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Dynamics of vole populations: an experimental evaluation of the influence of food resources

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Abstract: We studied responses of populations of *Microtus ochrogaster* and *M. pennsylvanicus* in east-central Illinois, USA to supplemental food in intermediate (bluegrass) and low (tallgrass prairie) food habitats. Whereas amplitudes of fluctuation of *M. ochrogaster* were higher in supplementally fed than in control sites in intermediate food habitat, mean population densities and patterns of fluctuation did not differ between the two sites in either habitat. Mean population densities of *M. pennsylvanicus* were higher in supplementally fed than in control sites only in low food tallgrass habitat. Supplemental food did not positively influence survival or maturation rates of *M. ochrogaster* in either habitat; the proportion of reproductively active adult females and adult male body mass were higher only in supplementally fed sites in intermediate food habitat. Supplemental food did not influence any variable of *M. pennsylvanicus* in bluegrass, nor survival in tallgrass, whereas maturation rates were shortened and proportion reproductively active females, immigration, and male body mass were greater in supplementally fed low food habitat. We conclude that food resources play only a minor role in driving the dynamics of populations of *M. ochrogaster* and *M. pennsylvanicus*.

Key words: Demography; Food resources; *Microtus ochrogaster*; *Microtus pennsylvanicus*; Supplemental feeding

鼠类种群动态：食物资源影响力的实验评估

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摘要：本研究在美国伊利诺斯州中东部测定了中等食物质量（莓系属的牧草）和低食物质量（高杆草牧场）栖息地内橙腹田鼠（*Microtus ochrogaster*）和草原田鼠（*M. pennsylvanicus*）种群对附加食物的响应。在中等食物质量栖息地内投放附加食物，橙腹田鼠种群的波动幅度高于对照样地，但同类型食物质量栖息地内，种群平均密度和波动模式无显著的差异。仅在低等食物质量的高杆草栖息地内，投放附加食物可导致草原田鼠的种群密度高于对照样地。附加食物不直接影响两种栖息地内橙腹田鼠的成活率或成熟率，在中等食物质量栖息地中投放附加食物，繁殖活跃的成熟雌性个体比例及雄性成体的体重高于对照。附加食物不影响莓系属牧草内草原田鼠，也不能影响该动物在高杆草环境中的存活率。然而，投放附加食物，可缩短低等食物质量栖息地内草原田鼠的成熟期，提高繁殖活跃雌性的比例和迁入个体比例，增加并引起雄性个体体重增加。据此，本研究证明食物资源在橙腹田鼠和草原田鼠种群动态中只起极小的作用。

关键词：数量统计；食物资源；橙腹田鼠；草原田鼠；附加食物
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Higher levels of food resources, whether naturally occurring or experimentally provided, have been shown to increase population densities or amplitudes of fluctuation of arvicoline (microtine) rodents (Meserve, 1971; Cole and Batzli, 1978; Taitt and Krebs, 1981; Desy and Thompson, 1983; Ford and Pitelka, 1984; Boutin, 1990; Batzli and Lesieutre, 1991; Hall *et al.*, 1991; Lofgren *et al.*, 1996; Prevot-Jul-

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liard *et al.*, 1999). Greater survival, higher reproduction, more rapid body growth, greater body mass, more rapid reproductive maturation, and increased immigration have been associated with higher population densities in habitats with abundant food (Cole and Batzli, 1978, 1979; Taitt and Krebs, 1981, 1983; Desy and Thompson, 1983; Desy and Batzli, 1989; Lofgren *et al.*, 1996; Prevot-Julliard *et al.*, 1999; Kasparian and Millar, 2004). Most studies involving food supplementation, however, have found that increased levels of food do not substantially alter the pattern of population dynamics (Krebs and DeLong, 1965; Cole and Batzli, 1978; Desy and Thompson, 1983; Boutin, 1990; Yoccoz *et al.*, 2001). Recent studies also indicate that food resources may not be the primary factor responsible for higher population densities of a species (Lin and Batzli, 2001; Getz *et al.*, 2005a).

Most evidence for the influence of food on population dynamics of arvicoline rodents comes from comparison of population dynamics in supplementally fed and control sites in the same habitat. There is no study evaluating the effects of supplemental feeding in habitats that provide different levels of food. Moreover, experimental studies of the influence of supplemental feeding on arvicoline population dynamics were usually of short duration, and thus did not provide insights into the influence of long-term effects of food supplementation on population dynamics.

As part of a long-term demographic study (Getz *et al.*, 2001), we conducted manipulative studies to examine the influence of food resources on population dynamics of the prairie vole, *Microtus ochrogaster*, and meadow vole, *M. pennsylvanicus*. Experimental manipulations involved supplemental feeding of populations for up to 10 years in habitats with presumed intermediate and low food resources. Specifically, we tested the hypotheses that both species would achieve only moderately higher population densities in supplementally fed than control intermediate food habitat, and much higher population densities in supplementally fed than control low food habitat.

1 Materials and methods

1.1 Study sites

The study sites were located in the University of Illinois Biological Research Area ("Phillips Tract"), 6 km NE of Urbana, Illinois, USA (40°15′N, 88°28′W). Populations of *M. ochrogaster* and *M. pennsylvanicus* were monitored monthly in two habitats: restored tallgrass prairie (a mixture of big bluestem, *Andropogon gerardii*; Indian grass, *Sorghastrum nutans*; and switch grass, *Panicum* spp.) and bluegrass, *Poa pratensis*. Tallgrass is a very low food habitat, while bluegrass provides an intermediate food source for the two species of vole (Thompson, 1965; Cole and Batzli, 1979; Getz *et al.*, 1979; Lindroth and Batzli, 1984).

1.2 Methods

All study sites were organized on a grid system with 10 m intervals between trap stations. 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; cracked corn was used for prebaiting and as bait in traps. Traps were set in the afternoon and checked at about 08:00 h and 15:00 h on the following three days. All animals were toe-clipped at first capture for individual identification (≤2 toes on each foot). All procedures were approved by the University of Illinois Laboratory Animal Care Committee and meet the guidelines recommended by the American Society of Mammalogists (Animal Care and Use Committee, 1998).

Species, grid station, individual identification, sex, reproductive condition (males, testes abdominal or scrotal; females, vagina open or closed, pregnant as determined by palpation, or lactating), and body mass to the nearest 1 g were recorded at each capture. Animals were grouped by age based on body mass: adult, >30 g; young, ≤29 g.

A 0.5 ha bluegrass study site was supplementally fed from June 1977 through December 1983. An adjacent 0.8 ha bluegrass site, separated from the supplementally fed site by a 15 m closely mown area, served as the control (Getz *et al.*, 2001). These were the same sites previously used by Cole and Batzli (1978). A 0.5 ha tallgrass site at the east end of the tallgrass prairie in Phillips tract (Getz *et al.*, 2001) was supplementally fed from September 1977 through May 1987. A similar size site at the west end of the prairie, 150 m from the supplementally fed site, served as the control. Both species of vole were present in all 4 sites. Because *M. pennsylvanicus* appeared to have a suppressing effect on *M. ochrogaster* in tallgrass (Getz *et al.*, 1987), all *M. pennsylvanicus* were removed from the supplementally fed and control tallgrass sites at each trapping from September 1984 - May 1987 to reduce the effects of *M. pennsylvanicus* on responses of *M. ochrogaster* to supplemental feeding.

A feeding station, consisting of a 0.5 liter glass bottle, was located at each trapping station. Purina rabbit chow (No. 5321), a high-quality diet for both *M. ochrogaster* and *M. pennsylvanicus* (Cole and Batzli, 1979), was used as supplemental food. The bottles were checked twice weekly and refilled as necessary to ensure food was present in them and in good condition at all times.

2 Data analysis

We analyzed our data within capture-mark-recapture (CMR) framework (Lebreton *et al.*, 1992, Williams *et al.*, 2001). We implemented CMR methods using Program MARK (White and Burnham, 1999) to estimate demographic parameters [apparent survival (ϕ) and maturation rates (Ψ)], to test specific hypotheses regarding these parameters, and to evaluate the effects of supplemental food. Specifically, we used Cormack-Jolly-Seber (CJS) models (Cormack 1964; Jolly, 1965; Seber, 1965) to estimate overall survival and recapture rates (ρ), and to test for variation in survival rates among experimental groups and through time. We applied goodness-of-fit tests using RELEASE TEST 2 + 3 (available in program MARK) to test if our global model fits the data. When the over-dispersion parameter ($\hat{c}$) was greater than 1, we corrected for over-dispersion using the calculated $\hat{c}$. Next, we used Akaike's information criterion corrected for small sample size and adjusted for quasi-likelihood (AIC_c) for model comparison, and for the identification of the most parsimonious model; the lower the AIC_c value, the more parsimonious the model. The most parsimonious model in the candidate model set was compared to neighbouring models based on the differences in AIC_c values, ΔAIC_c. If $\Delta AIC_c < 2$, both models are equally supported by the data. If $2 < \Delta AIC_c < 7$, there is considerable support for a real difference between the models, and if $\Delta AIC_c > 7$, there is a strong evidence for a difference between the models (Burnham and Anderson, 2002).

We used multi-state CMR models (Hestbeck *et al.*, 1991, Brownie *et al.*, 1993, Williams *et al.*, 2001, Fujiwara and Caswell, 2002) to estimate reproductive state-specific survival and maturation rates (probability that a nulliparous animal becomes reproductive). Each vole in our sample was classified either as a young (nulliparous) or an adult (reproductive). Once an animal became reproductive, it was considered as an adult and remained an adult for the rest of its life. These analyses allowed us to estimate and model apparent survival rates for young (ϕ_{yng}) and adult voles (ϕ_{ad}), and maturation rates (Ψ). Using the most parsimonious model obtained from CJS models, we investigated patterns in maturation and stage-specific survival rates.

We performed our analyses separately for 4 species-habitat combinations: (1) *M. ochrogaster* in bluegrass habitat, (2) *M. ochrogaster* in tallgrass, (3) *M. pennsylvanicus* in bluegrass habitat, and (4) *M. pennsylvanicus* in tallgrass habitat (Table 1). Our preliminary analysis showed that survival rates did not differ between sexes; therefore, we combined the data for both sexes in further analyses. We excluded the transient animals (adults captured only once) from the CMR analyses.

Table 1 Description of the four study sites: species, habitat, start and end date, and duration of the food supplementation experiment, and number of voles in control and experimental groups that were used in CMR analysis for each species-habitat combination

Species	Habitat	Start date	End date	Control No. voles	Food No. voles
M. ochrogaster	Bluegrass	1 - Jun - 1977	1 - Dec - 1983	315	258
M. ochrogaster	Tallgrass	1 - Nov - 1984	1 - Nov - 1986	416	296
M. pennsylvanicus	Bluegrass	1 - Jun - 1977	1 - Dec - 1982	845	473
M. pennsylvanicus	Tallgrass	1 - Sep - 1977	1 - May - 1984	768	899

Effects of food supplementation on survival, maturation, and recapture rates were analyzed by examining both combined and additive effect of food supplementation and time (Williams *et al.*, 2001). For example, a model denoted as ϕ (time* sup) contains the combined effects of time and food supplementation on survival, including main effects of time and food supplementation, and also the interaction between these two covariates, whereas ϕ (time + sup) represents only the additive effect of time and food supplementation on survival. To analyze the effect of density on temporal variation in the survival rate, we constrained the logit of survival rate to be a linear function of population density (Cooch and White, 2002). Population size for each occasion was estimated using the Jolly-Seber method (Pollock *et al.*, 1990).

We estimated persistence of voles first captured as young, and presumed to have been born on the study site, as follows. We assumed voles recorded as young in a given trapping session were born midway between that trapping session and the previous session. Voles that disappeared from a site were presumed to have done so midway between the last session they were captured and the subsequent session. Persistence as defined herein includes both in situ mortality and emigration; the former is presumed to be the most prevalent cause of disappearance (Verner and Getz, 1985). Owing to small monthly sample sizes, persistence data for the two sexes were combined.

We estimated the proportion of reproductively active adult females for each month. Because reproductive condition of females can be more accurately determined than that of males, only females were used in our analysis. We limited our comparisons of body mass to adult males to avoid bias from variation in the proportion of the population comprised of young voles and from variation in the reproductive status of females (i.e., changes in body mass due to pregnancy, parturition, and lactation; Ostermeyer, 1983). Individuals ≤29 g when first captured were presumed to have been born in the study site, while those weighing ≥30 g when first captured were assumed to have been born elsewhere and to have immigrated into the site since the last trapping session (Getz *et al.*, 2005b).

In our analysis of proportion of adult females reproductively active, we used data from every second month to increase independence of the data. For the analyses of body mass, we avoided bias from inclusion of the same individual in subsequent months by using data for each adult male only once, the first month it appeared as an adult in the capture data.

We used independent-sample *t*-tests to compare within each habitat proportion of reproductively active adult females, persistence of young, adult body mass, and number of immigrants between supplementally fed and control sites. Because most of these variables 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. For variables that included "zeros" we added 0.001 prior to transformation. This allowed us to test for differences using independent-sample *t*-tests. When degrees of freedom for *t*-tests are given in whole numbers, variances are equal (Levene's test for equality of variances). When variances were not equal, *df* is given to one decimal place. SPSS 10.0.7 for Macintosh (SPSS, Inc., 2001) was used for these statistical analyses.

All original capture data and explanatory files from the 25-year study are available to anyone wishing to make use of them at: http://www.life.uiuc.edu/getz/

3 Results

3.1 Population density

There was no difference in population densities of *M. ochrogaster* between supplementally fed and control sites in bluegrass habitat (Fig. 1; Table 2). *M. ochrogaster* was either absent or in very low numbers in both supplementally fed and control tallgrass sites from 1977 – 1984 and this did not differ between the two sites (Getz *et al.*, 1987). During November 1984 – December 1985, when *M. pennsylvanicus* were removed from both sites, there were large fluctuations in *M. ochrogaster* densities in tallgrass (Fig. 2). We used data only from this period in our analyses; densities of *M. ochrogaster* were higher in the control than supplementally fed site, but the difference was not significant (Table 2).

Table 2 Effects of supplemental feeding on the population density (no./ha), persistence of young on study sites (no. of months), proportion females reproductively active, and adult male body mass (g) of *M. ochrogaster* and *M. pennsylvanicus* in two habitats (bluegrass and tallgrass). Mean ± SE are presented for each variable. Results of 2-sample *t*-tests comparing each variable between control and experimental sites are given for each species-habitat combination

	Population density	Persistence	% Reproductive	Immigrants	Body mass
Bluegrass					
M. ochrogaster					
Supp fed	8.99 ± 1.77	1.81 ± 0.20	0.789 ± 0.053	3.3 ± 0.6	39.2 ± 0.5
Control	8.91 ± 1.46	1.64 ± 0.11	0.358 ± 0.039	2.6 ± 0.4	36.0 ± 0.4
t; *df*	0.04; 156	0.583; 165	6.250; 89	0.483; 140	3.759; 219
P	0.97	0.561	< 0.001	0.630	< 0.001
M. pennsylvanicus					
Supp fed	45.25 ± 7.61	2.03 ± 0.17	0.660 ± 0.057	7.1 ± 1.2	40.8 ± 0.8
Control	50.71 ± 4.63	2.11 ± 0.11	0.656 ± 0.037	5.0 ± 0.9	40.6 ± 0.4
t; *df*	0.61; 109	0.644; 396	0.167; 115	0.997; 144	0.500; 471
P	0.54	0.520	0.868	0.330	0.618
Tallgrass					
M. ochrogaster					
Supp fed	60.72 ± 14.02	1.45 ± 0.10	0.593 ± 0.101	8.8 ± 2.4	40.6 ± 0.7
Control	89.14 ± 20.70	2.06 ± 0.16	0.589 ± 0.081	9.6 ± 2.1	40.1 ± 0.5
t; *df*	1.14; 48	3.696; 268.6	0.761; 36	0.836; 58	0.520; 232
P	0.26	< 0.001	0.452	0.407	0.603
M. pennsylvanicus					
Supp fed	83.89 ± 6.20	2.64 ± 0.18	0.600 ± 0.036*	14.1 ± 1.6	42.0 ± 0.4
Control	57.63 ± 4.77	2.59 ± 0.15	0.485 ± 0.044	8.8 ± 1.0	39.4 ± 0.3
t; *df*	3.36; 150	–0.163; 417	2.23; 134.65	2.398; 158	5.751; 820.8
P	< 0.01	0.870	0.027	0.018	< 0.001

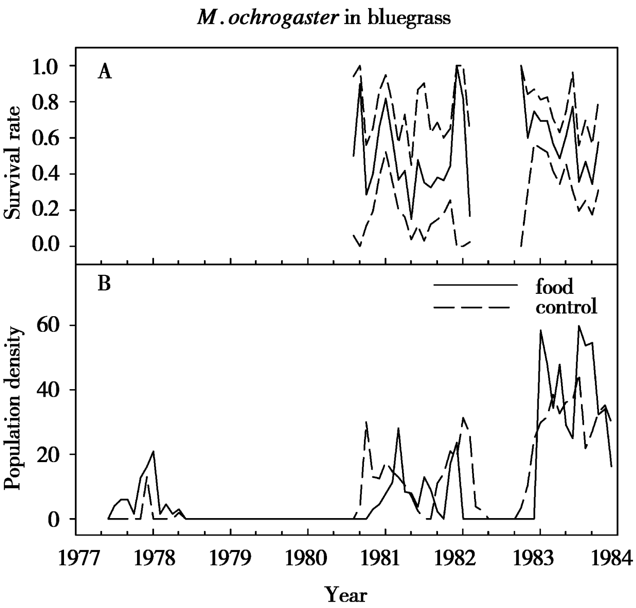

Fig. 1 (A) Temporal variation in monthly survival rates of *M. ochrogaster* in bluegrass habitat. Because food supplementation did not significantly influence survival, survival rates were estimated using the model $\{\phi(\text{time})\ \rho(\text{sup}^*\ \text{time})\}$ (Table 1). Dashed lines indicate 95% confidence intervals. (B) Monthly estimates of population densities (individuals/hectare) are given for food supplemented (food) and control sites.

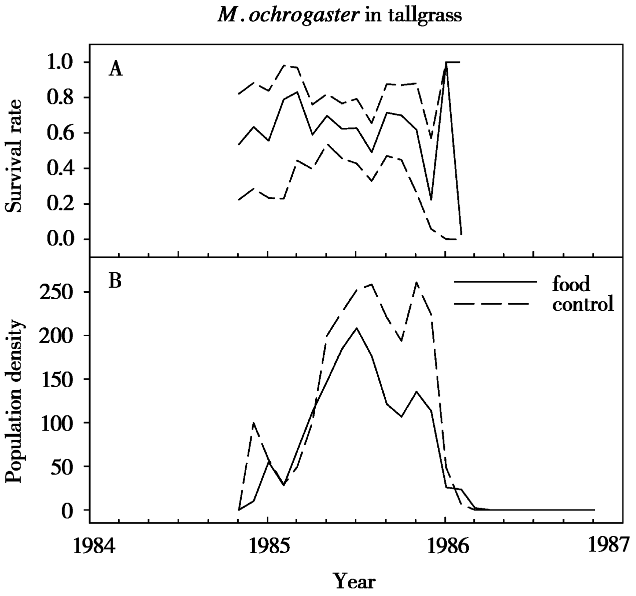

Fig. 2 (A) Temporal variation in monthly survival rates of *M. ochrogaster* in tallgrass habitat. Because food supplementation did not significantly influence survival, survival rates were estimated using the model $\{\phi(\text{time})\ \rho(\text{time})\}$ (Table 1). Dashed lines indicate 95% confidence intervals. (B) Monthly estimates of population densities (individuals/hectare) are given for food supplemented (food) and control sites.

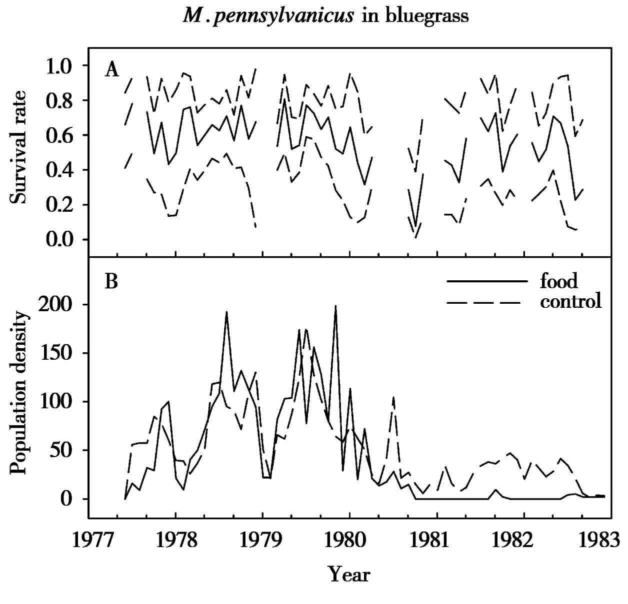

Fig. 3 (A) Temporal variation in monthly survival rates of *M. pennsylvanicus* in bluegrass habitat. Because food supplementation did not significantly influence survival, survival rates were estimated using the model $\{\phi(\text{time})\ \rho(\text{sup}^*\ \text{time})\}$ (Table 1). Dashed lines indicate 95% confidence intervals. (B) Monthly estimates of population densities (individuals/hectare) are given for food supplemented (food) and control sites.

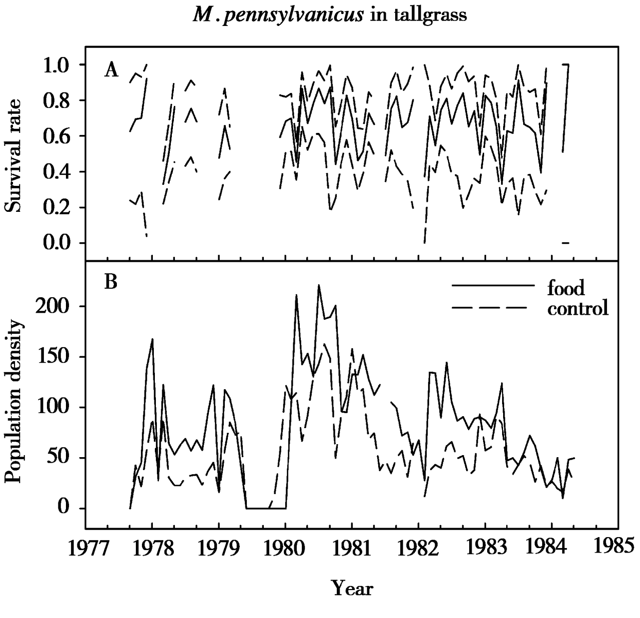

Fig. 4 (A) Temporal variation in monthly survival rates of *M. pennsylvanicus* in tallgrass habitat. Because food supplementation did not significantly influence survival, survival rates were estimated using the model $\{\phi(\text{time})\ \rho(\text{sup}+\text{time})\}$ (Table 1). Dashed lines indicate 95% confidence intervals. (B) Monthly estimates of population densities (individuals/hectare) are given for food supplementation (food) and control sites.

Population densities of *M. pennsylvanicus* in bluegrass did not differ between the control and supplementally fed sites (50.7 ± 4.6 and 45.2 ± 7.6 voles/ha, respectively; $t = 0.61$, $df = 109$, $P = 0.54$; Fig. 3; Table 2). *M. pennsylvanicus* populations in supplementally fed and control tallgrass sites were generally high at all times and higher in the supplementally fed than control site (83.9 ± 6.2 and 57.6 ± 4.8

voles/ha, respectively; $t = 3.36$, $df = 150$, $P < 0.01$), with no indication of distinct population fluctuations in either site (Fig. 4; Table 2).

3.2 Demographic variables

Goodness-of-fit tests (Table 3) indicated that our global CJS model fit the data with a moderate underdispersion ($\hat{c} < 1.0$) in two sites (*M. ochrogaster* in bluegrass, $\hat{c} = 0.79$; *M. pennsylvanicus* in bluegrass, $\hat{c} = 0.80$), an over-dispersion ($\hat{c} > 1$) in one site (*M. ochrogastger* in tallgrass, $\hat{c} = 2.57$, and an almost perfect fit in one site (*M. pennsylvanicus* in tallgrass, $\hat{c} = 1.10$). Where $\hat{c} > 1.0$, we used the value to correct for over-dispersion in parameter estimation and quasi-likelihood adjustment for model comparison. Our analyses using CJS models showed that the most parsimonious recapture rate model differed among the four species-habitat combinations (Table 4). The most parsimonious survival rate model included only the food supplementation effect for *M. ochrogaster* in tallgrass, and only the time-effect for *M. ochrogaster* in bluegrass, *M. pennsylvanicus* in bluegrass, and *M. pennsylvanicus* in tallgrass (Table 4).

Table 3 Results of goodness-of-fit tests for the global Cormack-Jolly-Seber models for each species-habitat combination. The values of the variance inflation factor ($\hat{c}$) also are given

Species	Habitat	Model Deviance	Degrees of freedom	$\hat{c}$
M. ochrogaster	Bluegrass	69.8	87	0.79
M. ochrogaster	Tallgrass	200.5	78	2.57
M. pennsylvanicus	Bluegrass	180.9	225	0.80
M. pennsylvanicus	Tallgrass	384.4	349	1.10

Although the effect of food supplementation was included in the most parsimonious model for *M. ochrogaster* in tallgrass, comparison of this and the neighboring model (without food supplementation effect) failed to detect a significant effect of food supplementation ($\Delta AIC_c < 2$). Thus, our results suggest that food supplementation did not affect the survival rates in any of the four species-site combinations. In *M. ochrogaster* in bluegrass and *M. pennsylvanicus* in tallgrass, survival rates significantly varied through time (Figs. 1 – 4). However, in *M. pennsylvanicus* in bluegrass, comparison of the time-effect model and the constant survival rate model revealed the lack of a significant effect of time on survival rates ($\Delta AIC_c < 1$). The AIC_c values for survival rate models, in which population density was used as a covariate, ranked much lower ($\Delta AIC_c > 20$) than the survival rate models with the time-effect, indicating that population density did not significantly influence observed temporal variation in survival rate.

Analyses of two-state models revealed a similar pattern of the influence of supplemental food on state-specific survival rates (Table 5). For *M. ochrogaster* in bluegrass, the most parsimonious model included only the effect of time on maturation rate, indicating that this parameter varied over time, but was not influenced by supplemental food. Although the interactive effects of food supplementation and time on maturation rate was included in the most parsimonious model for *M. ochrogaster* in tallgrass, comparison between this model and the neighboring model (with only time effect) failed to detect a significant effect of food supplementation ($\Delta AIC_c < 2$; Table 5).

For *M. pennsylvanicus*, maturation rates varied only temporally in bluegrass, but there was an interactive effect of supplemental food and time on maturation rate in tallgrass habitat (Table 5). Thus, our results indicate that supplemental food might have influenced maturation rate only in tallgrass habitat (Table 5). However, the influence of food supplementation on maturation rate was not apparent when temporal variation was ignored (Table 6).

Table 4 Akaike's information criterion corrected for small sample size and adjusted for quasi-likelihood (AIC_c), number of parameters and model deviance for the CJS models. Parameter ϕ is the apparent survival rate, ρ is the recapture rate, and sup indicates food supplementation. For model definitions, see text. Only four most parsimonious models are given for each species-habitat combination

	AIC_c	Num. Par.	Deviance
***M. ochrogaster* in bluegrass**			
ϕ (time) ρ (exp * time)	1449.24	70	399.09
ϕ (sup + time) ρ (sup * time)	1449.51	71	397.02
ϕ (sup * time) ρ (sup + time)	1465.94	81	389.67
ϕ (sup * time) ρ (time)	1476.12	82	397.45
***M. ochrogaster* in tallgrass**			
ϕ (sup) ρ (time)	1017.69	18	308.15
ϕ (sup) ρ (time)	1019.09	17	311.60
ϕ (sup) ρ (sup + time)	1019.27	19	307.67
ϕ (sup) ρ (sup + time)	1019.37	18	309.83
***M. pennsylvanicus* in bluegrass**			
ϕ (time) ρ (sup * time)	4747.60	146	1309.35
ϕ (time) ρ (sup * time)	4748.06	101	1410.25
ϕ (sup) ρ (sup * time)	4748.15	102	1408.15
ϕ (sup + time) ρ (sup * time)	4750.14	148	1307.33
***M. pennsylvanicus* in tallgrass**			
ϕ (time) ρ (sup + time)	6636.01	134	2513.95
ϕ (sup + time) ρ (sup + time)	6636.84	138	2506.09
ϕ (time) ρ (time)	6648.22	133	2528.33
ϕ (sup + time) ρ (time)	6649.21	135	2524.99

Supplemental food did not influence persistence of young *M. ochrogaster* in bluegrass (1.8 ± 0.2 and 1.6 ± 0.1 months, supplementally fed and control, respectively; $t = 0.58$, $df = 165$, $P = 0.56$) or the number of immigrants (3.3 ± 0.6 and 2.5 ± 0.4 voles/month; $t = 0.48$, $df = 140$, $P = 0.63$), but significantly increased the proportion of reproductively active adult females (0.80 ± 0.05 and 36 ± 0.04; $t = 6.25$,

$df = 89$, $P < 0.01$) and adult male body mass (39.2 ± 0.5 and 36.0 ± 0.4 g; $t = 3.76$, $df = 219$, $P < 0.01$). With respect to *M. ochrogaster* in tallgrass, none of the variables was significantly affected by supplemental feeding (persistence: 1.4 ± 0.1 and 2.1 ± 0.2 months, supplementally fed and control, respectively; $t = 3.70$, $df = 268.6$, $P < 0.01$. immigrants: 8.8 ± 2.4 and 9.6 ± 2.1 voles/month; $t = 0.84$, $df = 58$, $P = 0.41$. proportion females reproductive: 0.59 ± 0.10 and 0.60 ± 0.08; $t = 0.76$, $df = 36$, $P = 0.45$. body mass: 40.6 ± 0.7 and 40.1 ± 0.5 g; $t = 0.52$, $df = 232$, $P = 0.60$).

Table 5 Akaike's information criterion corrected for small sample size (AICc), number of parameters and model deviance for the multistate models fitted to the vole data. Parameter ϕ is the apparent survival rate, ρ is the recapture rate, Ψ is the maturation rate, and sup indicates food supplementation. For model definitions, see text. Only four most parsimonious models for each site are given

	AIC_c	Num. Par.	Deviance
M. ochrogaster in bluegrass			
ϕ_{yng} (time) ϕ_{ad} (time) ρ_{yng} (time) ρ_{ad} (time) Ψ (time)	1408.60	27	579.35
ϕ_{yng} (time) ϕ_{ad} (time) ρ_{yng} (time) ρ_{ad} (time) Ψ (time)	1450.74	28	619.36
ϕ_{yng} (time) ϕ_{ad} (time) ρ_{yng} (time) ρ_{ad} (time) Ψ (sup* time)	1537.11	94	554.03
ϕ_{yng} (time) ϕ_{ad} (time) ρ_{yng} (time) ρ_{ad} (time) Ψ (sup + time)	1562.74	96	574.68
M. ochrogaster in tallgrass			
ϕ_{yng} (time) ϕ_{ad} (time) ρ_{yng} (time) ρ_{ad} (time) Ψ (sup* time)	2584.51	48	942.37
ϕ_{yng} (time) ϕ_{ad} (time) ρ_{yng} (time) ρ_{ad} (time) Ψ (time)	2585.89	42	956.57
ϕ_{yng} (time) ϕ_{ad} (time) ρ_{yng} (time) ρ_{ad} (time) Ψ (sup + time)	2587.50	43	956.05
ϕ_{yng} (time) ϕ_{ad} (time) ρ_{yng} (time) ρ_{ad} (time) Ψ (sup + time)	2609.25	30	1005.26
M. pennsylvanicus in bluegrass			
ϕ_{yng} (time) ϕ_{ad} (time) ρ_{yng} (time) ρ_{ad} (time) Ψ (time)	5099.81	210	1889.40
ϕ_{yng} (time) ϕ_{ad} (time) ρ_{yng} (time) ρ_{ad} (time) Ψ (sup + time)	5110.02	212	1894.76
ϕ_{yng} (time) ϕ_{ad} (time) ρ_{yng} (time) ρ_{ad} (time) Ψ (sup + time)	5157.42	184	2009.11
ϕ_{yng} (time) ϕ_{ad} (time) ρ_{yng} (time) ρ_{ad} (time) Ψ (sup)	5173.84	189	2013.70
M. pennsylvanicus in tallgrass			
ϕ_{yng} (time) ϕ_{ad} (time) ρ_{yng} (time) ρ_{ad} (time) Ψ (sup * time)	7711.13	258	3353.92
ϕ_{yng} (time) ϕ_{ad} (time) ρ_{yng} (time) ρ_{ad} (time) Ψ (time)	7765.88	246	3436.73
ϕ_{yng} (time) ϕ_{ad} (time) ρ_{yng} (time) ρ_{ad} (time) Ψ (sup + time)	7767.22	247	3435.74
ϕ_{yng} (time) ϕ_{ad} (time) ρ_{yng} (time) ρ_{ad} (time) Ψ (sup)	7848.76	219	3581.99

Table 6 Estimates (mean ± SE) of the monthly apparent survival and maturation rates for each species-habitat combination. See Tables 3 – 4 for symbols and model definitions

Species/habitat	**Site**	$\phi_{overall}$	ϕ_{young}	ϕ_{adult}	Ψ
M. ochrogaster					
Bluegrass	Control	0.522 ± 0.024^{a}	0.507 ± 0.052^{d}	0.562 ± 0.028^{d}	0.414 ± 0.073^{d}
	Supp fed	0.581 ± 0.033^{a}	0.633 ± 0.056^{d}	0.505 ± 0.032^{d}	0.377 ± 0.066^{d}
Tallgrass	Control	0.670 ± 0.028^{b}	0.573 ± 0.034^{d}	0.748 ± 0.020^{d}	0.267 ± 0.038^{d}
	Supp fed	0.588 ± 0.036^{b}	0.487 ± 0.043^{d}	0.672 ± 0.026^{d}	0.324 ± 0.056^{d}
M. pennsylvanicus					
Bluegrass	Control	0.642 ± 0.012^{a}	0.676 ± 0.027^{d}	0.648 ± 0.013^{d}	0.392 ± 0.035^{d}
	Supp fed	0.610 ± 0.019^{a}	0.618 ± 0.041^{d}	0.557 ± 0.022^{d}	0.334 ± 0.052^{d}
Tallgrass	Control	0.652 ± 0.012^{c}	0.694 ± 0.022^{d}	0.655 ± 0.014^{d}	0.332 ± 0.028^{d}
	Supp fed	0.696 ± 0.010^{c}	0.718 ± 0.021^{d}	0.686 ± 0.011^{d}	0.337 ± 0.027^{d}

Model structure used for each estimate (for details, see Tables 4 – 5):

[a] {ϕ (sup) ρ (sup* time)}; CJS model

[b] {ϕ (sup) ρ (time)}; CJS model

[c] {ϕ (sup) ρ (sup + time)}; CJS model

[d] {ϕ_{yng} (sup) ϕ_{ad} (sup) ρ_{yng} (time) ρ_{ad} (time) Ψ (sup)}; Multistate model

Food supplementation did not influence persistence (2.0 ± 0.2 and 2.1 ± 0.1 months, supplementally fed and control, respectively; $t = 0.64$, $df = 396.6$, $P = 0.52$), number of immigrants (7.1 ± 1.2 and 5.0 ± 0.9 voles/month; $t = 1.00$, $df = 144$, $P = 0.33$), proportion of reproductively active adult females (0.66 ± 0.06 and 0.66 ± 0.04; $t = 0.17$, $df = 115$, $P = 0.87$), or body mass (40.8 ± 0.8 and 40.6 ± 0.4 g; $t = 0.50$, $df = 471$, $P = 0.62$) of *M. pennsylvanicus* in bluegrass. In tallgrass, however, supplemental feeding significantly increased the proportion of reproductively active adult females (0.60 ± 0.04 and 0.48 ± 0.04, supplementally fed and control, respectively; $t = 2.23$, $df = 34.6$, $P = 0.03$), number of immigrants (14.1 ± 1.6 and 8.8 ± 1.0 voles/month; $t = 2.40$, $df = 158$, $P = 0.02$), and adult male body mass (42.0 ± 0.4 and 39.4 ± 0.3 g; $t = 5.75$, $df = 820.8$, $P < 0.01$); there was, however, no effect of supplemental feeding on persistence of young (2.6 ± 0.2 and 2.6 ± 0.2 months; $t = 0.16$, $df = 417$, $P = 0.87$) *M. pennsylvanicus* in tallgrass

4 Discussion

Our hypotheses were not supported by the results of this study. Although peak densities of *Microtus ochrogaster* population fluctuations tended to be slightly higher in the supplementally fed than in the control intermediate food bluegrass site, neither the mean population densities nor the basic pattern of fluctuation differed between the two sites. The only significant response of *M. ochrogaster* to supplemental feeding in intermediate food habitat was a higher proportion of adult females that were reproductively active in the supplementally fed site as compared to the control site.

Body mass of adult male *M. ochrogaster* also was greater in the supplementally fed site than in the control site, suggesting a positive response in physical condition to supplemental feeding. Whereas, greater reproduction may have resulted in higher peak densities during population fluctuations, there was no influence on densities at other times. *M. ochrogaster* did not respond, in respect to population density or any variable, to supplemental feeding in low food tallgrass habitat.

Population density of *M. pennsylvanicus* displayed a positive response to supplemental feeding only in low food tallgrass. Population densities in tallgrass were significantly higher in the supplementally fed site than in the control site. A higher proportion of reproductively active adult females, greater immigration, and greater adult male body mass were associated with higher densities of *M. pennsylvanicus* in the supplementally fed sites in low food tallgrass.

From CMR analysis we detected temporal variation in survival rates in *M. ochrogaster* in bluegrass and *M. pennsylvanicus* in tallgrass. However, we failed to detect a significant effect of food supplementation on overall survival rates in all species-site combinations. Analyses of multistate CMR models further indicated significant temporal variation in maturation rates in all four species-habitat combinations. However, the interactive effect of food supplementation and time on maturation rates of both species in tallgrass suggested that, although maturation rates varied over time, they were also positively influenced by supplemental food.

That neither species displayed major positive demographic responses to supplemental feeding in intermediate food bluegrass suggests that natural food levels were sufficient for population success of both species. These results are consistent with those reported for *M. ochrogaster* by Cole and Batzli (1978) from the same study sites; amplitudes of fluctuation were higher in the supplementally fed site than in the control, but the patterns of fluctuation were similar in the two sites. *M. ochrogaster* did not respond to supplemental feeding in low food tallgrass; this suggests that factors other than food availability restricted population success in tallgrass. Getz *et al.* (2005a) concluded differential survival, unrelated to food availability, was responsible for differential population success of *M. ochrogaster* among habitats.

Although *M. pennsylvanicus* effectively utilizes monocots, supplemental feeding with a high quality diet resulted in modestly, but significantly, higher densities in the supplementally fed than in the control site in low food tallgrass. Survival, proportion of reproductive females, number of immigrants, and adult male body mass were greater in supplementally fed than control sites in low food tallgrass. More rapid maturation rates may have resulted in greater reproductive success and contributed to the slightly higher densities in supplementally fed than control tallgrass sites.

From these results, food does not appear to be the primary factor influencing population density of either species in the intermediate food bluegrass habitat. The slight response of *M. ochrogaster* and lack of response by *M. pennsylvanicus* to supplemental food in bluegrass are consistent with our prior conclusions that bluegrass provides adequate food for *M. pennsylvanicus* and marginal food for *M. ochrogaster* (Getz *et al.*, 2005a). *M. pennsylvanicus* was slightly more successful in supplementally fed low food habitat, tallgrass, but *M. ochrogaster* was unaffected by supplemental feeding in this habitat. The results of supplemental feeding in tallgrass are not consistent with presumed food availability for the two species in this habitat. While tallgrass has few dicots, the preferred food for both species, *M. pennsylvanicus* can utilize monocots (Haken and Batzli, 1996) and thus we would have predicted a greater response from *M. ochrogaster* than *M. pennsylvanicus*. That *M. pennsylvanicus* makes use of monocots may account for its modest response to supplemental feeding in tallgrass.

Results of this study are similar to those of shorter-term studies which indicated the pattern of population dynamics of arvicoline rodents was not substantially altered by supplemental feeding in habitats in which food is perceived to be scarce (Krebs and DeLong, 1965; Cole and Batzli, 1978; Desy and Thompson, 1983; Boutin, 1990; Yoccoz *et al.*, 2001). Our results are inconsistent, however, with those of studies indicating higher food leads to higher population densities and amplitudes of fluctuation (Cole and Batzli, 1978, 1979; Taitt and Krebs, 1981, 1983; Desy and Thompson, 1983; Desy and Batzli, 1989; Lofgren *et al.*, 1996; Prevot-Julliard *et al.*, 1999; Kasparian and Millar, 2004), whereas they are in agreement with conclusions of Lin and Batzli (2001) and Getz *et al.* (2005a) that food resources are not the primary factor responsible for population densities in a site.

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