relationship observed between abundance of shrews and amount of litter during 1984–1996 supported this assertion.

Precipitation during time period of January–September and amount of litter explained nearly 90% of variation in abundance of short-tailed shrews on Konza Prairie. Precipitation apparently was the driving force that caused annual variation in abundance of these shrews, both directly and indirectly. Litter was the 2nd most important factor and increased the percentage of variation explained in abundance of shrews by 28%.

Relationships between abundance of short-tailed shrews and soil moisture and precipitation were similar, whether we included summer or season-long values in our analyses. Season-long measurements of precipitation yielded a model that explained considerably more about the variation in abundance of shrews (59%) than did precipitation in summer (32%). We expected precipitation in summer to influence shrew populations in autumn through survival and possibly reproduction during late summer more than overall wetness of year. However, higher level of variation explained by

season-long precipitation may reflect positive influence of an overall wet year on the size of breeding populations in spring, and on the increase in growing-season population and, thereby, the abundance of shrews in autumn. In contrast to precipitation, soil moisture in summer explained more about the variation in abundance of shrews (47%) than did season-long values (37%). This difference may be of little importance. However, magnitude of soil moisture in summer may have a greater influence on shrews during autumn than average season-long soil moisture. During hot, dry summers, moisture loss from soils is mitigated by a layer of plant litter (Knapp et al. 1998). As a result, soil moisture in summer may reflect the amount of precipitation that occurred, as well as the amount of litter that was present at the different sampling sites. Abundance of shrews was related negatively to season-long values for average maximum temperature, but the pattern was less clear for maximum temperature in summer.

Our data suggest that abundance of shrews in autumn largely is a result of how much of the wetness of the year (reflected in precipitation and soil moisture) is available in the environment in relatively xeric locations such as the Great Plains. Litter, because of its ability to mitigate loss of soil moisture, likely is the 2nd most important factor after precipitation that influences abundance of shrews. As a result, factors that influence development or maintenance of a litter layer, such as fire and grazing, also influence moisture conditions experienced by shrews. Further, litter conditions are expected to have greater influence on shrews in years of low precipitation because of buffering effect on loss of soil water. As a result, autumn or peak abundance of Elliot's short-tailed shrews in landscapes of the Great Plains should reflect wetness of year or growing season (i.e., precipitation). Local occurrence or abundance of shrews should reflect suitable conditions, at least in relatively dry years that largely are influenced by amount of plant litter. How-

ever, the spatial scale at which litter conditions are important or influence abundance of shrews remains unknown.

Our findings suggest that climate change, especially increased temperature and decreased precipitation, may have a dramatic impact on shrews in the Great Plains. These changes in climate likely will lead to changes in abundance and distribution of shrews throughout the plains. Based on patterns observed in our data, we suggest that shrews may function as an indicator species of effects of climate change on mammalian fauna of the Great Plains. Additionally, information described herein may prove useful in attempts to model the effects of climate change on abundance and distribution of shrews in the plains.

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