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COMMUNITY STRUCTURE OF *ELEODES* BEETLES  
(COLEOPTERA: TENEBRIONIDAE) IN THE SHORTGRASS STEPPE:  
SCALE-DEPENDENT USES OF HETEROGENEITY

Nancy E. McIntyre<sup>1</sup>

ABSTRACT.—Patterns in the community structure of darkling beetle (9 *Eleodes* spp., Coleoptera: Tenebrionidae) assemblages in the shortgrass steppe of north central Colorado were monitored by live pitfall trapping for 4 summers. There were significant correlations among weather (temperature and precipitation), species richness, and number of individuals per species captured; effects from weather conditions also displayed 1-month and 1-yr delayed effects. Population densities of 2 eleodid species were monitored by mark-recapture methods. Densities of these species varied relatively little among years and sites, although density was correlated with temperature and precipitation. Abiotic influences on both density and richness differed between 2 macrohabitat types (shortgrass upland, shrub floodplain). The 4 largest species were most abundant in the floodplain, whereas the smallest species was most common in the upland. Affinities with cactus and shrub microhabitats (and an avoidance of bare soil) were evident, although a preference for shaded microhabitats was not detected. These results do not conform well to previous explanations of why darkling beetle assemblages are spatially and temporally heterogeneous, which primarily focused on predation and thermoregulation. Therefore, an alternative mechanism concerning scale-dependent uses of heterogeneity and mobility is proposed to account for eleodid community patterns.

*Key words:* Coleoptera, community diversity, darkling beetle, *Eleodes*, population density, precipitation, richness, shortgrass steppe, temperature, Tenebrionidae.

The shortgrass steppe of western United States is one of the least studied ecosystems in North America. Disparagingly called “the Great American Desert” by early explorers and homesteaders because of its apparent monotony and harsh climate, this biome is in fact a spatio-temporally dynamic ecosystem (Knopf and Samson 1997). The long-standing and persistent misperception of the shortgrass steppe as homogeneous may stem from the coarse perceptual scale of observers. Many of its other occupants, however, may more readily perceive the heterogeneous nature of the shortgrass steppe, owing to differences in body size and mobility. In this paper I examine evidence for scale-dependent uses of heterogeneity in various species of darkling beetle (*Eleodes* spp., Coleoptera: Tenebrionidae) of the northern shortgrass steppe of Colorado.

Darkling beetles (eleodids) are among the most abundant macroarthropods of the shortgrass steppe, with as many as 9 species occurring in narrow sympatry (Bell 1971, Kumar et al. 1976). They live most of their lives as soil-inhabiting larvae that feed on roots and detritus.

Upon eclosion, they may live for 2 yr as adults (Allsopp 1980). Adults are detritivorous, feeding mainly on grasses and forbs, and there is a high degree of dietary overlap among species (Yount 1971, Doyen and Tschinkel 1974, Slobodchikoff 1978, Rogers et al. 1988). Although flightless, the beetles are highly mobile and wander over great distances (Kramm and Kramm 1972, Calkins and Kirk 1973, Doyen and Tschinkel 1974). Individuals are active when temperatures permit. On the southern shortgrass steppe and in desert ecosystems, activity is usually crepuscular and nocturnal from spring through autumn; on the northern shortgrass and mixed-grass prairies and shrub-steppe, darkling beetles are mostly diurnal from late spring through early autumn, with peaks of activity in early morning and early evening (Kramm and Kramm 1972, Wise 1981b, Kenagy and Stevenson 1982, Richman et al. 1982, Whicker 1983, Marino 1986, Whicker and Tracy 1987, Stapp 1997a). More detailed information on darkling beetle ecology may be found in Doyen and Tschinkel (1974), Allsopp (1980), Parmenter and MacMahon (1984), Sheldon

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and Rogers (1984), Whicker and Tracy (1987), Rogers et al. (1988), and Parmenter et al. (1989b).

The similarity of life history, diet, range, and behavior among species prompts the question of how the darkling beetle community is structured in space and time. Factors that account for spatio-temporal patterns of darkling beetle community composition have been subject to much speculation by past researchers. A high degree of niche overlap suggests that environmental factors may play more important roles in structuring eleodid assemblages and populations than do biotic factors such as competition and predation (Wiens and Rotenberry 1979, Wise 1981a; but see Abrams 1980), which may play only minor roles in determining the abundance and distribution of darkling beetles (Wise 1981a, 1985, Parmenter and MacMahon 1988).

Previous studies have demonstrated that darkling beetle activity and occurrence are influenced by various environmental factors, including soil texture (Calkins and Kirk 1975, Krasnov and Shenbrot 1996, 1997, Stapp 1997a), abundance of food resources (McIntyre 1997), shrub cover (Parmenter et al. 1989b, McIntyre 1997, Stapp 1997a), and thermoregulatory resources (Rickard 1971, Slobodchikoff 1983, Whicker 1983, Whicker and Tracy 1987, Parmenter et al. 1989c). However, none of these studies examined the interaction between abiotic (weather) and environmental factors in influencing eleodid communities and populations. In this study, I investigated habitat occupancy at 2 spatial scales and variations in eleodid density and diversity over a 4-yr period. In particular, I focused on how eleodids respond to temperature, precipitation, and the presence of shrubs.

Some eleodid species are more abundant in and move to areas with greater shrub cover (Parmenter and MacMahon 1988, McIntyre 1997), possibly because shrubs provide protection from vertebrate predators (Parmenter and MacMahon 1988, Stapp 1997b) as well as shade. I investigated both factors.

#### Hypotheses

First, I tested the hypothesis (A1) that eleodids prefer shrub-dominated areas because of thermoregulatory resources that shrubs provide. This hypothesis was addressed by comparing pitfall-trap captures among naturally

shaded, artificially shaded, and unshaded traps. I then tested 2 alternative hypotheses (B1 and B2, below) regarding the relationships among predation risk, body size, and shrub cover. Although eleodids can produce unpalatable quinones when threatened with predation (Tschinkel 1975a), they are sometimes preyed upon by birds and rodents (Wiens et al. 1974, Wiens and Rotenberry 1979, Stapp 1997b). If eleodids partition habitat according to risk of predation, then that partitioning may take 1 of 2 forms as related to body size:

- (B1) Larger species, being more obvious to vertebrate predators, should be more abundant in areas with greater shrub coverage because shrubs serve as refugia from predators; smaller eleodids, being less vulnerable to predation because of their more inconspicuous size, should be widespread.
- (B2) Smaller species should be more abundant in areas with numerous refugia from predators (i.e., areas with finely textured clays with cracks that serve as refugia; such soils do not support high densities of shrubs); larger species, being less vulnerable to predation because of their size (being unmanageably large for a predatory rodent or bird), should be widespread (Stapp 1997a, 1997b).

To test these hypotheses, I compared the presence and abundance of eleodids that differ in body size in areas differing in amount of shrub cover.

Eleodid species exhibit different preferences in ambient temperatures in which they are active, perhaps reflecting species-specific differences in ability to conserve water (Kramm and Kramm 1972, Campbell and Smith 1975, Slobodchikoff 1983, Whicker 1983, Whicker and Tracy 1987, Parmenter et al. 1989c). I therefore examined 2 hypotheses of how eleodid richness and abundance might vary with temperature and precipitation. Because temperature and precipitation are negatively correlated variables, these hypotheses combine both temperature and precipitation rather than test each variable singly:

- (C1) If eleodids are heat sensitive, they should vary negatively with temperature and positively with precipitation.
- (C2) If eleodids are cold sensitive, they should vary positively with temperature and negatively with precipitation.

Inasmuch as the shortgrass steppe is in the cool-temperate zone, I assumed that temperature and precipitation should have a negative relationship with species richness and abundance. Because shrubs can provide both cooler- and warmer-than-ambient microclimates at different times of day (Stapp 1997a), however, hypotheses C1 and C2 were modified to generate the following hypothesis, which was tested against the null hypothesis that eleodids are indifferent to temperature:

- (D1) Eleodids in areas with lower shrub coverage should exhibit a greater number of strong correlations with weather variables than beetles in areas with greater shrub coverage.

Results from these tests are discussed with respect to interactions between darkling beetle presence and abundance, body size, and movement capacity and mobility, producing new insights into how spatio-temporal variations in eleodid community structure may be an expression of the different ways in which different species interact with the same spatial structure.

## METHODS

### Study Site

Research was conducted during May–August 1994–1997 at the 6280-ha Central Plains Experimental Range (CPER) on the Pawnee National Grassland, Colorado. Characterized by gently rolling topography, the site possesses primarily sandy loam and loamy sand soils. Approximately 1630 m in elevation ASL, the area receives 322 mm average annual precipitation, generally in the form of spring rains and summer convective thunderstorms. The climate is semiarid, with mild summers and cold, dry winters. Perennial warm-season C4 shortgrasses (primarily *Bouteloua gracilis* and *Buchloë dactyloides*) comprise most of the vegetative biomass (Lauenroth and Milchunas 1991). Forbs (particularly *Aster tanacetifolia*, *Astragalus* spp., *Gaura coccinea*, *Helianthus petiolaris*, *Leucocrinum montanum*, *Lomatium cous*, *Oenothera albicaulis*, *Oxytropis* spp., *Plantago patagonica*, *Sphaeralcea coccinea*, and *Thelesperma filifolium*) account for most vegetative diversity of the ecosystem. There are also low shrubs (*Atriplex canescens*) in sandy floodplains associated with ephemeral

creek channels. Soapweed (*Yucca glauca*) is abundant on rocky hilltops. Prickly-pear cactus (*Opuntia polyacantha*), found throughout the region, is especially abundant in upland areas with finely textured soils. There are also numerous small areas of bare ground and vegetative detritus (McIntyre 1997). There is little free-standing permanent water, with the few stream channels present containing water only sporadically in most locations. Topography, soils, climate, and biota of the shortgrass steppe have been described in more detail by Lauenroth and Milchunas (1991).

Visually, the shortgrass steppe appears to be composed of 2 coarsely defined habitat types that extend for dozens of square kilometers: upland areas dominated by shortgrasses with few shrubs and lowland floodplains with numerous shrubs. To determine whether this macrohabitat categorization was valid, 6 circular 638-m<sup>2</sup> sites were used. Three of these sites were located in each of the 2 putative macrohabitat types. Within a macrohabitat, sites were separated by 1–3 km; a 4-km separation existed between sites differing in macrohabitat type. Vegetational composition (proportion of grass/forb, shrub, bare soil, cactus, and vegetative detritus) was measured at each site in July of each year by determining percent basal cover along 2 randomly located 29.25-m line-intercept transects (diameter of trapping-area circle). A hierarchical cluster analysis (using average-neighbor distances and pooled covariance matrices) was then performed on the arcsine/square-root transformed percentages, with clustering distance correlations >0.50 accepted as clusters. Cluster analysis provided a means of quantifying similarities and differences in the 6 sites rather than relying on subjective categorization (Johnson and Wichern 1992). Soil type and elevation at each site were also recorded.

### Community Richness

Darkling beetles were live-trapped in 480 pitfall traps in six 638-m<sup>2</sup> trapping webs of 80 unbaited traps each. One trapping web was situated in each of the 6 study locations. Each pitfall trap was a 500-mL Barber-style trap (Weeks and McIntyre 1997). Traps were spaced 1.5 m apart in 8 lines along the 8 primary cardinal directions to create 10 concentric rings of traps (McIntyre 1995). Traps were checked

once daily for 7 consecutive days (6 nights) during the 3rd wk of each month from May through August 1994–1997 (46,080 total trap-nights). Changes in community composition with month and year were noted by assessing eleodid species richness each month from May through August of each year for each trapping web.

Weather data have been collected daily at the CPER since 1961, and data for the period 1961–1990 were compiled to give 29-yr averages in precipitation and temperature (compiled weather data at Internet sites <http://lter.net.edu/im/climate/climdes/sgs/sgsclim.htm> and [http://sgs.cnr.colostate.edu/data/data\\_cat/climateindex.html](http://sgs.cnr.colostate.edu/data/data_cat/climateindex.html)). Weather data collected during the weeks I trapped were compared to these 29-yr averages. A Spearman rank correlation was used to detect a significant relationship among species richness, daily minimum and maximum air temperatures, and daily amount of precipitation averaged over each trapping week. Rank correlations were also performed on temperature and precipitation data with 1-month and 1-yr time lags to determine whether eleodids exhibit a delayed response to weather. Because many climatic variables are non-monotonic, making linear regression susceptible to biases from data points at the extremes of the response distribution, outliers (defined as occurring  $\geq 2$  standard deviations away from the mean) were omitted from analyses.

#### Population Density Estimation

*Eleodes extricata* and *E. hispilabris* individuals that were captured in the pitfall trapping array were marked on the elytra with colored enamel paint to distinguish recaptured individuals from new captures. These 2 species were chosen for population monitoring because they are among the most widespread and abundant eleodids at CPER (Bell 1971, Whicker 1983, McIntyre 1997). The computer package DISTANCE was used to estimate population densities of these species (Buckland et al. 1993). DISTANCE uses distance-sampling theory, whereby the spacing between captures is used to derive significantly fitted models of detection probabilities to estimate population density (Wilson and Anderson 1985, Laake et al. 1994). Only new captures are used in fitting these models so as to eliminate bias from trap-happy individuals. Although DISTANCE may

not perform well for highly mobile organisms such as darkling beetles (Parmenter et al. 1989a), producing inflated density estimates, it has been used in a variety of field studies (Anderson et al. 1983, Parmenter et al. 1989a, McIntyre 1995) and performs well when capture rates are not extremely low ( $< 15$  individuals). Low capture rates necessitate calculating density either from number of animals trapped per area (which may give inflated density estimates) or from data pooled among dates or sites to calculate density for coarser spatio-temporal scales (Anderson et al. 1983).

Numbers of *E. extricata* and *E. hispilabris* were tallied each month from May through August of each year for each trapping web. Preliminary analyses revealed that capture rates were highly variable. Variation in capture rates may cause some assumptions to be violated and thus can bias density estimations made with DISTANCE, but this can be corrected by pooling data across time (Buckland et al. 1993, Laake et al. 1994). Therefore, data were pooled across months and density calculated for each year for each trapping web. Ninety-five percent confidence intervals (95% CI) were constructed around the mean estimated density of individuals per square meter within each trapping web. Densities in trapping webs where  $< 15$  beetles were captured were estimated as number of beetles caught per trapping web area ( $638 \text{ m}^2$ ) and have no confidence intervals associated with them. A Spearman correlation was used to detect significant relationships among beetle densities, daily minimum and maximum air temperatures, and daily amount of precipitation. Correlations were also performed on temperature and precipitation data with 1-month and 1-yr time lags.

#### Multiple-scale Habitat Analyses

Differences in macrohabitat use by eleodids were assessed with analysis of variance (ANOVA), using clusters from the hierarchical cluster analysis based on vegetation as blocks of variance. Species richness and population density were compared among blocks. Significant factors in ANOVA models were then compared among blocks with Tukey's Studentized Range (HSD) test for post-hoc comparisons.

To assess differences in microhabitat use by eleodids, a 25-cm-diameter circle centered on

each pitfall trap was characterized by the following microhabitat types: grass, bare ground (unvegetated areas at least as large as the opening of a pitfall trap), cactus, vegetative detritus, and shrub. Each trap was then categorized as having caught either at least as many as or fewer than the average number of eleodid individuals (obtained by taking the total number of individuals captured in a trapping web during a given year and dividing by the 80 traps present in a web). Trap "success" was therefore a binary quantity comprising 2 mutually exclusive categories. Representing trap success as a binary quantity in this manner rather than as a continuous response variable circumvents the assumption that the data assume a Poisson distribution, which is not present in this case (mean and variance differed significantly,  $\chi^2 = 960.65$ ,  $P = 0.0001$ ). Binomial logistic regression was used to correlate a trap's success with the microhabitats surrounding it. Data were pooled by site and year; pooling is justified because calculating trap success in the manner described above accounts for any among-site and -year variation and allows for general trends to emerge. If eleodids are attracted to certain microhabitat types, then traps surrounded by those microhabitats should capture more beetles (as determined by a Wald  $\chi^2$  analysis; SAS Institute Inc. 1996).

#### Effects of Shade on Eleodid Captures

One of the 3 shrub-floodplain sites (site 4) was selected at random for experimental manipulation of the effects of shade on eleodid captures. Each of the 80 pitfall traps present was classified as being naturally shaded by shrubs or unshaded (following the criterion of Rickhard and Haverfield 1965). A random subset of the unshaded traps was provided with artificial shade in the form of paper "parasols" (25-cm-diameter circles supported atop 20-cm-high nails placed adjacent to a trap). To provide a balanced design, equal numbers of naturally shaded, artificially shaded, and unshaded traps were selected at random for analysis ( $N = 26$  traps per 3 treatments). These traps were open for 6 consecutive days in July 1994, with eleodid captures in each trap type tallied each day. Average eleodid captures were then compared among trap types using a Kruskal-Wallis test.

## RESULTS

### General Community Patterns

Nine darkling beetle species were captured (Figs. 1, 2). ANOVA revealed that there were significant differences in species richness among months within 1995 but not within the other years (Table 1). In 1995 the highest diversity of species was trapped in August; trapping in May, June, and July captured similar numbers of species (HSD = 2.09,  $df = 20$ ,  $P < 0.05$ ). Significantly more species were trapped in each of the 6 trapping sites in 1997 than in the other 3 yr (HSD = 1.99,  $df = 92$ ,  $P < 0.05$ ).

For abundance, significant differences among months were found in 3 of 4 yr studied (1994, 1995, and 1997; Table 1). In 1994 the greatest number of eleodid individuals was trapped in May, with the remaining 3 months not significantly different from one another (HSD = 3.96,  $df = 20$ ,  $P < 0.05$ ). In 1995 the reverse was true, with significantly more individuals per species being captured in June, July, and August than in May (HSD = 3.96,  $df = 20$ ,  $P < 0.05$ ). In 1997 most individuals were captured in July, least in June (HSD = 3.96,  $df = 20$ ,  $P < 0.05$ ). Significantly more individuals for each of the 9 species were trapped in 1994 than in the other years, and the least number of eleodids was captured in 1995 (HSD = 1.99,  $df = 92$ ,  $P < 0.05$ ).

Of the 9 eleodids captured, most were found throughout the 4-month trapping period. Certain species, however, were more abundant early in the season (*E. extricata* and *E. fusiformis*), whereas others were more common in late summer (*E. longicollis* and *E. obsoleta*). *E. suturalis* and *E. tricostata* were most abundant in midsummer. All 9 species were captured each year.

### Multiple-scale Habitat Analyses

Cluster analysis quantitatively supported the visual separation of 2 macrohabitat types within the shortgrass steppe, based upon percent basal vegetation coverage (basal branching of sites 1–3: normalized root mean squared correlation = 0.61; basal branching of sites 4–6: normalized root mean squared correlation = 0.77). Three trapping webs were located within upland shortgrass areas (sites 1–3), which were characterized by extensive grass

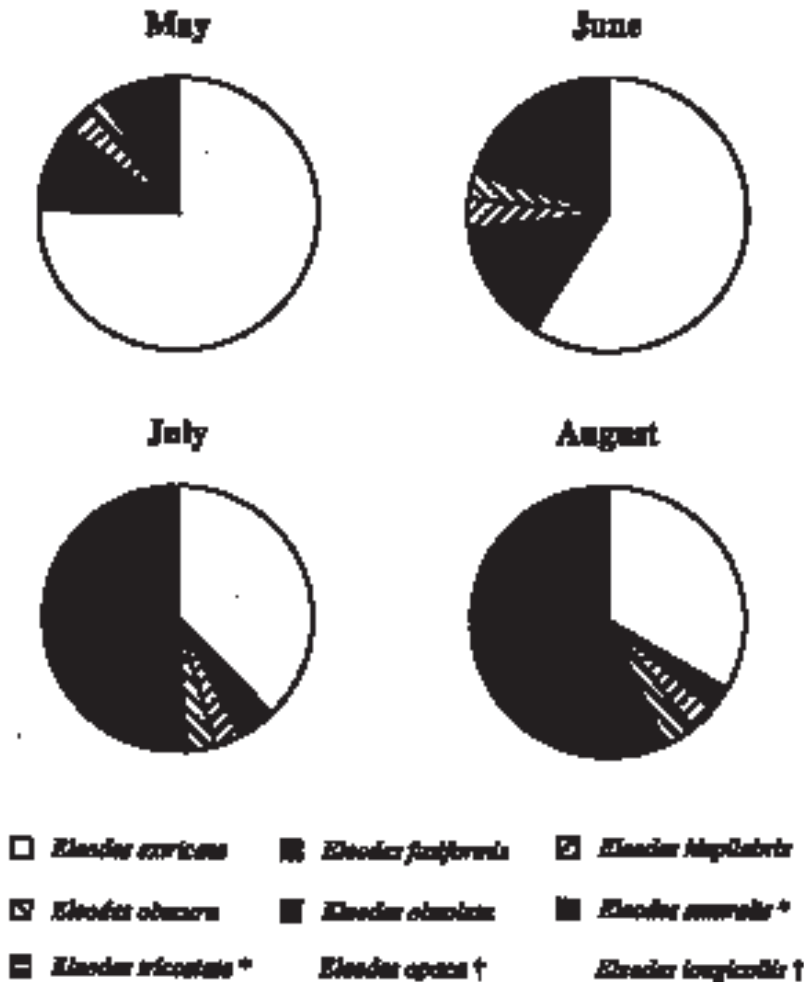


Fig. 1. Species composition (%) of pitfall-trap captures by month for shortgrass upland macrohabitat. Years (1994–1997) pooled. Species marked with an asterisk (\*) comprised <1% of captures for all months. Species marked with a dagger (†) were not captured in any month.

coverage (mean basal ground cover = 86.97%), few shrubs (1.53%) and cactus (0.92%), little vegetative detritus (1.21%), and moderate amounts of bare ground (7.13%). These sites had fine sandy loam soils and averaged 1643 m in elevation. The other 3 trapping areas were located within shrub floodplains (sites 4–6) and had higher amounts of shrubs (14.66%), vegetative detritus (5.12%), cactus (1.08%), and bare ground (16.80%) but less extensive grass coverage (60.65%). These sites had loamy and loamy sand soils and averaged 1621 m in elevation. Significant correlates with eleodid species richness among the 6 trapping areas were macrohabitat type ( $F = 203.86$ ,  $df$

= 1,  $P = 0.0001$ ) as well as year ( $F = 7.79$ ,  $df = 3$ ,  $P = 0.0020$ ) and month ( $F = 5.34$ ,  $df = 3$ ,  $P = 0.0024$ ).

More eleodid species were trapped in floodplains than in uplands ( $F = 203.86$ ,  $df = 1$ ,  $P = 0.0001$ ; HSD: 2.825,  $df = 64$ ,  $P < 0.05$ ). Densities of *E. extricata* and *E. hispilabris*, however, did not differ significantly between the 2 macrohabitats (Fig. 3; *E. extricata*:  $F = 0.98$ ,  $df = 7$ ,  $P = 0.4778$ ; *E. hispilabris*:  $F = 1.12$ ,  $df = 7$ ,  $P = 0.3972$ ) or among years (*E. extricata*:  $F = 1.78$ ,  $df = 3$ ,  $P = 0.1921$ ; *E. hispilabris*:  $F = 1.17$ ,  $df = 3$ ,  $P = 0.3520$ ), probably because of high variance associated with the density estimates.

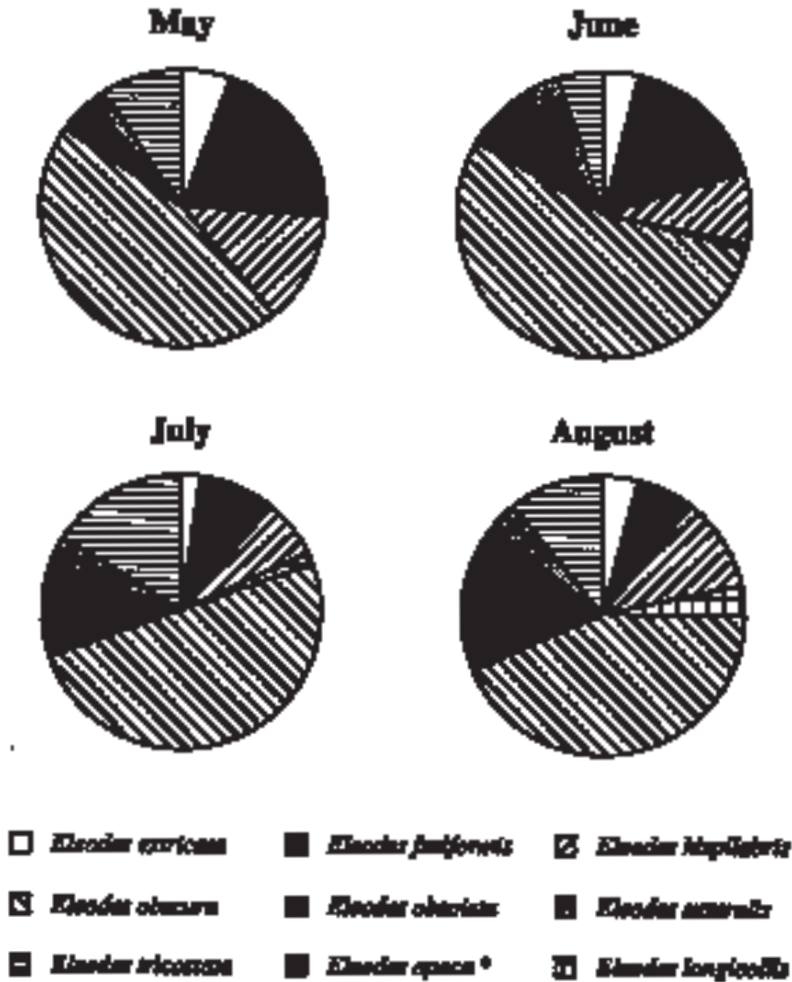


Fig. 2. Species composition (%) of pitfall-trap captures by month for shrub floodplain macrohabitat. Years (1994–1997) pooled. Species marked with an asterisk (\*) comprised <1% of captures for all months.

Some significant microhabitat affinities were revealed. Traps located near cactus caught an average of 1 more beetle per trap than did traps where cactus was absent (model goodness-of-fit: log-likelihood = 107.9292,  $P = 0.0000$ ;  $\chi^2 = 12.2047$ ,  $P = 0.0005$ ). A similar relationship was noted for traps near shrubs, which caught an average of 3 more individuals per trap (model goodness-of-fit: log-likelihood = 49.1869,  $P = 0.0000$ ;  $\chi^2 = 11.8918$ ,  $P = 0.0006$ ). Conversely, traps located near bare ground caught an average of 2 fewer beetles per trap (model goodness-of-fit: log-likelihood = -132.3717,  $P = 0.0000$ ;  $\chi^2 = 5.3276$ ,  $P = 0.0210$ ). No significant relationships were

TABLE 1. ANOVA results for differences in number of species (richness) and abundance among months for 1994–1997; ns = not significant.

Year	F	df	P
----- Effect: richness among months -----			
1994	2.43	3	0.0956 ns
1995	6.03	3	0.0043
1996	0.55	3	0.6571 ns
1997	0.69	3	0.5709 ns
----- Effect: abundance among months -----			
1994	13.96	3	0.0001
1995	4.32	3	0.0167
1996	1.12	3	0.0719 ns
1997	3.35	3	0.0395



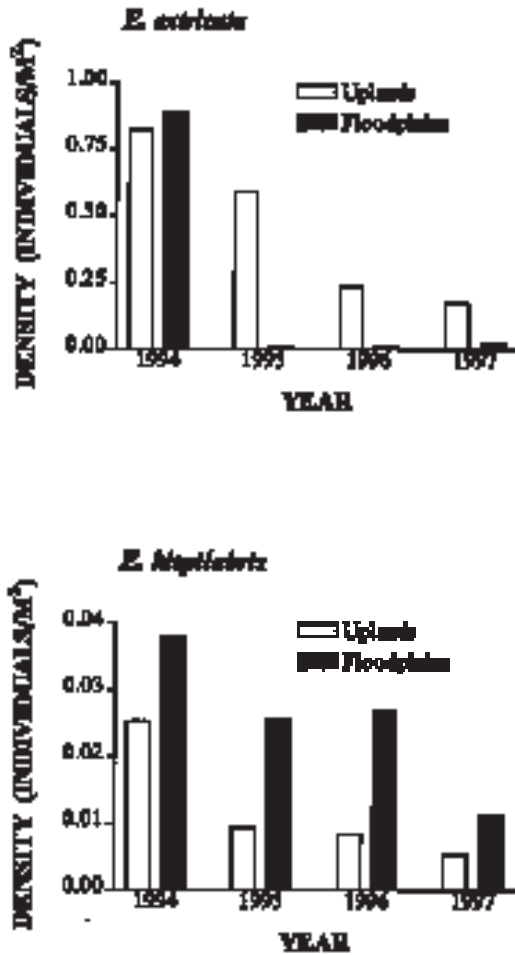


Fig. 3. Average estimated population density for *E. extricata* (top) and *E. hispidulabris* (bottom) in 2 macrohabitat types (shortgrass upland and shrub floodplain) at the Central Plains Experimental Range, Colorado, 1994–1997. Open bars represent shortgrass upland sites; filled bars represent shrub floodplain sites. Note differences in scale of y-axes. Density values are averaged across the 3 sites within each of 2 macrohabitat types for clarity of presentation. Confidence intervals are not shown for sake of clarity (site and year effects nonsignificant; see text for statistics).

noted for the presence of grass or vegetative detritus.

Differences in captures with shade

No significant differences were found in average eleodid captures among naturally shaded (39.8 individuals), artificially shaded (40.5), and unshaded (36.6) pitfall traps ( $\chi^2 = 0.44015$ ,  $df = 2$ ,  $P = 0.8025$ ).

Shrub Cover, Predation Risk, and Body Size

Although most species were widespread, certain species attained higher numbers in one or the other macrohabitat type (Table 2; Figs. 1, 2). The larger species (*E. hispidulabris*, *E. longicollis*, *E. obscura*, and *E. suturalis*) were more abundant in the shrub floodplains (body size information from Whicker 1983 and Crist et al. 1992), and one of these (*E. longicollis*) occurred only in the shrub-floodplain sites. The smallest species (*E. extricata*) was more common in the shortgrass uplands, but it overlaps considerably in size with other species that were more abundant in floodplain sites (*E. fusiformis* and *E. tricostata*), found only in floodplain sites (*E. opaca*), or were equally abundant in both macrohabitat types (*E. obsoleta*).

Weather

Precipitation was highly variable in timing and amount during the 4-yr study period (Table 3). While 1994 was drier than the 29-yr average, the years 1995–1997 were wetter. There was also variation among months within each year, with May receiving most precipitation in most years (except 1997, when August received the most rainfall). The years of my study were also cooler than the 29-yr average. Although maximum daily air temperatures in 1994 and 1995 fell within the 29-yr range, 1996 and 1997 were consistently cooler by 2–3°C.

Some weather variables were significantly correlated with richness during some months and years in certain trapping sites. For example, precipitation levels were significantly negatively correlated with eleodid species richness only at 2 trapping sites in a single year (Table 4). The number of species trapped at sites 1, 2, and 6 in 1995 was positively correlated with maximum air temperature and negatively correlated with minimum air temperatures and daily air temperatures. Other relationships were not significant.

There were also some significant effects on eleodid richness from weather conditions of the previous year or month, and these effects were also mediated by site. Temperatures in 1994 were significantly correlated with richness at trapping site 1 in 1995, for example, and temperatures in the summer of 1995 significantly affected richness at site 4 in 1996.

TABLE 2. Average number of individuals captured by species in each of the 2 macrohabitat types (SU = shortgrass upland, SF = shrub floodplain). Values averaged across 3 sites within each macrohabitat type, across 4 months, and across 4 yr for clarity of presentation. EXTR = *E. extricata*, FUSI = *E. fusiformis*, HISP = *E. hispilabris*, LONG = *E. longicollis*, OBSC = *E. obscura*, OBSO = *E. obsoleta*, OPAC = *E. opaca*, SUTU = *E. suturalis*, TRIC = *E. tricostata*.

	EXTR	FUSI	HISP	LONG	OBSC	OBSO	OPAC	SUTU	TRIC
SU	42.61	6.52	2.64	0	2.40	20.30	0	0.04	0.27
SF	6.50	21.70	16.23	2.44	82.04	19.54	0.40	5.25	18.17

TABLE 3. Weather data, 1994–1997, compared to historical data collected 1961–1990. PPT = precipitation (mm), AIRMAX = maximum daily air temperature (°C), AIRMIN = minimum daily air temperature (°C), TEMP = average daily air temperature (°C). A dash (—) indicates no data available.

Year	PPT	AIRMAX	AIRMIN	TEMP
<b>Historic</b>	282.7	17.28	1.13	9.27
<b>1994</b>	135.0	17.81	-0.45	8.63
May	11.8	28.96	7.88	19.19
June	0	31.38	10.36	21.31
July	0	34.05	11.01	22.85
August	1.0	32.15	14.76	22.66
<b>1995</b>	302.9	17.37	-0.97	7.66
May	4.31	16.69	-6.83	7.69
June	—	—	—	—
July	0	26.13	11.03	17.89
August	0	29.58	12.13	23.65
<b>1996</b>	423.4	16.89	-0.66	7.99
May	0.25	15.98	5.81	7.48
June	1.02	26.86	11.84	20.12
July	0.25	29.42	12.14	20.12
August	0	30.46	10.44	20.22
<b>1997</b>	408.8	15.36	-1.02	7.07
May	—	—	—	—
June	4.32	27.02	10.83	17.99
July	0	31.56	11.71	22.44
August	13.72	29.02	13.91	20.93

Precipitation in 1996 negatively affected richness in site 5 in 1997. Precipitation levels in May 1994 affected the number of eleodid species trapped in June at sites 2, 3, and 5; and maximum air temperatures in June 1996 were negatively correlated with the number of species trapped at site 3 in July. Other relationships were not significant.

Densities of *E. extricata* and *E. hispilabris* populations were affected by some weather variables (Table 5). *E. extricata* densities were primarily affected by weather conditions of the previous year, and this effect was mediated by site. For example, at trapping sites 1, 3, and 5, density was significantly correlated with daily mean temperature of the previous year. At sites 2, 4, and 6, densities responded to precipitation levels and temperature maxima.

*E. hispilabris* numbers were significantly correlated with weather variables of the current and previous years, depending on site. For instance, density was significantly correlated with the current year's minimum and daily mean air temperatures at site 1 and precipitation and maximum air temperature at site 6. Densities at sites 3 and 4 were affected by both current and prior weather conditions. Other relationships were not significant.

#### DISCUSSION

Eleodid community composition of the northern shortgrass steppe showed as much variation among months within a year as among years. Some eleodid species experienced irregular increases and declines in abundance in

TABLE 4. Spearman rank correlation matrix for number of species captured and weather variables, 1994–1997. Values are  $r_s(P)$ . “Current year” indicates correlations performed on data within a year, whereas “1-yr lag” indicates weather data from year prior to the one listed and “1-month lag” indicates correlations performed with weather data from the month prior to the one listed within a year. PPT = precipitation, AIRMAX = maximum daily air temperature, AIRMIN = minimum daily air temperature, TEMP = average daily air temperature. Only significant correlations are shown for sake of clarity.

Time	Site	PPT	AIRMAX	AIRMIN	TEMP
----- Current year -----					
1995	1		0.96(0.0005)	-0.92(0.0014)	-0.99(0.0001)
1995	2	-0.93(0.0011)	0.96(0.0004)	-0.90(0.0012)	-0.97(0.0003)
1995	5	-0.99(0.0001)			
1995	6		0.97(0.0003)	-0.90(0.0009)	-0.97(0.0003)
----- 1-yr lag -----					
1995	1				0.83(0.0026)
1996	4				0.86(0.0028)
1997	5	-0.90(0.0019)			
----- 1-month lag -----					
6/1994	2	-0.97(0.0003)			
	3	-0.97(0.0003)			
	5	-0.97(0.0003)			
7/1994	3		-0.90(0.0019)		

response to weather (primarily precipitation and minimum air temperatures), although population densities of the 2 focal species remained relatively stable across years and sites.

Most of the 9 eleodid species present at CPER were widespread, occurring in both macrohabitat types (shortgrass uplands and shrub floodplains), although certain species were more abundant in one or the other macrohabitat (Figs. 1, 2). The 4 largest species (*E. hispilabris*, *E. longicollis*, *E. obscura*, and *E. suturalis*) were more abundant in shrub floodplains. Most smaller species were more abundant in floodplain sites (*E. fusiformis*, *E. opaca*, and *E. tricostata*), although 1 species (*E. obsoleta*) was equally abundant in both macrohabitat types. The smallest species (*E. extricata*) was more common in shortgrass uplands. These results are consistent with Whicker (1983), Parmenter and MacMahon (1984), and Stapp (1997a). Beetles were captured more often in traps located near cactus and shrub microhabitats in both macrohabitats, and significantly lower capture rates were noted for traps associated with bare soil (see also Stapp 1997a).

Most eleodids were widespread over time, being present throughout most of the summer, although there was some phenological turnover in species abundance and community composition (Figs. 1, 2). In addition, most

species were present every year, suggesting that I sampled the entire local eleodid species pool (see also Kumar et al. 1976).

#### Shrubs and Shade

No significant shrub-shade effects (hypothesis A1) were found, probably because beetles were captured during a thermally favorable “window” of time (Whicker 1983), a daily period when beetles can be active (and thus trapped). During most of this window, beetles do not need to seek out thermoregulatory sites associated with shrubs. Therefore, it is not surprising that beetle captures were similar between shaded and unshaded traps. Parmenter and MacMahon (1984) reported similar negative results from a shrub-removal experiment in the shrub-steppe of Wyoming (~40% shrub coverage), which suggests that shade may not be an important resource provided by shrubs when eleodids are active (although it may be important during other portions of the day or at night; Stapp 1997a).

As a word of caution, however, the shortgrass steppe has a relatively low amount of shrub coverage ( $\leq 14\%$ ), and so any favorable microhabitats created by shrubs would be relatively rare. In habitats with shrub canopy coverage  $\geq 90\%$ , however, microclimate differences associated with shrubs may be more pronounced, and some microhabitat partitioning by eleodids has been revealed under such

TABLE 5. Spearman rank correlation matrix for population density of *E. extricata* (EXTR) and *E. hispilabris* (HISP) and weather variables. Values are  $r_s(P)$ . "Current year" indicates correlations performed on data within a year, whereas "1-yr lag" indicates weather data from the previous year. PPT = precipitation, AIRMAX = maximum daily air temperature, AIRMIN = minimum daily air temperature, TEMP = average daily air temperature. Only significant correlations are shown for sake of clarity.

Species	Year	Site	PPT	AIRMAX	AIRMIN	TEMP
----- Current year -----						
HISP	1996	1			-0.90(0.0031)	0.97(0.0003)
HISP	1996	2				
HISP	1996	3	-0.99(0.0001)			
HISP	1996	4		-0.96(0.0005)		
HISP	1996	5				
HISP	1996	6	-0.99(0.0001)	0.90(0.0001)		
----- 1-yr lag -----						
EXTR	1995	1				0.99(0.0001)
EXTR	1995	2	-0.99(0.0001)	-0.92(0.0008)		
EXTR	1995	3				0.99(0.0001)
EXTR	1995	4	-0.99(0.0001)	-0.92(0.0008)		
EXTR	1995	5				0.99(0.0001)
EXTR	1995	6	-0.99(0.0001)	-0.92(0.0008)		
HISP	1997	3			-0.99(0.0001)	
HISP	1997	4	-0.99(0.0001)			

circumstances (Parmenter et al. 1989b, 1989c). In particular, *Eleodes extricata* is usually associated with open, shrub-free areas (this study, Whicker and Tracy 1987, Parmenter et al. 1989b, 1989c).

#### Shrubs, Predation Risk, and Body Size

Regarding the hypotheses about body-size differences in predation risk by macrohabitat/degree of shrub cover, my data do not completely support either alternative. With alternative B1, for example, although some smaller eleodid species were more abundant in upland sites, others were more abundant in shrub floodplains with coarsely textured soils that do not provide refugia, and larger species were not widespread. With alternative B2, smaller species were not widespread, with some being more abundant in uplands and others achieving higher numbers in floodplains (Figs. 1, 2). In other words, neither hypothesis explains why there were fewer individuals of only some of the smaller eleodid species in shrub floodplains and simultaneously why there were lower numbers of the larger species in uplands.

Rodent-removal experiments have shown that eleodid populations may increase by as much as 63% in the absence of predators (Parmenter and MacMahon 1988). Even so, some eleodid species may prefer shrub-dominated areas although predators are more numerous

there. Predacious rodents, for example, attain densities 8–16 times higher in shrub-dominated areas of the shortgrass steppe, and more species of rodents that prey upon eleodids are found in areas with shrubs (Stapp 1996).

Parmenter and MacMahon (1988) found that most larger-bodied tenebrionids showed little response to predator removal, which they attributed to better chemical (quinone) defenses. Although most *Eleodes* species are assumed to possess chemical defenses (Tschinkel 1975a, 1975b, Allsopp 1980), not all species have been tested to determine whether this is true. In this study I observed such chemicals in only 4 species: *E. extricata* (small species, most abundant in uplands; defensive chemical also found in this species by Parmenter and MacMahon [1988]), *E. fusiformis* (small species, most abundant in shrub floodplains), *E. hispilabris* (large species, most abundant in shrub floodplains), and *E. obsoleta* (small species, found in both macrohabitats). Therefore, no clear patterns of habitat occupation with defensive capabilities emerged, and no conclusions can be drawn about potential differences in predation risk among the different species (and different body sizes) in the shortgrass steppe without further study.

Given this information as well as the paucity of empirical data on differential rates of species-specific eleodid predation, these hypotheses of why eleodid communities are structured as

they are must be viewed with skepticism. Instead, eleodids may prefer areas with shrubs because of resources that shrubs provide or because of environmental (particularly edaphic) factors that are correlated with, but independent of, shrub presence (Parmenter and MacMahon 1984, Parmenter et al. 1989b, McIntyre 1997, Stapp 1997a).

#### Shrubs and Weather

Species-specific differences in physiological tolerance of weather variables may account for phenological turnovers in species richness and abundance I observed each year, but there is a high degree of overlap in physiological tolerances among the different species I studied (Whicker 1983, Whicker and Tracy 1987). Thus, it is perhaps not surprising that I observed overlap in community composition and population density among weather conditions and years (Figs. 1, 2).

Species-specific physiological differences may be compromised by habitat effects. For example, the avoidance of bare-soil microhabitats may reflect an avoidance of areas in which thermoregulation is difficult (cf. McIntyre in press) or where food resources are absent. In addition, because insectivorous rodents create areas of bare soil during burrow excavations (Stapp 1997b), eleodids may be more exposed to predation in bare-ground areas and hence avoid such areas. This microhabitat avoidance was not reflected in macrohabitat occupation, however, because shrub-floodplain sites possessed more bare soil. Different mechanisms of habitat selection may be operating at different scales, creating this apparent paradox of habitat occupancy (see also McIntyre 1997).

Hypothesis D1 received only partial support, suggesting that the eleodid community is somewhat insensitive to weather. Because darkling beetles are ectotherms, it comes as no surprise that they responded to some weather variables (see also Hinds and Rickard 1973), but it is surprising that they did not respond more strongly and consistently to weather variables. This weak relationship may be artificial, however, because the test of hypotheses C1 and C2 included a hidden bias. Pitfall trapping is influenced by both insect abundance (with more abundant species exhibiting higher capture rates) and insect activity (with more mobile species being captured more often

than sedentary species; Southwood 1966). Eleodids are active only during a thermally favorable window of time each day (Whicker 1983). Beetles are trapped only when they are active, with the daily timing and duration of their activity window determined by the weather. Therefore, beetles may in fact respond strongly to temperature and precipitation, insofar as these variables determine when beetles can be active, but not density or diversity.

In general, larger ectotherms are less affected by weather conditions than are smaller ones because of the negative relationship between body size and convective heat loss. Larger beetles may be exposed to greater heat gain than are smaller species by virtue of their smaller surface-area-to-volume ratio. Thus, larger species may require shrub microclimates more so than smaller species, which may explain why the 4 largest eleodid species were consistently more abundant in shrub floodplains. This relationship does not explain the more complicated community-habitat patterns of the smaller species, however.

#### An Alternative Explanation for Patterns Observed

Various forms of habitat partitioning seem to offer only partial explanations for the spatio-temporal characteristics of the eleodid community of the shortgrass steppe. Can other mechanisms provide a more comprehensive explanation of the abundance and distribution of eleodids on the shortgrass steppe?

Because all eleodid species are highly vagile, they are presumably not excluded from one or another macrohabitat type because of an inability to reach it. The presence of at least a few individuals of nearly all species in both macrohabitat types indicates this is true, and the macrohabitats themselves are interspersed throughout the shortgrass steppe, being separated by no more than a few kilometers. Because macrohabitats are defined by differences in vegetative structure (e.g., presence vs. absence of shrubs), differences in this structure may be driving the eleodid community patterns by acting as filters to movement, the process by which animals achieve habitat selection. This idea was first hinted at by Roughgarden (1974) with respect to how different scales of environmental heterogeneity affect population dynamics by affecting dispersal distances; it was further modified by

Wiens and Milne (1989), Crist et al. (1992), Crist and Wiens (1995), Keitt et al. (1997), and Wiens et al. (1997).

Different macrohabitats, by virtue of their differences in physiognomic structure, possess different "viscosities." Species that differ in their movement behaviors (*capacity* and *mobility*, defined below) would therefore respond differently to different portions of a landscape (Roughgarden 1974, Rolstad 1991). Overall movement *capacity* (distance traveled in a given time period) is affected by body size, with larger species able to cover greater distances than smaller species (With 1994, Keitt et al. 1997). An animal's *mobility* (ease of movement) is also affected by its body size because animals interact with environmental features according to the scale of those features. For example, large, mobile animals are able to disregard fine-grained features such as small variations in topography or vegetative physiognomy. Small species, on the other hand, are affected by these small features, which are (relative to themselves) not small at all. Large eleodids do indeed move over features that smaller beetles circumambulate (Crist et al. 1992). Thus, large, mobile species perceive landscapes as more connected because they interact with spatial features at a broader (coarser) scale (Levins 1968, Kotliar and Wiens 1990). If a structure is very large relative to the size of an animal, the structure in its entirety may be disregarded and interactions made only with its component parts (Rolstad 1991).

To a large eleodid beetle, then, shortgrass poses no obstructions to movement; to a small beetle, however, shortgrass may represent a veritable thicket. Large beetles would be forced to interact with shrubs, however, but small beetles may be able simply to move through small gaps in aboveground roots and leaf litter. Therefore, larger species should accumulate in areas with coarse physical structure (i.e., shrub macrohabitats), whereas smaller species should be found more often in areas with finer-textured vegetation that is sufficiently large to detain them (i.e., shortgrass uplands). This scale-dependent mobility explains why there were more individuals of the large eleodid species in the shrub floodplains, why some small species were more abundant in the shrub floodplains than in the shortgrass uplands, and why the smallest species was most abundant in the uplands.

Scale-dependent uses of heterogeneity may also explain how an individualistic behavior such as movement can translate into population- and community-scale patterns (Crist and Wiens 1995). For example, adult eleodids may move to areas with favorable oviposition and larval-development sites, resulting in higher eleodid abundances there the following year. Very little is known about egg and larval requirements, however, and nothing is known about larval movements. More studies are needed about other life stages of eleodids if we are to understand fully their community organization.

The shortgrass steppe has an abundant, diverse, and understudied arthropod fauna. Its darkling beetle community possesses some spatio-temporal dynamics that resist straightforward explanations. Continued long-term monitoring of eleodids and weather in both shortgrass-upland and shrub-floodplain macrohabitat types may reveal how abiotic and environmental factors interact to influence darkling beetle community structure. Particular attention should be paid to how environmental heterogeneity may be perceived at different scales to create dynamic community patterns.

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