EFFECTS OF SUPPLEMENTAL FOOD ON POPULATION DYNAMICS OF COTTON RATS, *SIGMODON HISPIDUS*¹

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Abstract. Variation in resource abundance affects population dynamics by altering demographic processes and interactions among individuals in the population. For small mammals, food is likely to be a critical resource. Population densities should vary directly with food abundance, but the underlying demographic changes are more difficult to predict. We experimentally increased food available to populations of hispid cotton rats, *Sigmodon hispidus*, to examine how rates of recruitment and disappearance varied with food abundance. We expected supplemental food to increase winter survival and to increase recruitment, perhaps advancing the date of first reproduction in the spring. We also thought larger, behaviorally dominant animals might dominate the point sources of supplemental food, altering age or size ratios and producing an excess of transient animals.

Supplemental food increased population densities but did not dampen pronounced seasonal fluctuations. Supplemented populations contained proportionately more juveniles and small adults than did controls; social behavior may have limited increases in numbers of large adults. Survival rates did not change; density increases were due to increased reproduction and immigration. In supplemented populations, reproductive effort by females increased, but the proportion of reproductive females decreased. Reproductive females and nonreproductive animals of both sexes were less likely to be transients than were reproductive males. Transients constituted higher proportions of control populations because of successful settlement, primarily by juveniles and small adults, into supplemented areas. The strongly seasonal climatic conditions under which northern *S. hispidus* populations exist produce contrasting selective pressures which might favor season-specific foraging strategies. Our data support a scenario of territorial females and wandering males in the reproductive season, with females maximizing resource acquisition for production of offspring. During winter, both sexes may restrict foraging time (and exposure to predators and weather) to the minimum required for survival.

Key words: cotton rats; density dependence; experiment; Kansas; population dynamics; recruitment; seasonality; *Sigmodon hispidus*; supplemental food; survival.

INTRODUCTION

Most life history theories are based on the assumption that energy is a finite resource that must be allocated among maintenance, growth, and reproduction (Boyce 1988). Species that are energy (i.e., food) limited typically must balance energetic costs of growth against reproduction. Such species could respond to increased food in several ways: increased individual growth rates, resulting in more rapid maturation and higher frequencies of adults; increased reproductive effort per adult; or increased survivorship. Any of these responses could lead to increased population densities. Ultimately, tradeoffs that individuals make in allocation of resources to life history parameters will determine population responses to changes in food abundance (Boyce 1988).

Effects of food abundance on demography may be mediated by the social system of a species. In territorial species, territory holders accrue resources that are then unavailable to other individuals (Krebs and Davies 1987). Fretwell (1972) presented a theoretical framework to explain how territoriality could affect the distribution of resources and variation in fitness among individuals. If territories remain fixed in size as resources increase, territorial individuals may increase their fitness while holding densities of reproductive adults constant (Fretwell 1972). If territories can be compressed, new individuals will be added in the interstices and per capita resource abundance, hence fitness, will remain relatively unchanged (Fretwell 1972, Mares et al. 1976). Thus, an absolute increase in resource abundance may translate into variable per capita responses that depend on interactions among conspecifics.

Populations of the cotton rat, *Sigmodon hispidus* (Rodentia: Cricetidae), provide a good system to experimentally examine the interplay between resource abundance, social behavior, and population dynamics. Cotton rats show considerable intraspecific variation in

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body and litter size across their geographic range, which may result from seasonality in both climatic conditions and the abundance and quality of food (Cameron and McClure 1988). In Kansas, near the northern edge of the species' range, cotton rats encounter relatively harsh winters during which individual growth slows, reproduction stops, and survivorship is poor (Fleharty et al. 1972, Cameron and Spencer 1981, Slade and Swihart 1983). For populations to persist, precipitous declines during winter must be offset by substantial reproduction in warmer seasons (Goertz 1964, Fleharty et al. 1972). Seasonal variation in food abundance or quality may contribute to both the winter decline and the rapid rate of increase in warmer months for *Sigmodon hispidus* (Goertz 1964, Fleharty et al. 1972, Kincaid et al. 1983, Batzli 1985, Kincaid and Cameron 1985, Cameron and McClure 1988).

Population densities and habitat use by cotton rats may be regulated by social dominance (Goertz 1964, Ramsey and Briese 1971, Fleharty and Mares 1973, Bigler et al. 1977, Spencer and Cameron 1983, Cameron and Spencer 1985, Kincaid and Cameron 1985). Cotton rats use a variety of open-field, grass-dominated habitats (Goertz 1964, Baker 1971), but show preferences for specific habitat types that presumably provide them greater access to critical resources (Fleharty and Mares 1973, Cameron and Spencer 1985). In preferred habitats, numbers of cotton rats may reach relatively stable levels, while population density over a larger area continues to increase (Goertz 1964, Ramsey and Briese 1971, Bigler et al. 1977). Although behavioral dominance may limit cotton rat numbers within preferred habitats, the effects on population dynamics have not been well documented.

We provided supplemental food to test hypotheses about the effects of food abundance and social dominance on population dynamics of *Sigmodon hispidus*. Population densities of other mammals are known to increase in response to supplemental food (Fordham 1971, Cole and Batzli 1978, Taitt 1981, Taitt and Krebs 1981, Saitoh 1989, Boutin 1990, Sullivan 1990). If populations of *Sigmodon* are food limited, then densities should increase with extra food. However, if *Sigmodon* populations also are limited by intraspecific interactions, there may be little or no increase in densities of adult residents, even though numbers of juveniles and transients might increase.

With supplemental food, population densities of sciurids, microtines, and cricetines consistently have increased, although demographic responses such as survivorship and per capita reproduction vary (Boutin 1990). If survivorship and reproduction are food limited, those processes should increase as food increases. Increased food abundance could lessen the impact of unfavorable climatic conditions in winter or increase growth rates and reproduction of *S. hispidus* during warm months. If intraspecific behavioral interactions constrain demographic responses, survivorship and re-

production might not increase or might increase differentially among genders or size classes with supplemental food.

Both survival and reproduction can be influenced by body size variation within populations of vertebrates (Sauer and Slade 1987), as has been demonstrated for *Sigmodon hispidus* (Sauer and Slade 1985). Alterations of size structure might also indicate behavioral mediation of the effects of additional food. Therefore, we tested whether or not supplemental food altered size structure within the population. Increased proportions of juveniles, indicating increased birth or juvenile survival rates (Ricklefs 1990), might result from increases in size-specific fecundities or changes in size structure of the reproductive portion of the population. Increased frequencies of adults would be expected with increased rates of individual growth (i.e., maturation), survivorship (Boyce 1988), or adult immigration (Fretwell and Lucas 1970).

Increases in densities of food-supplemented populations also could be accounted for by greater frequencies of transients, animals that moved through, but did not become established in populations (Koford 1992). We evaluated this by comparing frequencies of transients in control and food-supplemented populations.

METHODS

Study area and field methods

We used four trapping grids established at The University of Kansas' John H. Nelson Environmental Study Area, located in Jefferson County, ≈ 14 km north-northeast of Lawrence, in northeastern Kansas. All grids encompassed open-field habitat and included patches that were dominated by forbs, grasses, or a mixture of grasses and forbs. Each trapping station was characterized by the dominant vegetation type in the 225-m² area centered on the traps. In forb-dominated habitat, goldenrods (primarily *Solidago canadensis*) and asters (primarily *Aster pilosus* but also *A. praelius*) were the most common components of the vegetation, with sunflowers (*Helianthus* sp.) and a variety of other forb species also common. In grass-dominated habitat, brome (*Bromus inermis*) was the most common species, but bluegrass (*Sporobolus* sp.), fescue (*Festuca* sp.), and bluegrass (*Poa pratensis*) also were common locally.

The first three grids (A–C) were separated from each other by 50–100 m, and each comprised 64 trap stations arranged in an 8 $\times$ 8 grid with minor variations. The fourth grid (D), used in a long-term monitoring project, was located ≈ 400 m from the nearest of the other three grids, and comprised 99 trap stations on a 10 $\times$ 10 grid. All trap stations on each grid were placed at 15-m intervals. At each trap station two Sherman live traps (either 8 $\times$ 9 $\times$ 23 cm or 8 $\times$ 9 $\times$ 30 cm) were placed within 1–2 m of the station and 10–30 cm of each other.

One piece of plywood was placed over both traps to provide some protection from sun and precipitation, and to reduce disturbance by birds and medium-to-large mammals.

In estimating the area sampled by each grid, we included a 7.5-m boundary strip. Grid B, entirely in open-field habitat, had an effective area of 1.44 ha. The second rows of Grids A and C ran along the margin of a patch of secondary oak-hickory forest habitat. Thus, the first row of eight trap stations on both grids was ≈ 15 m inside the forest; these traps were excluded from our analysis, so each grid had an effective area of 1.17 ha of open-field habitat. Grid D, described in detail elsewhere (Slade and Swihart 1983), encompassed abandoned fields and pastures, a road, and hedgerows. Grid D spanned 2.25 ha and had an effective area of 2.0 ha of open-field habitat.

Trapping was conducted for 3-d periods at monthly intervals from June 1990 through May 1992. Traps were set the afternoon prior to the 1st d and were checked the next three consecutive mornings and the intervening afternoons. Traps were locked open the last morning and left in place between trapping periods. Traps were baited with commercial scratch grain (a mixture of cracked corn, *Zea mays*; wheat, *Triticum aestivum*; and grain sorghum, *Sorghum vulgare*) and polyester fiberfill was placed in the traps as nesting material during cold weather (generally November through March).

Every animal was uniquely marked with a numbered metal ear tag on first capture. For each capture of an animal, identification number, sex, mass, reproductive condition, and location were recorded. Mass was measured to the nearest gram using Pesola spring scales. Males were classified as reproductive (testes scrotal) or not (testes abdominal). For females, reproductive condition was determined by vaginal condition (perforate or imperforate), nipple size (small, medium, or large), and pubic symphyseal opening (closed, partly open, or fully open). Because single external characters are not always accurate for determining reproductive status of female *S. hispidus* (McCravy and Rose 1992), females were classified as reproductive only if they were obviously pregnant, or if at least two of the three external features indicated reproductive activity.

Supplemental food was a mixture of grain sorghum, millet seed (*Panicum miliaceum*), and commercial rabbit chow (Purina No. 5315). This mixture was used because *S. hispidus*, although primarily herbivorous, will readily eat seeds (Menhusen 1963, Fleharty and Olson 1969, Cameron and Spencer 1981, Randolph et al. 1991). Cotton rats briefly held in the laboratory (Campbell and Slade 1993) ate grain rather than standard rat chow. We used rabbit chow (primarily pelleted alfalfa) because it provided a high-quality herbaceous component known to be eaten by herbivorous rodents (Saitoh 1989). Supplemental food was provided in 355-mL aluminum beverage cans (feeder cans) from which

one end had been removed. One can containing 50 g of each of the three foods was placed on its side, between the traps and under the board covering them, at every trap station on the experimental grids. At ≈ 2 -wk intervals, each feeder can was removed and replaced by another can of food. Feeder cans were not replaced < 1 wk prior to the initiation of a trapping period.

The amount of supplemental food provided was chosen to increase available food (Saitoh 1989) but not to make food available *ad libitum*. We did not measure primary productivity, but 400 (Knapp et al. 1993) to 600 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ (Whittaker 1975) is a reasonable estimate of primary production of unburned temperate grasslands or crop land. Dyer et al. (1991) reported 515 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ for unfertilized *Bromus inermis*. At 17.78 kJ/g (data expressed in kcal/g by Whittaker [1975]; 1 cal = 4.184 J), natural vegetation in the 225 m^2 surrounding each trap station could yield 1602–2402 MJ/yr. Fifty grams of each of our three supplemental foods provided an additional 2.47 MJ each two weeks (rabbit chow = 15.23 kJ/g, D. Ettel of Ralston Purina, *personal communication* [in kcal]; millet = 16.15 kJ/g and sorghum = 18.07 kJ/g, National Research Council (USA), Subcommittee on Feed Composition 1971 [using kcal]). Supplemental food provided 62.8 MJ/yr, roughly a 2.5–4% energy increase. We provided pulsed rather than continuously available food to reduce the probability of resource monopolization by dominant individuals. During trapping sessions, 1 wk after replacement, feeder cans typically were empty; occasionally a few stations retained small amounts of food during early spring trapping periods when *Sigmodon* densities were lowest. In the first few weeks of the study, we weighed food remaining in the cans after 2 wk but quickly stopped doing so because food was present rarely.

Of the four trapping grids, two were maintained as experimental grids and two as control grids at all times throughout this study. For the entire study, grid D was a control and supplemental food was provided on grid B. To reduce the influence of any site (grid) biases, feeder cans were switched from grid A to grid C at the beginning of June 1991, the end of the first year of this study.

Data analysis

For some analyses, monthly trapping data were pooled by season: Spring = March, April, and May; Summer = June, July, and August; Autumn = September, October, and November; Winter = December, January, and February.

Numbers of individuals on each grid were estimated as minimum number known alive (MNKA; number of individuals captured at time t , plus individuals not captured at but captured both before and after time t). MNKA is known to provide an underestimate of population density unless every animal is captured in its

first and last trapping periods on the area (Nichols and Pollock 1983, Pollock et al. 1990). We also estimated numbers with the computer program CAPTURE (Otis et al. 1978, White et al. 1982). CAPTURE assumes a closed population over our 3-d trapping intervals, tests that assumption, and provides a series of models based on different assumptions about behavior of the animals being sampled. When the closure assumption was met and probabilities of capture were >0.20 , we used the estimator from an appropriate model of capture if it exceeded MNKA. When there was no estimator for the most appropriate model, the best alternative model with an estimator was used, but only if the selection value for the alternative model was ≥ 0.75 (Otis et al. 1978). For 3-d trapping periods and <50 animals on a grid, the model selection procedure of CAPTURE also may lead to negatively biased estimates of population density (Menkens and Anderson 1988), but other estimation procedures such as Jolly-Seber models are no more reliable (Blair 1992).

Estimated numbers in each trapping period were converted to densities per hectare to account for differences in grid size. For statistical analyses, density estimates were square-root transformed to normalize distributions. A general linear model (GLM) procedure for ANOVA (Minitab 1991) was used to test for significant effects of treatment (control or supplement), season, and year.

Jolly-Seber estimates of weekly survivorship were obtained using model A of the computer program JOLLY (Pollock et al. 1990). Survivorship estimates were arcsine-transformed and distributions checked for normality. Variation in survivorship among treatments, seasons, and years was tested by a GLM procedure. Because sample sizes varied among trapping periods, survivorship was weighted by number of individuals captured (Minitab 1991), so only those months and grids with cotton rats present were used. Survivorship analyses were conducted only with data from residents, i.e., those individuals caught at least once in each of two or more monthly trapping periods, whether consecutive or not. This procedure introduces a positive bias into estimated survivorships (residents must survive at least 1 mo), but that bias is constant for both control and supplemented populations.

We estimated monthly probabilities of capture with JOLLY to avoid variation among days within the month and variation caused by use of more than one model with CAPTURE. Differences in capture probabilities between treatments and among trapping periods were tested with a GLM procedure (Minitab 1991), after probabilities were arcsine-transformed and distributions were checked for normality.

Effects of food abundance on reproduction by *S. hispidus* were examined using chi-square tests on sums of monthly numbers of reproductive adults (>60 g mass; Glass and Slade 1980) between gender and adult size classes and among seasons. In this and several other

tests of frequency distributions (e.g., size distributions), cotton rats that persisted on grids for several months were tallied in each month. To further examine effects of food abundance on reproduction, any female that appeared ready to give birth when captured was held for up to 5 d in a laboratory building adjoining grid D (Campbell and Slade 1995). If the female gave birth, her postpartum mass, number of pups in the litter, and mass of the litter were recorded. Females and any pups were released at the point of capture. Litter size, mother's mass, and litter mass per mother's mass were analyzed by Kruskal-Wallis tests, as those variables were not normally distributed.

Effects of treatment and season on frequencies in three size (mass) classes: 0–60 g (juveniles), 61–120 g (small adults), and >120 g (large adults), were assessed with log-linear techniques (Fienberg 1970, Kincaid and Cameron 1985) using the SAS procedure CATMOD (SAS 1985).

Recruitment, i.e., numbers per ha of individuals captured for the first time on a grid, was examined for juveniles and all adults (>60 g). Recruitment was compared by paired *t* tests between supplemented and control populations for each trapping period; for this analysis, replicate grids were pooled because numbers of recruits were small for many months. Chi-square tests were used to determine whether or not seasonal patterns in recruitment were significantly different between treatments. To estimate per capita recruitment, number of juvenile recruits was divided by number of adult females. Resulting rates of recruitment were examined with a GLM procedure (Minitab 1991) incorporating treatment, month, and season as independent variables.

Transients were defined as those animals caught in only one monthly trapping period. Frequencies of transients were compared by chi-square tests to determine whether supplemental food, size class, reproductive status, or gender affected the probability of an individual's being a transient. Because the distinction between transients and residents was made once per individual, cotton rats were assigned to categories based on their status at first capture, and each individual was counted once regardless of length of persistence on the grid. The proportion of transients in each month's census was determined separately for each month, so residents were included more than once in those estimates and the proportion of transients in a monthly census was lower than the probability that a recruit would become a transient.

RESULTS

Probability of capture

Mean (± 1 SE) probabilities of individuals being captured at least once in a 3-d trapping period did not differ significantly between control (0.829 ± 0.256) and supplemented (0.826 ± 0.184) populations ($F_{1,45}$

TABLE 1. Area of open field habitat, treatments maintained, estimated densities (N) of cotton rats, *Sigmodon hispidus*, and frequency of capture from June 1990 through May 1992 on each study grid in northeastern Kansas.

Grid	Area (ha)	1990–1991		1991–1992		Mean captures per individual
		Treatment	Mean number (N -ha ⁻¹ -mo ⁻¹)	Treatment	Mean number (N -ha ⁻¹ -mo ⁻¹)	
A	1.17	Supplement	35.82	Control	15.38	3.73
B	1.44	Supplement	33.62	Supplement	27.72	3.32
C	1.17	Control	8.69	Supplement	13.03	2.92
D	2.00	Control	16.79	Control	12.42	3.64

= 0.50, $P = 0.485$) nor among trapping periods ($F_{22,45} = 0.83$, $P = 0.674$).

Population density

During this study, 1240 *Sigmodon hispidus* individuals were captured a total of 4272 times on the four trapping grids (Table 1), with numbers captured per hectare highest on grid B, which was supplemented both years. On all four grids, under both treatments, there was a single annual peak in population density in autumn followed by sharp declines throughout the winter and early spring (Fig. 1). Maximum density of cotton rats under control conditions was 39.5 individuals/ha on grid D, while maximum density with supplemental food was 100 individuals/ha on grid B, both in November 1990.

Population densities differed between treatments ($F_{1,85} = 29.21$, $P < 0.001$), among seasons ($F_{3,85} =$

47.06, $P < 0.001$) and between years ($F_{1,85} = 5.93$, $P = 0.017$). The treatment-by-season interaction was not significant ($F_{3,85} = 2.46$, $P = 0.069$), although interactions between treatment and year ($F_{1,85} = 13.28$, $P < 0.001$) and season and year ($F_{3,85} = 13.28$, $P < 0.001$) were.

Survivorship

Survivorship varied among seasons ($F_{3,70} = 8.76$, $P < 0.001$) but neither the main effect of supplemental food ($P = 0.919$) nor the supplemental food-by-season interaction ($P = 0.920$) was significant (Table 2). For both treatments, seasonal mean survivorships (Table 2) were lowest in winter but indistinguishable in spring, summer, and autumn.

Reproduction

Reproduction was strongly seasonal, and supplemental food did not alter this pattern (Table 3). Pro-

FIG. 1. Estimated monthly cotton rat population densities (no./ha) from June 1990 through May 1992 in study grids in northeastern Kansas. Error bars represent two standard errors for estimates calculated by program CAPTURE. Values without error bars are minimum numbers known alive.

TABLE 2. Probabilities of survivorship per week for cotton rats, with or without supplemental food, averaged over replicate grids and months within seasons in northeastern Kansas. Adjusted means ($\bar{X}$) were determined from general linear model (GLM) analysis weighting estimated survivals by number of residents present in each month from June 1990 through May 1992. Sample size (n) is the number of grid-months with some residents.

Treatment	Period	Survivorship per week		n
		$\bar{X}$	SE	
Control	All seasons	0.9299	0.0027	42
	Spring	0.9570	0.0097	7
	Summer	0.9492	0.0031	11
	Autumn	0.9489	0.0018	12
	Winter	0.8645	0.0028	12
Supplement	All seasons	0.9210	0.0022	42
	Spring	0.9166	0.0154	7
	Summer	0.9523	0.0058	11
	Autumn	0.9413	0.0032	12
	Winter	0.8736	0.0052	12

portions of adults that were reproductive did not differ significantly between treatments (Table 3) in any season for either sex ($P > 0.085$), except that in summer, control populations had a higher proportion of reproductive females than did supplemented populations ($P = 0.049$). In winter, only two reproductive individuals, one male and one female, were identified during the study.

Proportionately more large adults than small adults were reproductive for both genders and both treatments ($\chi^2 > 44.0$, $P < 0.001$, $df = 1$ for all four tests; Table 4). However, within size classes the effect of the treatment varied with gender (Table 4). Relative frequencies of reproductive cotton rats were not different between treatments for small adult ($P = 0.303$) or large adult males ($P = 0.397$). Higher proportions of females were reproductive on control grids for both small adults ($\chi^2 = 4.56$, $df = 1$, $P = 0.033$) and large adults ($\chi^2 = 9.61$, $df = 1$, $P = 0.002$).

Median postpartum masses of mothers that gave birth in the laboratory were indistinguishable between con-

trol (122.5 g, $n = 28$) and supplemented (126.0 g, $n = 16$) populations ($H < 0.01$, $df = 1$, $P = 0.990$), pooled over replicate grids and years. The same was true for median number of pups per litter (control, 7.0; supplement, 7.5; $H = 1.28$, $df = 1$, $P = 0.259$), and median litter mass (control, 44.5 g; supplement, 46.5 g; $H = 2.34$, $df = 1$, $P = 0.127$). However, median ratio of litter mass to mother's mass was slightly greater ($H = 3.91$, $df = 1$, $P = 0.048$) in supplemented (0.3795) than in control (0.3448) populations. (Campbell and Slade 1995 present more detailed analyses.)

Recruitment

Mean numbers of recruits per hectare were significantly greater in supplemented populations than in controls (Table 5) for all individuals ($t = 2.59$, $df = 23$, $P = 0.017$), juveniles ($t = 2.18$, $df = 23$, $P = 0.039$), and adults ($t = 2.91$, $df = 23$, $P = 0.008$). General linear model (GLM) analysis showed that juvenile recruitment per adult female varied among months ($F_{11,44} = 5.90$, $P < 0.001$) but was not affected significantly by supplemental food ($P > 0.439$), nor was any other main effect or interaction significant ($P > 0.395$). Peaks in recruitment for both juveniles and adults (Fig. 2) coincided with peaks in population density (Fig. 1) and reproduction (Table 3). Supplemental food produced a greater increase in recruitment of juveniles than adults (Fig. 2, Table 5).

Transients

Although numbers of transients were higher in supplemented populations (Table 6), transients comprised a lower proportion ($\chi^2 = 23.36$, $df = 1$, $P < 0.001$) of the monthly population estimates in supplemented (21.0%) than in control (27.9%) populations. Size distributions of transients might represent random samples from resident populations (Table 6) in control ($\chi^2 = 1.99$, $df = 2$, $P < 0.370$), but clearly not in supplemented ($\chi^2 = 15.09$, $df = 2$, $P < 0.001$) populations. On supplemented grids, juveniles were more likely to become residents than were adults (Table 6). Size struc-

TABLE 3. Variation in proportion of reproductive adult (>60 g) cotton rats compared between treatments and among seasons from June 1990 through May 1992 in northeastern Kansas. Sample size (n) is the sum of adults captured each month. Individuals were tallied once for each month in which they were present.

Season	Treatment	Males		Females	
		Proportion reproductive	n	Proportion reproductive	n
Spring	Control	0.500	20	0.385	13
	Supplement	0.721	43	0.164	55
Summer	Control	0.905	74	0.672	64
	Supplement	0.848	99	0.511	86
Autumn	Control	0.186	145	0.295	129
	Supplement	0.122	237	0.234	252
Winter	Control	0.000	93	0.016	64
	Supplement	0.006	154	0.000	154

TABLE 4. The influence of size (body mass) on proportions of reproductive adult cotton rats in supplemented vs. control treatments. Sample size (n) is the sum of number of adults captured in each month from June 1990 to May 1992 on four study grids in northeastern Kansas. Individuals were tallied once for each month in which they were present.

Gender	Treatment	Small adults (61–120 g)		Large adults (>120 g)	
		Proportion reproductive	n	Proportion reproductive	n
Male	Control	0.225	262	0.643	70
	Supplement	0.193	451	0.707	82
Female	Control	0.154	201	0.812	69
	Supplement	0.096	427	0.592	120

ture of transients and residents on control grids shows similar trends (Table 6).

Proportions of adults that were transients for a single month were significantly ($\chi^2 = 88.64$, $df = 1$, $P < 0.001$) higher among reproductive (32.8%) than among nonreproductive (12.8%) cotton rats. Similar patterns were found when individual recruits (first time captures) were classified as transients or residents (Table 6). Among reproductive animals, significantly higher proportions of males than females were transients (Table 7) in both control ($\chi^2 = 4.94$, $df = 1$, $P < 0.026$) and supplemented ($\chi^2 = 5.03$, $df = 1$, $P = 0.025$) populations; among nonreproductives, there were no significant differences between genders (Table 7) in control ($\chi^2 = 0.60$, $df = 1$, $P = 0.439$) or supplemented ($\chi^2 = 1.36$, $df = 1$, $P = 0.756$) populations.

Size structure

Monthly proportions of animals in three size classes varied with treatment (Table 8; $\chi^2 = 7.13$, $df = 2$, $P = 0.023$); control populations contained higher proportions of juveniles and supplemented populations higher proportions of small adults. Seasonal differences in size distributions (Table 8) were highly significant ($\chi^2 = 360.09$, $df = 6$, $P < 0.001$). Higher order interactions involving size class were not significant ($P > 0.05$).

Vegetation of the grids

The proportions of open field dominated by forbs, grass, and mixed vegetation were 0.20, 0.51, and 0.29 on grid A ($n = 57$ stations); 0.39, 0.38, and 0.24 on

grid B ($n = 64$); 0.39, 0.31, and 0.30 on grid C ($n = 56$); and 0.21, 0.43, and 0.36 on grid D ($n = 89$), respectively. The grids differed in vegetative composition ($\chi^2 = 13.04$, $df = 6$, $P = 0.042$), with grids A and D having fewer and grids B and C more stations dominated by forbs, but all three vegetation types were occupied by cotton rats. There were no indications that population processes were more similar between grids A and D or B and C when they served as replicates of the same treatment (the 2nd yr) than between replicates in the 1st yr.

DISCUSSION

In our experiment, as with other studies of rodents (Boutin 1990), density increased in food-supplemented populations, indicating that food can be a limiting resource for cotton rats (Fig. 1). Mean population density was higher on supplemented grids in both years, but the difference was most pronounced in the 1st yr (Table 1), confirmed by a significant treatment-by-year interaction in the GLM. The increase of cotton rats with supplemental food on grid C in the 2nd yr of study was not as large as the decline on grid A following the removal of the supplement. This may indicate that grid A offered better habitat than grid C, as suggested by a reviewer. However, population densities in the 2nd yr averaged $\approx 25\%$ lower on both grids B and D, which received the same treatments in both years; therefore we maintain that the modest (50%) increase on grid C with supplemental food, the only grid with an increase in a poor year, is evidence that supplemental food results in increased populations of cotton rats. We also

TABLE 5. The influence of supplemental food on densities and seasonal distribution of newly marked juvenile (≤ 60 g) and adult (> 60 g) cotton rats from July 1990 through May 1992 in grids in northeastern Kansas. Sample size (n) is the total number of recruits. Densities of recruits were averaged over grids and months within seasons, weighting each grid equally.

Recruit age group	Treatment	Individuals $\text{ha}^{-1} \cdot \text{mo}^{-1}$		Seasonal distribution of recruits (proportion)				n
		Mean	SE	Spring	Summer	Autumn	Winter	
All	Control	5.8	1.04	0.039	0.349	0.539	0.073	460
	Supplement	10.9	2.12	0.057	0.219	0.688	0.036	693
Juvenile	Control	3.1	0.70	0.037	0.280	0.622	0.061	246
	Supplement	6.3	1.52	0.069	0.144	0.772	0.015	403
Adult	Control	2.7	0.47	0.042	0.421	0.448	0.089	214
	Supplement	4.5	0.76	0.041	0.314	0.579	0.066	290

FIG. 2. Densities of juvenile and adult recruits to cotton rat populations from June 1990 through May 1992 on treatment grids in northeastern Kansas. $\blacktriangle$, males; ∇ , females. Shaded regions indicate periods of supplemental food.

found evidence of a cumulative effect across years (Fig. 1). Spring densities on grids A and B were similar and higher than on control grids in the 2nd yr, but following the switch of feeder cans from grid A to C, grid B

reached higher peak densities than either grid C or grid A. Our data may also imply some density-dependence: starting from higher density in the spring, Grid B increased fourfold from May to October 1991, while grid

TABLE 6. Effect of supplemental food on size structure (mass) of transient and resident cotton rats in northeastern Kansas, from June 1990 to May 1992. Sample size (n) is the number of cotton rats categorized by size at initial capture on a grid.

Treatment	Residency	Proportion			n
		Juvenile (≤ 60 g)	Small adult (61–120 g)	Large adult (> 120 g)	
Control	Transient	0.518	0.344	0.138	247
	Resident	0.580	0.314	0.106	207
Supplement	Transient	0.498	0.398	0.104	317
	Resident	0.612	0.346	0.042	402

TABLE 7. Effect of supplemental food on the relative frequency of transient adult cotton rats in northeastern Kansas from June 1990 to May 1992. Sample size (n) is the number of cotton rats categorized by gender and reproductive condition at initial capture on a grid.

Reproductive status	Treatment	Gender	Proportion transient	n
Nonreproductive	Control	Male	0.531	64
		Female	0.457	46
	Supplement	Male	0.495	99
		Female	0.414	104
Reproductive	Control	Male	0.735	68
		Female	0.500	28
	Supplement	Male	0.667	81
		Female	0.438	32

C increased 17-fold in the same year. Thus, high population densities in the spring may influence the height of annual peaks, but not in a strictly linear fashion. Whatever the mechanisms, our data demonstrate that the magnitude of response to supplemental food varies between years.

It is difficult to determine what impact one should expect from supplemental food. Our supplement probably was a small increment in the total energy available (net primary productivity) to cotton rats on our study area, but it was of high quality, concentrated in space (perhaps making it defensible) and pulsed uniformly throughout the year. It also was available to a variety of consumers, e.g., ants, granivorous birds, and other mammals, so it is difficult to predict what proportion of the supplement was available to a single species. Clearly the extra food attracted additional cotton rats to the supplemented grids and did so throughout the year. We did not expect a pronounced effect during the growing season when natural food was abundant, but thought the impact might be more pronounced in the winter.

The hypothesis that winter declines in *S. hispidus* populations are the result of food shortage (Kincaid and Cameron 1985) led us to expect higher winter survival and less severe declines with supplemental food. The modest increases in winter and spring densities that we observed were a carry-over from higher fall

densities, but did not stem from increased winter survival rates. Winter survival rates were unaffected by supplemental food and were lower than in other seasons, in contrast to earlier analyses of *S. hispidus* populations on our study area (Sauer and Slade 1985, Campbell and Slade 1993). We attribute our lower winter survival to our having restricted survival estimates to residents, whereas earlier estimates combined transients and residents, as we have defined them. Our results indicate that disappearance rates in warm seasons reported by Sauer and Slade (1985) and Campbell and Slade (1993) were overestimates of mortality.

Lack of a significant increase in survivorship in populations provided with extra food is not unusual. Previous studies of food-supplemented rodent populations reported varied responses in survivorship. Higher survivorship was found in some groups (Cole and Batzli 1978 [adult prairie voles], Dobson and Kjelgaard 1985 [juvenile *Spermophilus columbianus*], Young and Stout 1986 [*Ochrotomys nuttalli*]). In other groups, there was no change in survivorship (Dobson and Kjelgaard 1985 [yearlings and adults], Saitoh 1989 [*Clethrionomys rufocanus*]), and in one case survivorship decreased (Young and Stout 1986 [*Peromyscus gossipinus*]).

In Kansas, winter declines of *Sigmodon hispidus* populations result from cessation of reproduction and from decreased survivorship. Both of these may reflect insufficient energy intake, even in the presence of ad-

TABLE 8. The influence of supplemental food and season on size structure of cotton rat populations on study grids in northeastern Kansas from June 1990 through May 1992. Sample size (n) is the sum of number of animals captured in each trapping period. Individuals were tallied once in each trapping period for which they were present.

Season	Treatment	Proportions in age classes			n
		Juvenile (≤ 60 g)	Small adult (61–120 g)	Large adult (> 120 g)	
Spring	Control	0.250	0.568	0.182	44
	Supplement	0.222	0.508	0.270	126
Summer	Control	0.327	0.332	0.341	205
	Supplement	0.245	0.445	0.310	245
Autumn	Control	0.396	0.485	0.119	454
	Supplement	0.410	0.489	0.101	829
Winter	Control	0.230	0.735	0.034	204
	Supplement	0.130	0.847	0.023	354

ditional food. Porter and McClure (1984) modeled energetics and predicted seasonal reproduction for northern cotton rats because of limited food in winter. Howard (1951) showed that small mammals have higher energy requirements at lower ambient temperatures, and used the term "cold weather starvation" for the combined effect of low temperature and insufficient food. Our supplemental feeding did not alter survival or the timing of breeding, which might imply no increase in food available to the average individual. It appears that winter declines were determined more by intraspecific competitors or harsh environmental conditions restricting access to food (Dunaway and Kaye 1961, Goertz 1964, Sauer 1985) rather than by abundance of food (Kincaid and Cameron 1985).

Because survival probabilities were unchanged, increased densities of supplemented populations must have resulted from increased recruitment of both juveniles (reproduction) and adults (immigration). Supplemented grids averaged twice as many juvenile and 1.5 times as many adult recruits per hectare as did the control areas (Table 5). Separating the sources of recruits based on size or age at first capture can involve some error (Dueser et al. 1984, Tamarin 1984), but our attributing recruits that weighed <60 g to reproduction on the grid seems reliable. Of the 194 pups marked at birth, 61 were eventually recaptured, all were captured in the first trapping period following release, and only four weighed >60 g. Therefore juvenile recruits (<60 g) were <2 mo old (Campbell and Slade 1993) and likely to have been born on the grid, whereas adult recruits (>60 g) were likely to be immigrants. By these criteria, increases in population density with supplemental food were due less to immigration than to reproduction.

Density of all females on supplemented grids averaged about twice control densities (sex ratios were unaffected by supplemental food, Doonan 1993). Correcting for the proportion that were reproductive (Table 3), densities of reproductive females on supplemented grids were ≈ 1.5 times control levels. It might appear that increased reproduction was due solely to the number of reproductive females in supplemented populations because median litter size did not increase. However, considering only median litter size conceals a response to added food at the individual level; median ratio of litter mass to maternal mass increased on supplemented grids. This also was demonstrated by performing an analysis of covariance on litter mass as a function of supplemental food and maternal mass (Campbell and Slade 1995). Further, neither pup size nor pup survival changed with supplemental food, so increased litter mass translated into increased numbers of surviving pups per litter (Campbell and Slade 1995). Changes in reproductive effort with changes in food abundance support the hypothesis that reproductive output of female *S. hispidus* is a phenotypically plastic trait, whose expression is at least partially determined

by energy availability (Cameron and Spencer 1981, Cameron and McClure 1988). Increased reproductive effort was hidden when litter size was averaged over all breeding females, because our sample from supplemented populations had higher proportions of small adults that produce relatively small litters.

The proportion of animals that are reproductively active generally has been found to increase in food-supplemented populations (Watts 1970, Fordham 1971, Cole and Batzli 1978), although at least one study (Hansen and Batzli 1979) found no change in frequency. The only increase in proportion of reproductive animals that we found was among males in spring. Higher proportions of reproductive males in spring may indicate that males were more responsive than females to increased food early in the year. Becoming reproductive earlier than females would enable males to take advantage of the earliest available breeding opportunities. If such a strategy were employed, it would be analogous to mating systems in ground squirrels in which males emerge from hibernation early and await the later emergence of females (Slade and Balph 1974). In addition, it might be expected that large reproductive males, most of which were transients, would be attracted to supplemented grids that had high densities of females. However, over the entire breeding season, neither proportion of reproductive adults nor size structure differed between control and supplemented grids.

This is the first study to report a *decrease* in the proportion of reproductive females in populations provided with supplemental food. One possible explanation for decreased proportions of reproductive females is that in growing populations, the age or size structure tends to be biased toward younger, nonreproductive size classes (Ricklefs 1990). Two points argue against this as the main explanation for lower frequencies of reproductive females in our study. On supplemented grids, size structure was relatively unchanged from controls and, more importantly, the proportion of reproductives decreased within both size classes of adult females on the supplemented grids.

Social dominance seems a more plausible explanation for reduced proportions of reproductive females in supplemented areas. Territoriality has been suggested in previous studies examining patterns of habitat use in *Sigmodon* (Goertz 1964, Fleharty and Mares 1973, Spencer and Cameron 1983, Cameron and Spencer 1985). Large numbers of small nonreproductive adult females on our supplemented grids suggest that these animals are tolerated more readily than are reproductives, whereas restricted numbers of large reproductive females may indicate dominance systems that would restrict access to critical resources (Brown 1969, Spencer and Cameron 1983).

Social dominance also is consistent with our data on fecundity. Even though we found no changes in median litter size, we did find an increase in litter mass as a proportion of maternal mass (reproductive effort) in

the supplemented populations. This may reflect increased energy available for reproduction, but how additional energy is invested depends on body size (Campbell and Slade 1995). Size-specific analyses (Campbell and Slade 1995) showed large females in supplemented populations had larger litters and lower reproductive effort than those in controls. In contrast, small females had higher reproductive effort but produced fewer recruits, compared to control populations. Thus, larger females produced more offspring at potentially lower cost with extra food, but smaller females might do better under control conditions. This is consistent with large females obtaining higher proportions of available resources. Small females in supplemented populations actually may have reduced access to those resources because of the increased densities of competitors.

Social dominance may have been weaker or less spatially restricted among adult males than females, as there was no change in size structure or proportion of reproductive males in supplemented populations. Reduced spatial affinity among males also was supported by higher proportions of transients among reproductive adult males than among other animals. Transients are more likely to be individuals moving large distances, and reproductive males are the most mobile segment of *S. hispidus* populations (Fleaharty and Mares 1973, Slade and Swihart 1983). Increased mobility by reproductive males is consistent with Ostfeld's (1985) model relating territoriality to resource acquisition. He suggested that territoriality should not be as pronounced among males because they must cover a larger area to acquire mates, the limiting resource for male fitness (Ostfeld 1985). However, increased mobility of males is advantageous only in species with mating systems that allow multiple matings. Currently the mating system of *S. hispidus* is unknown.

Koford (1992) suggested that transient individuals, attracted by extra food, would be trapped more frequently in food-supplemented populations and could bias comparisons of population densities between control and supplemented populations. In this study, however, frequencies of transients actually were slightly lower in supplemented populations. Lower frequencies of transients resulted from higher rates of settlement (higher mean numbers of adult recruits per hectare) in food-supplemented populations, as would be predicted by one hypothesis of habitat selection (Fretwell and Lucas 1970). The ideal free distribution model of Fretwell and Lucas predicts that individuals with preferences in habitat use should settle in the highest quality habitats they encounter. Cotton rats have demonstrated clear preferences in habitat use in other studies (Goertz 1964, Fleaharty and Mares 1973, Spencer and Cameron 1983, Randolph et al. 1991). In our study, extra food appeared to increase habitat quality as evidenced by higher densities, higher retention of juveniles, and higher reproductive effort in supplemented popula-

tions. Therefore, higher rates of settlement by transient cotton rats in food-supplemented populations would be expected until densities reduce the quality of the supplemented habitat to the equivalent of the control areas. There is some evidence, i.e., similar winter survival rates and lower proportions of large females on supplemented grids, that densities may have reached levels offering equal habitat qualities to new immigrants.

Previous studies have indicated that size frequency distributions of dispersing *S. hispidus* are not different from frequency distributions of source populations (Joule and Cameron 1975, Stafford and Stout 1983). If it is assumed that transient individuals were dispersers, then the results of this study are not in agreement with this "template" hypothesis. Frequencies of adults were higher among transients than among residents for both treatments, although the difference was statistically significant only for the supplemented populations. This implies that juvenile cotton rats may reside on a grid for >1 mo before they disperse. This seems at odds with the proposition that cotton rats disperse prior to reaching sexual maturity (at ≈ 60 g, Cameron and Spencer 1981), as does our finding of a large number of reproductive adults moving onto or through the grid.

Results of this study indicate that effects of resource abundance on dynamics of cotton rat populations vary with environmental conditions. During the reproductive season, population dynamics seemed to be dominated by individuals directing most of their acquired resources into reproductive output; with supplemental food, population densities and reproductive output both increased. In winter, supplemental food increased neither reproduction nor survival of residents. Harsh temperatures and decreased cover in winter may increase costs of activity outside the nest, restricting an individual's ability to profit from additional food. These contrasting sets of conditions under which northern *S. hispidus* populations exist could produce contrasting selective pressures; selection for increased reproductive output would be constrained by requirements for surviving harsh conditions in winter. This might induce contrasting season-specific foraging strategies (Stephens and Krebs 1986), energy maximizing in the reproductive season and time minimizing in winter. This is consistent with predictions of Sauer and Slade (1985) for *S. hispidus*, based on sensitivity analysis of stage transition matrices.

CONCLUSIONS

This experiment demonstrates some of the complexity in relationships between population limitation, regulation, and social behavior. Population densities increased with additional food; thus food levels were limiting. Density increases appeared to be cumulative, but per capita rates of increase were lower in the second year of supplementation as compared to a newly supplemented population in that same year, indicating

some density dependence, i.e., regulation. Survival rates of residents were relatively unaffected by supplemental food, whereas rates of reproduction and immigration increased. While large adult females seemed better able to exploit added food for reproduction, their density showed some evidence of constraint, perhaps through territoriality. Newly resident females on supplemented grids were likely to be nonreproductive. Thus, density dependence seemed most evident among reproductive females. Densities of reproductive males, both residents and transients, also increased, but our observed density increases were not due to increased frequency of transients, as might occur in a social system with strong dominance by residents. Seasonality dramatically influenced demography, and severe seasonal declines persisted even with supplemental food. In our populations, density responded to food levels, but climatic variation and suspected social interactions mediated the response. Both density dependence and environmental stochasticity are likely to be important considerations in dynamics of these populations.

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