Population dynamics of the northern short-tailed shrew, *Blarina brevicauda*: insights from a 25-year study

Lowell L. Getz, Joyce E. Hofmann, Betty McGuire, and Madan K. Oli

Abstract: The population demography of the northern short-tailed shrew, *Blarina brevicauda* (Say, 1823), was studied for 25 years in bluegrass, alfalfa, and tallgrass habitats in east-central Illinois. The population in bluegrass had higher over-winter population density, began increasing earlier in the year, peaked earlier in the year, had higher mean monthly densities and amplitudes of fluctuation, and remained higher for longer than did populations in alfalfa and tallgrass. Survival rates were greater in bluegrass and tallgrass than in alfalfa. The species displayed annual population fluctuations with little variation in amplitude among years in all three habitats. Seasonal reproduction appeared to be responsible for the annual fluctuations. Survival did not vary in relation to season, but was positively correlated with annual peak densities, whereas reproduction was not. There was no correlation between population densities of voles during April–August and annual peak densities of *B. brevicauda*. We conclude that annual fluctuations in *B. brevicauda* populations are driven by seasonal reproduction, while variation in mortality, most likely from predation, may explain differences in the amplitudes of annual peaks.

Résumé : La démographie de la musaraigne à queue courte, *Blarina brevicauda* (Say, 1823), a été étudiée pendant 25 ans dans des habitats de pâturin, de luzerne et d’herbes hautes du centre-est de l’Illinois. La population vivant dans le pâturin possède une densité de population en hiver plus grande que les populations dans la luzerne ou les herbes hautes; de plus, elle commence à croître et atteint son maximum plus tôt dans l’année; elle a des densités moyennes mensuelles plus élevées et des fluctuations plus importantes et elle maintient sa densité élevée plus longtemps. Les taux de survie sont plus forts dans le pâturin et les herbes hautes que dans la luzerne. L’espèce subit des fluctuations annuelles de densité dont l’amplitude varie peu d’une année à l’autre dans les trois habitats. La reproduction saisonnière semble expliquer les fluctuations annuelles. La survie ne varie pas en fonction de la saison; en effet, la survie est en corrélation avec la densité maximale annuelle, mais la reproduction ne l’est pas. Il n’y a pas de corrélation entre les densités des populations de campagnols en avril–août et les densités maximales annuelles de *B. brevicauda*. En conclusion, les fluctuations annuelles de *B. brevicauda* s’expliquent par la reproduction saisonnière, alors que la variation de la mortalité, très vraisemblablement due à la prédation, peut expliquer les différences d’amplitude des maximumsannuels.

Introduction

Although the short-tailed shrew, *Blarina brevicauda* (Say, 1823), is one of the more common small mammals in eastern North America, there have been relatively few long-term demographic studies of the species (Getz 1989, 1994). High


L.L. Getz.1 Department of Animal Biology, University of Illinois, 505 South Goodwin Avenue, Urbana, IL 61801, USA.

J.E. Hofmann. Illinois Natural History Survey, 607 East Peabody Drive, Champaign, IL 61820, USA.

B. McGuire. Department of Biological Sciences, Smith College, Northampton, MA 01063, USA.


1Corresponding author (e-mail: L-GETZ@life.uiuc.edu).
Buckner 1966; Smith et al. 1974; Grant 1976; Yahner 1983; Lima et al. 2002). Further, preliminary analyses of data from the first 18 years of this study (Getz 1989, 1994) indicated that *B. brevicauda* displayed annual fluctuations, with little year-to-year variation in peak density.

*Blarina brevicauda* has been proposed as a predator on arvicoline rodents (Eadie 1944, 1948, 1952). Although the ability of *B. brevicauda* to kill free-living adult voles has been questioned by Barbehenn (1958) and Lomolino (1984), the latter suggested that the species is an important predator on juvenile *M. pennsylvanicus*. Getz et al. (1992) concluded from studies in seminatural environments that *B. brevicauda* might be an important predator on *M. pennsylvanicus* nestlings but not on *M. ochrogaster* nestlings. If such findings can be applied to the field, we might expect the population densities of *M. pennsylvanicus* and *B. brevicauda* to affect one another. If voles, especially young, are an important food source for *B. brevicauda*, we would expect a positive correlation between population densities of voles (either species alone or the two species combined) and that of *B. brevicauda*. If, however, the main effect of *B. brevicauda* predation on voles was increased mortality of voles, we would expect a negative correlation between population densities of voles and that of *B. brevicauda*.

*Blarina brevicauda* has high water requirements (Chew 1951) and is associated with mesic habitats (Pruitt 1953, 1959; Getz 1961). The population demography of *B. brevicauda* in drier habitats would be expected to be influenced by variation in precipitation. Matlack et al. (2002) found a correlation between precipitation and population densities of *Blarina hylophaga* Elliot, 1899. Smith et al. (1974) suggested that precipitation the previous autumn has an impact on shrew population densities the following year.

We used *B. brevicauda* data from the entire 25 years of the study to test the following predictions: (i) the species will display annual rather than multi-annual population fluctuations, (ii) population densities and annual peaks will be higher during years of high precipitation, and (iii) population densities will be correlated with those of *M. pennsylvanicus* but not those of *M. ochrogaster*.

**Study sites and procedures**

**Study sites**

The study sites were located in the University of Illinois Biological Research Area (“Phillips Tract”) and Trelease Prairie, both 6 km northeast of Urbana, Illinois (40°15′N, 88°28′W). Populations of *B. brevicauda* were monitored from 1972 to 1997 in three distinct habitats: bluegrass, *Poa pratensis* L., alfalfa, *Medicago sativa* L., and restored tallgrass prairie. Getz et al. (1987, 2001) provided detailed descriptions of the study areas; only brief descriptions are given here.

Vegetative cover was most dense in bluegrass and least so in alfalfa. Vegetative cover, including a mat of dead grass litter, 5–25 cm above the surface was very dense throughout the year in bluegrass; *B. brevicauda* made use of voles’ surface runways through the vegetation and litter. Larger forbs provided considerable cover up to 1–2 m above the surface during summer – late autumn. Vegetative cover in alfalfa was more dense from mid-spring through early winter than during late winter – early spring, when much of the surface was exposed. During mid-spring – early winter, alfalfa plants were less than 0.5 m tall, and only scattered taller plants provided cover up to 1.0 m above the surface. Vegetative cover in tallgrass was dense throughout the year. During spring – early summer, grasses formed cover 0.5–1.0 m high; from late summer to early winter, there was dense vegetative cover 1.0–1.5 m above the surface. During the entire year, recumbent dead grasses formed a dense layer approximately 25 cm above the surface. Owing to the bunch growth-form of the tall grasses, the area between the bases of tall grass clumps was relatively open up to 10 cm above the surface at all times. The tallgrass sites were burned in April or May, when invading grasses, shrubs, and trees were deemed to be impacting habitat quality. There were four burns during the study: 1977, 1979, 1984, and 1987. All vegetation and litter was consumed by the burns. Prairie grasses recovered and were 1.5–2.0 m high by late August; the recumbent litter layer was reestablished during the following winter. Trapping was not conducted during the summer following a burn, but resumed in September. *Blarina brevicauda* and vole populations recovered by September or October following the burns.

All study sites, except for a small (=0.1 ha) area in the Trelease Prairie tallgrass site (trapped only in 1972–1977), were well-drained and relatively dry except following heavy rains. Weather data were compiled from the Illinois State Water Survey climatological data records. The weather station was located on the campus of the University of Illinois, approximately 6.6 km southwest of the study sites.

**Trapping procedures**

A grid system with 10-m intervals was established in all study sites. One wooden multiple-capture live trap (Burt 1940) was placed at each station. Each month a 2-day prebaiting period was followed by a 3-day trapping session. Because the study was designed for voles, cracked corn was used for prebaiting and as bait in the traps. Cracked corn is not a suitable food for shrews. We used vegetation or aluminum shields to protect the traps from the sun during the summer. The wooden traps provided ample insulation in the winter, so nesting material was not placed in the traps at any time. Traps were set in the afternoon and checked at approximately 0800 and 1500 on the following 3 days. All live shrews were toe-clipped at first capture for individual identification (maximum of two toes on each foot). The field protocol was reviewed periodically by the University of Illinois Laboratory Animal Resource Committee throughout the study and approved, based on University and Federal guidelines as well as those recommended by the American Society of Mammalogists, in effect at the time.

**Data analysis**

Of the 7203 individuals captured during the study, 1933 (26.8%) were dead at first capture. Another 957 were found dead in traps at subsequent captures, for a total trap mortality of 40.1%. While obviously having an impact upon the populations, trap mortality did not appear to disrupt the overall dynamics of our study population or unduly bias our conclusions. *Blarina brevicauda* did not enter traps until they were at least three-fourths grown, so we could not dis-
tistinguish young animals from small adults; thus, we did not separate our data by age class. Estimates of population density were compiled manually, based on the minimum number known alive method (Krebs 1999). Owing to very few captures for many months, often 1 or 2, or no captures at all, and few repeated captures, other models of estimating population density were not appropriate. Population data from all sites within each habitat (Getz 1994) were combined for analysis. Thus, population densities represent averages for all sites within each habitat.

Survival rates were calculated as the proportion of individuals present one month that were trapped the subsequent month. We could not distinguish between mortality and emigration in the monthly survival analyses. Since fewer than 30% of the individuals survived for more than 1 month (see Results), survival data for sequential months are sufficiently independent that they do not create a serious problem with interpretation of statistical analyses. Further, survival curves are based on independent data; individuals are included only once in the analyses.

Owing to difficulty in determining sex and reproductive condition of *B. brevicauda* from external examination, we did not record sex or reproductive condition of most live animals. Reproductive condition was recorded from live males with enlarged testes and from females that were obviously pregnant (confirmed by palpation) or lactating (enlarged nipples); such records constituted fewer than 5% of the total animals recorded as reproductive. Most reproductive data came from necropsy of animals dead in the traps; thus, monthly reproductive data represent independent samples. Males were recorded as reproductive if the testes were ≥3 mm in length; females were recorded as reproductive if the uteri were ≥2 mm in diameter or embryos were present.

Seasonal analyses were based on the following periods: spring (March–May), summer (June–August), autumn (September–November), and winter (December–February). Comparisons of effects of precipitation on peak densities were grouped according to periods with greatest potential for impact: September–December of the previous year and April–August of the same year. April–August is the period of maximum population growth in most years.

We examined correlations between (i) *B. brevicauda* population densities in January–March and peak densities that year, (ii) vole densities in April–August and *B. brevicauda* peak densities that year (the latter typically occurred during the period when vole reproduction was greatest and thus nesting voles would be most available as food for *B. brevicauda*), (iii) total precipitation in the previous September–December and in April–August of the present year and *B. brevicauda* peak densities, (iv) mean monthly survival rates during April–August and peak densities, (v) total precipitation in April–August and mean monthly survival rates, (vi) the proportion of *B. brevicauda* that were reproductive during April–August and peak densities, and (vii) precipitation and the proportion of *B. brevicauda* that were reproductive in April–August.

All monthly *B. brevicauda* population densities and all original vole capture data files from this study are available to anyone wishing to make use of them at http://www.life.uiuc.edu/getz/ [created 28 July 2004].

**Statistical analyses**

Because most of the variables used in our analyses did not meet the requirements for normality (population densities and demographic variables were non-normal at the 0.05 level [Kolmogorov–Smirnov test]; Zar 1999), all variables were log-transformed so that we could use parametric analysis of variance (ANOVA) or Pearson’s correlation analysis. Significant one-way ANOVAs were followed by Tukey’s honestly significant difference (HSD) post hoc multiple comparisons for significance at α = 0.05. We used SPSS® version 10.0.7 for Macintosh (SPSS Inc. 2001) for the above statistical analyses. Chi square tests with Yates’ correction were also employed.

**Results**

**Population densities**

Mean monthly population densities of *B. brevicauda* in bluegrass, alfalfa, and tallgrass were 10.3 ± 0.5, 6.9 ± 0.5, and 5.2 ± 0.3/ha (mean ± SE), respectively, and varied among habitats ($F_{[2,88]} = 48.302, P < 0.001$). Densities in bluegrass were significantly higher than those in alfalfa and tallgrass (Tukey’s HSD test, $P < 0.05$); differences between alfalfa and tallgrass were not significant ($P > 0.05$).

*B. brevicauda* densities displayed annual fluctuations in all three habitats (Fig. 1). Mean annual peak densities were 24.2 ± 1.9/ha in bluegrass, 20.9 ± 1.5/ha in alfalfa, and 16.2 ± 1.3/ha in tallgrass, and varied among habitats ($F_{[2,72]} = 5.219, P = 0.008$). Only the difference between bluegrass and tallgrass was significant (Tukey’s HSD test, $P < 0.05$). The amount of deviation from the mean annual peak density did not vary among the three habitats ($F_{[2,72]} = 1.440, P = 0.244$). Only the significant difference in mean amplitudes of fluctuation among habitats was lower amplitudes (annual low to peak density) in tallgrass than in the other two habitats ($F_{[2,72]} = 4.331, P = 0.017$; Tukey’s HSD test, $P < 0.05$).

The overall annual fluctuation varied among habitats (Fig. 2). Population density increased rapidly in both bluegrass and alfalfa, beginning in May, while increases in tallgrass were more gradual and began later (Fig. 2). On average, population density reached the annual peak in July in bluegrass and in October in both alfalfa and tallgrass ($F_{[2,72]} = 4.234, P = 0.018$); only the difference in the month of peaks in bluegrass and tallgrass was significant (Tukey’s HSD test, $P < 0.05$). Densities in bluegrass declined gradually from the peak through December, before dropping rapidly to a low in March. Population densities in both alfalfa and tallgrass dropped rapidly from the October peak to a low in March.

Population densities declined to zero for at least 1 month each year during 20 years in alfalfa, 15 years in tallgrass, and only 3 years in bluegrass. Mean monthly population densities during the 3 months of lowest densities (January–March; Fig. 2) were 4.4 ± 0.6, 1.7 ± 0.3, and 2.0 ± 0.2/ha in bluegrass, alfalfa, and tallgrass, respectively ($F_{[2,71]} = 14.357, P < 0.001$). January–March densities in bluegrass were significantly higher than those in alfalfa and tallgrass;
there was no difference between alfalfa and tallgrass (Tukey’s HSD test, $P > 0.05$).

Survival

Monthly survival rates for the entire 25 years were significantly lower in alfalfa than in bluegrass and tallgrass (0.331 ± 0.024, 0.466 ± 0.014, and 0.398 ± 0.022, respectively; $F_{[2,33]} = 10.760$, $P < 0.001$). There was no difference between bluegrass and tallgrass (Tukey’s HSD test, $P > 0.05$). Mean monthly survival was slightly higher in bluegrass than the other two habitats during all months except February, July, and August, when survival was highest in tallgrass (Table 1). Survival did not vary seasonally within the three habitats (Table 1; alfalfa: $F_{[3,8]} = 0.811$, $P = 0.522$; bluegrass: $F_{[3,8]} = 0.208$, $P = 0.888$; tallgrass: $F_{[3,8]} = 3.207$, $P = 0.083$).

Survival curves for the three habitats indicated higher survival rates in bluegrass than in alfalfa and tallgrass (Fig. 3). There was no difference in survival among the three habitats the first month following first capture ($\chi^2 = 3.31$, df = 2, $P > 0.05$). Only 27.5% of the $B.\ brevicauda$ in alfalfa, 29.6% in bluegrass, and 31.9% in tallgrass survived for more than 1 month. Survival was significantly greater in bluegrass than in alfalfa and tallgrass during the following 3 months (second month: $\chi^2 = 9.76$, df = 2, $P < 0.02$; third month: $\chi^2 = 14.32$, df = 2, $P < 0.01$; fourth month: $\chi^2 = 26.13$, df = 2, $P < 0.01$). Thereafter the numbers involved were too low for comparisons. Only 2.1% of the 5270 animals survived for 6 months; 6 individuals remained for 12 months.

Reproduction

Overall, the proportions of males and females that were reproductive tended to be smaller in tallgrass than in either bluegrass (males: $\chi^2 = 4.484$, $P = 0.05$; females: $\chi^2 = 13.382$, $P < 0.01$) or alfalfa (males: $\chi^2 = 18.964$, $P < 0.01$; females: $\chi^2 = 12.383$, $P < 0.01$); the proportions of reproductive males and females were similar in the latter two habitats (males: $\chi^2 = 2.721$, $P > 0.05$; females: $\chi^2 = 1.089$, $P > 0.05$). There was a tendency for fewer males and females to be reproductive during the winter than in other seasons (Table 2). A greater proportion of males than females were reproductive during the winter ($\chi^2 = 28.253$, $P < 0.01$) (Table 3). The proportion of reproductive males and females was highest during the spring in all three habitats (Table 3). The increase in the proportion of reproductive males began 2 months earlier than that of females (January and March, respectively; Table 2). Females continued to display indications of reproductive activity, including pregnancy and lactation, approximately 3 months longer than did males: July and October, respectively (Table 2).

Amplitudes of population fluctuations

There was no correlation between January–March population densities (see above) and peak densities for the year
Fig. 3. Survival of *B. brevicauda* following first capture in three habitats. Numbers in parentheses are sample sizes.

![Graph showing percentage surviving vs months]

Mean population densities of neither *M. ochrogaster* nor *M. pennsylvanicus*, nor total vole densities, during April–August were correlated with peak *B. brevicauda* densities for the year in any of the three habitats (alfalfa: *M. ochrogaster*, *r* = –0.344, *n* = 25, *P* = 0.092; *M. pennsylvanicus*, *r* = –0.017, *n* = 25, *P* = 0.935; total voles, *r* = –0.072, *n* = 24, *P* = 0.738; bluegrass: *M. ochrogaster*, *r* = 0.207, *n* = 25, *P* = 0.321; *M. pennsylvanicus*, *r* = 0.133, *n* = 25, *P* = 0.528; total voles, *r* = 0.222, *n* = 25, *P* = 0.286; tallgrass: *M. ochrogaster*, *r* = 0.111, *n* = 25, *P* = 0.598; *M. pennsylvanicus*, *r* = –0.094, *n* = 25, *P* = 0.654; total voles, *r* = –0.40, *n* = 24, *P* = 0.259).

Survival during April–August was not correlated with mean vole densities during these months (*M. ochrogaster*: *r* = –0.006, *n* = 19, *P* = 0.980; *M. pennsylvanicus*: *r* = –0.429, *n* = 19, *P* = 0.067; total voles: *r* = 0.430, *n* = 19, *P* = 0.073). Reproduction was negatively correlated with population density of *M. ochrogaster* during April–August (*r* = –0.488, *n* = 19, *P* = 0.034); reproduction was not correlated with densities of *M. pennsylvanicus* (*r* = 0.008, *n* = 19, *P* = 0.973) or total vole densities (*r* = –0.293, *n* = 19, *P* = 0.224).

Partial correlation analyses of peak densities in bluegrass with precipitation, survival, reproduction, and total vole densities were made, while holding the other three factors constant. Only survival was correlated with peak densities (precipitation: *r* = 0.418, *n* = 14, *P* = 0.107; survival: *r* = 0.625, *n* = 14, *P* = 0.010; reproduction: *r* = 0.139, *n* = 14, *P* = 0.608; total vole densities: *r* = –0.023, *n* = 14, *P* = 0.993).

### Discussion

Densities and amplitudes of fluctuation of *B. brevicauda* populations varied among bluegrass, tallgrass, and alfalfa habitats, with generally higher densities in bluegrass. Variation in survival among the three habitats was the primary factor responsible for higher population densities of *B. brevicauda* in bluegrass. Differential protection from predators provided by vegetative cover most likely explains variation in survival among habitats. Lin and Batzli (1995) list 21 common predators in our study areas (8 mammals, 8 birds, and 5 snakes). Of these, 3 mammalian predators (least weasel, *Mustela nivalis* L., 1766; long-tailed weasel, *Mustela frenata* Lichtenstein, 1831; and mink, *Mustela vison*

Table 2. Total monthly proportions of *B. brevicauda* that were reproductive during 1972–1997.

<table>
<thead>
<tr>
<th>Months</th>
<th>Males</th>
<th>Females</th>
</tr>
</thead>
<tbody>
<tr>
<td>January</td>
<td>0.367</td>
<td>0.074</td>
</tr>
<tr>
<td>February</td>
<td>0.739</td>
<td>0.061</td>
</tr>
<tr>
<td>March</td>
<td>0.938</td>
<td>0.765</td>
</tr>
<tr>
<td>April</td>
<td>0.871</td>
<td>0.767</td>
</tr>
<tr>
<td>May</td>
<td>0.846</td>
<td>0.827</td>
</tr>
<tr>
<td>June</td>
<td>0.607</td>
<td>0.752</td>
</tr>
<tr>
<td>July</td>
<td>0.422</td>
<td>0.586</td>
</tr>
<tr>
<td>August</td>
<td>0.275</td>
<td>0.515</td>
</tr>
<tr>
<td>September</td>
<td>0.378</td>
<td>0.471</td>
</tr>
<tr>
<td>October</td>
<td>0.250</td>
<td>0.265</td>
</tr>
<tr>
<td>November</td>
<td>0.175</td>
<td>0.116</td>
</tr>
<tr>
<td>December</td>
<td>0.079</td>
<td>0.083</td>
</tr>
</tbody>
</table>

Note: Data from all three habitats are combined. Numbers in parentheses are sample sizes.

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Table 3. Total seasonal proportion of *B. brevicauda* that were reproductive in three habitats during 1972–1997.

<table>
<thead>
<tr>
<th></th>
<th>Males</th>
<th>Females</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Bluegrass</td>
<td>Alfalfa</td>
</tr>
<tr>
<td>Spring</td>
<td>0.858a (113)</td>
<td>0.824a (17)</td>
</tr>
<tr>
<td>Summer</td>
<td>0.457a (223)</td>
<td>0.480a (50)</td>
</tr>
<tr>
<td>Autumn</td>
<td>0.246a (228)</td>
<td>0.257a (109)</td>
</tr>
<tr>
<td>Winter</td>
<td>0.361a (97)</td>
<td>0.316a (19)</td>
</tr>
<tr>
<td>Total</td>
<td>0.439 (661)</td>
<td>0.369 (195)</td>
</tr>
</tbody>
</table>

Note: Within columns, values followed by a different letter are significantly different at the 0.05 level (Tukey’s HSD test). Numbers in parentheses are sample sizes.

Schreber, 1777) and all the snakes feed below the vegetation. The remaining predators feed above the vegetation.

Vegetative cover, including a mat of dead grasses at the surface, was dense year-round in bluegrass, while cover was relatively sparse in alfalfa during all seasons, and especially in winter. Although vegetative cover was present year-round in tallgrass, except during summer and autumn following a burn (there were only four burns during the study), there was considerable open space up to 10 cm above the surface in most places. In bluegrass, *B. brevicauda* would be protected from predators hunting from above (large mammals, owls, and other raptors) and at the surface (mink, weasels, and snakes); weasels and snakes would be restricted mainly to hunting within vole surface runways. In tallgrass, there would be protection from predators hunting from above, but less protection from those hunting at the surface. Both groups of predators would be less impeded while hunting in alfalfa than in the other two habitats. Differences in reproduction among the three habitats, as indicated by the proportion of reproductive males and females, appeared to be less important than differential survival in generating higher population densities of *B. brevicauda* in bluegrass than in the other two habitats. The presence of proportionately fewer reproductive males and females in tallgrass than in alfalfa and bluegrass, however, may have contributed to lower population densities in tallgrass than in the latter two habitats.

*Blarina brevicauda* displayed annual population fluctuations, with peak densities during early summer – early autumn, in all three habitats throughout the 25 years of the study. These observations are consistent with several previous accounts of the demography of *B. brevicauda* (Harper 1929; Blair 1948; Manville 1949; Grant 1976), but differ from those of Lima et al. (2002), who found long-term erratic fluctuations. Although it is an important factor in among-habitat differences in population density and peak densities, differential survival did not appear to be responsible for generating annual fluctuations of *B. brevicauda* populations. There was no seasonal pattern to survival in the three habitats.

Seasonal variation in reproduction, coinciding with the annual fluctuations of *B. brevicauda* populations, appears to drive annual population fluctuations in this species. However, the factors responsible for seasonality in reproduction were not obvious. For example, precipitation was not seasonal in our study region (records of the Illinois State Water Survey). Further, food availability did not appear to be a proximate factor involved in the late summer – early autumn decline in reproduction; insect and other invertebrate populations remain high until at least the first autumn frost (Metcalfe and Metcalfe 1993). In east-central Illinois, the mean date of the first frost is 14 October; reproduction of *B. brevicauda* in our study sites began to decline before this date. Trapping sessions in this study were normally completed during the first half of each month. The main decline in the proportion of reproductive females occurred between mid-September and early October, well before the typical date of the first frost. Low food availability could, of course, be a factor in the low level of reproduction during winter. Declines in reproduction also were not related to low-temperature stresses; reproduction began declining in June (males) and September (females), well before late-autumn temperature declines (records of the Illinois State Water Survey). Wayne and Rissman (1990) and Chang et al. (1999) indicated that reproductive activation of male house shrews, *Suncus murinus* (L., 1766), was controlled, in part, by photoperiod. Churchfield (1990) also suggested that reproduction in shrews is related to photoperiod. Because of small monthly sample sizes, we were unable to test for specific effects of photoperiod on reproduction.

Whereas seasonal variation in reproduction appeared to be responsible for the annual population fluctuations, reproduction was not involved in variation in peak densities among years. There was no correlation between April–August reproduction and peak densities in given years. Variation in mortality seemed to be the factor most likely responsible for variation in peak densities among years. Although seasonal variation in survival did not appear to be responsible for driving annual population fluctuations, variation in mean monthly survival in April–August was positively correlated with peak densities achieved in given years in bluegrass (the only habitat for which sample sizes were adequate for analysis). Lima et al. (2002) also concluded that variation in survival was more important than variation in reproduction in explaining fluctuations in *B. brevicauda* populations. These authors suggested that such changes were intrinsic, and did not address the role of predation in survival.

We found no evidence to support the suggestion by Smith et al. (1974) that precipitation during the previous autumn impacted population densities the following year. April–August precipitation and peak densities of *B. brevicauda* were correlated, however, in bluegrass and tallgrass but not
alfalfa. We suggest that less cover in alfalfa and higher mortality from predation offset the influence of precipitation in this habitat. The dense mat of dead vegetation over the surface in bluegrass and tallgrass also may have resulted in more moist conditions than in the open alfalfa. Getz (1965, 1971) found, however, that although relative humidities were higher where vegetative cover was denser, absolute humidities did not differ; the latter are more important than relative humidities in the respiratory water balance of small mammals (Getz 1968). Matlack et al. (2002) suggested that greater numbers of Elliot’s short-tailed shrew, Blarina hylophaga Elliot, 1889, in areas of dense vegetative cover may have involved greater food availability as a result of moister soil and air conditions. Pankakoski (1985) also suggested that breeding success of the Eurasian shrew, Sorex araneus L., 1758, was promoted by improved food availability due to high precipitation during the breeding season.

While variation in precipitation was positively associated with peak densities of B. brevicauda in bluegrass and tallgrass, neither survival nor reproduction was correlated with precipitation. Partial correlation analysis of effects among precipitation, reproduction, and survival revealed that only survival was correlated with peak densities. During an extreme drought, in June–September 1988, survival rates were >30% lower than the 25-year mean for these months (Getz 1994). Reproduction, on the other hand, was not adversely affected by the drought.

If adult or nestling voles were a major food source for B. brevicauda, densities of B. brevicauda should have been high when vole densities were high, owing to increased food availability. Peak densities of B. brevicauda were not correlated with population densities of either species of vole during the period of annual population growth of B. brevicauda (April–August) in any habitat. That neither survival nor reproduction of shrews during April–August was correlated with population densities of voles during this period further suggests that predation on voles was not a major factor influencing population densities of B. brevicauda.

We conclude that seasonal reproduction was the major factor generating annual population fluctuations of B. brevicauda, but not variation in peak densities among years. Differential mortality, most likely from predators, appeared to be the primary factor responsible for variation in annual peak densities. Because B. brevicauda populations fluctuate annually, while voles show erratic multi-annual fluctuations (Getz et al. 2001), we suggest that B. brevicauda experienced predation effects different from those of the voles, and that such differential survival did not drive annual population fluctuations of B. brevicauda. Similar conclusions regarding effects of predators on shrews have been drawn from studies of Fennoscandian shrews (Skaren 1972; Hansson 1984; Henttonen 1985; Kaikusalo and Hanski 1985; Korpinen 1986; Sonerud 1988; Henttonen et al. 1989; Korpinen and Nordahl 1989). Shrew populations in Fennoscandia, especially those of S. araneus, displayed erratic seasonal fluctuations that typically were not in synchrony with cyclic fluctuations of voles.

Getz (1994) discusses the potential impact of predation by mammals, birds, and snakes on fluctuations of B. brevicauda populations, based on analysis of the first 18 years of this study. He concluded that varying effects of generalist bird, mammal, and snake predators were involved in differential mortality of B. brevicauda among habitats. Results of the entire 25-year study agree with those conclusions.

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**References**


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