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Source: Journal of Mammalogy, 86(1) : 46-55

Published By: American Society of Mammalogists

URL: https://doi.org/10.1644/1545-1542(2005)086<0046:IOFSAM>2.0.CO;2

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Journal of Mammalogy, 86(1):46–55, 2005

IMPACT OF FOOD SUPPLEMENTATION AND METHIONINE ON HIGH DENSITIES OF COTTON RATS: SUPPORT OF THE AMINO-ACID-QUALITY HYPOTHESIS?

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Considerable research supports the tenet that quantity and quality of food limit vertebrate populations. We evaluated predictions that increased availabilities of food and the essential amino acid methionine were related to population limitation of the hispid cotton rat (*Sigmodon hispidus*). Effects of supplemental food and methionine on density, survival, and reproductive parameters of wild cotton rats were assessed in north-central Oklahoma in 1998–1999. Twelve enclosed groups of 16 adult cotton rats each (8 male, 8 female) were randomly assigned to either no supplementation (control), supplementation with a mixed ration that had methionine at slightly below maintenance levels (0.20%), or a methionine-enhanced mixed ration (1.20%). In general, densities of cotton rats were twice as high and were sustained longer with dietary supplementation, and methionine-supplemented populations maintained the highest densities. Treatment effects on survival depended on time of year, with higher survival in supplemented enclosures in October and November. Per capita recruitment was highest with methionine-enhanced food. Treatment effects on proportions of overall and female cotton rats in reproductive condition depended on sampling date, but males were most reproductively active with methionine supplementation. Methionine supplementation resulted in an earlier and longer reproductive season. Density-dependent and density-independent factors no doubt interplay to determine population dynamics of cotton rats, but our results suggest that methionine plays a role in the population dynamics of wild cotton rats, apparently by enhancing overall density, recruitment, and reproductive activity of males.

Key words: amino-acid nutrition, food supplementation, hispid cotton rats, methionine, Oklahoma, population response, *Sigmodon hispidus*

Among the many theories to explain limitations to populations of mammalian herbivores, forage quality and quantity have been centrally important (Batzli and Lesieutre 1991; Cole and Batzli 1979; Doonan and Slade 1995; Eshelman and Cameron 1996; Jones 1990; Keith 1983; Sinclair et al. 1982; Sullivan et al. 1983). Food-supplementation experiments have demonstrated the importance of forage quantity in influencing population density, body mass, reproductive timing and effort, and sociality (Boutin 1990; Doonan and Slade 1995). Relative to forage quality, White (1978) and Mattson (1980) implicated nitrogen as the major limiting factor to most organisms (nitrogen limitation hypothesis)—a postulate with considerable empirical support at all trophic levels (Lochmiller 1996; White 1993). While overall nitrogen availability is often limited seasonally or in certain habitats (e.g., xeric ecosystems—Newsome and Corbett 1975), which can influence growth and reproduction of herbivores (Cameron and Eshelman 1996; Randolph et al. 1995), it is equally tenable that specific amino acids can act to limit populations even when overall nitrogen appears adequate (Schetter et al. 1998).

Protein in the diet supplies essential amino acids that cannot be synthesized in adequate amounts by an organism. The

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ability of a dietary protein to supply a proper balance of these essential amino acids determines the quality of that protein (Oser 1959) and can limit population abundance (i.e., amino-acid-quality index—Prestidge and McNeill 1983; White 1993). The ideal protein is balanced in terms of its content of essential amino acids and supply of total nitrogen as nonessential amino acids necessary for growth, maintenance, and reproduction (Moughan et al. 1988; Robbins 1993). Studies of protein quality in diets of waterfowl (Krapu and Swanson 1975; Sedinger 1984), upland game birds (Peoples et al. 1994; Steen et al. 1988), cottontail rabbits (*Sylvilagus floridanus*—Lochmiller et al. 1995), and hispid cotton rats (*Sigmodon hispidus*—Schetter et al. 1998) suggest that individual amino acids may be deficient in some wild populations and may have a prominent role in population limitation.

Schetter et al. (1998) noted that concentrations of some essential amino acids were 43% higher in diets of cotton rats from high-density populations compared with diets from low-density populations. They posited that sulfur-containing cystine and methionine were involved fundamentally with limiting wild populations of cotton rats, but they presented no direct evidence for this contention. Cystine is not an essential amino acid, but methionine is an indispensable component of the diet that supplies sulfur for cystine synthesis when it is absent or deficient in the diet (Rose 1937; Williams et al. 1954). In the absence of dietary methionine, laboratory rats (*Rattus*) rapidly lose body mass and eventually die, even if abundant cystine is supplied (Rose 1937). If methionine is supplied in levels that permit maintenance or slow growth, addition of cystine greatly improves the quality of the diet. Thus, cystine stimulates growth only when dietary methionine is present but in suboptimal quantities (Rose 1937). Cystine can furnish at least one-half of the total sulfur amino-acid requirement of the laboratory rat, but if dietary methionine levels are adequate, cystine does not need to be present in the diet (Nelson and Evans 1958).

The hispid cotton rat (Rodentia: Muridae) is a common generalist herbivore that occurs in grassland habitats in southeastern and south-central North America, Central America, and northern South America (Cameron and Spencer 1981). Cotton rats typically are the dominant rodent species in tallgrass prairies in the south-central Great Plains of North America—the northernmost extent of their distribution. Populations of cotton rats do not display multiannual patterns in their abundance (Brady and Slade 2004), although their densities can vary widely among habitats and years (Doonan and Slade 1995; Goertz 1964; McMurry et al. 1994). Generally, peak densities occur in late summer or early autumn, and the lowest densities occur in early spring.

Because abundance of quality food resources can dictate peak densities of cotton rats (Cameron and Eshelman 1996; Doonan and Slade 1995; Randolph et al. 1995; Schetter et al. 1998), we evaluated the hypotheses that food supplementation in general, and methionine in particular, play roles in the population dynamics of wild cotton rats. We manipulated both quantity (= food supplementation) and quality (= methionine supplementation) of food fed to high densities of wild-caught cotton rats maintained in enclosures because few studies have evaluated impacts at very low or very high densities (Boutin 1990; Yunger 2002). We reasoned that effects of food and methionine supplementation would be most apparent when density-dependent constraints were maximized and predicted that cotton rats receiving supplementation would maintain higher densities, higher survival, and higher reproductive potential longer than cotton rats in control enclosures. In keeping with the conclusion of Boutin (1990) that the overall pattern of population change throughout the year is not affected by food supplementation, we predicted that, regardless of supplementation, cotton rat numbers would decline as the experiment progressed, although most rapidly for nonsupplemented cotton rats.

Materials and Methods

Study area and experimental design.—Our experiment was conducted about 20 km west of Stillwater, Oklahoma (97°10′W, 36°03′N) on Oklahoma State University's Zoology Research Area. The general landscape of the area was gently rolling hills covered by forests of blackjack oak (*Quercus marilandica*) and post oak (*Q. stellata*) and grasslands dominated by little bluestem (*Schizachyrium scoparium*), switchgrass (*Panicum virgatum*), and indiangrass (*Sorghastrum nutans*—Webb 2000; Webb et al. 2003).

Twelve 0.1-ha enclosures were constructed with galvanized sheet metal and were cleared of all resident mammals prior to the beginning of an experiment that started in November 1998 and ended in December 1999. We actually started our research in November 1996 but faced considerable challenge from cotton rats, which were placed in the enclosures at the beginning of the experiment, escaping under the sheet-metal panels (Webb 2000). Ultimately, the 2-m high sheet-metal panels had to be buried in the ground $\geq$25 cm deep to eliminate cotton rats escaping by digging. While data were obtained from April to November 1997 (Webb 2000), we believe that they were somewhat equivocal because of the shortened monitoring period, and therefore they were not analyzed here.

Wild-caught cotton rats were trapped from local populations (0–18 km from enclosures) using Sherman live traps (H. B. Sherman Traps, Tallahassee, Florida) baited with oats. Sixteen nonreproductive adult cotton rats (8 male, 8 female) were toe clipped to indicate unique identification numbers, weighed, and placed in each enclosure (Animal Care and Use Committee 1998; protocol approved by Oklahoma State University's Animal Care and Use Committee). Adult status was determined by body mass: $<$60 g = juvenile, 60–89 g = subadult, and $\geq$90 g = adult (Eifler and Slade 1998; Schetter et al. 1998; Stafford and Stout 1983). To assess impacts of food supplementation at high densities, we set our initial density in experimental enclosures at 160 cotton rats/ha, which exceeded local wild populations by 2–80 times (Schetter et al. 1998).

The 12 enclosures were assigned randomly in a 3 $\times$ 4 block design to 3 treatments: (1) no supplementation (control); (2) supplementation with a pelleted ''mixed ration'' of 47.0% corn, 50.75% beet pulp, 3.0% dried molasses, and 0.25% vitamin and mineral mix by dry weight (9.5% crude protein); or (3) supplementation with the mixed ration and added methionine (4 enclosures/treatment). The mixed ration contained 0.20% methionine, which was slightly below the maintenance requirement of 0.22% for laboratory rats (Williams et al. 1954). Because the total sulfur-containing amino-acid requirement for optimal lactation in laboratory rats is 1.11–1.24% of the diet (Nelson and Evans 1958), D-L-methionine was incorporated into the pelleted mixed ration to increase it to 1.20%. Natural vegetation in the

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enclosures was not manipulated. Feeders were placed at the center and each corner of each enclosure; empty feeders were placed in the control enclosures. Covered feeders limited loss of nutrient in pellets from exposure to weather. Rations were provided ad libitum and replenished every 7–10 days. No evidence of removal of food by other species (e.g., birds) was noted during the experiment.

Assessment of cotton rats.—To assess populations of cotton rats, 25 Sherman live traps were set about 5 m apart in a 5 × 5 grid in each enclosure. All enclosures were trapped simultaneously for 3 consecutive nights each month, except during the normal breeding season in April–November when they generally were trapped for two 3-day sessions per month. Traps were baited with oats in the late afternoon and checked the next morning. For each cotton rat captured, body mass (g), sex, age class (i.e., juvenile, subadult, adult), reproductive condition, and toe-clip number were recorded. If the cotton rat had not been toe clipped (i.e., was a recruit), it was assigned a new identification number, via toe clipping, before being released. Males were considered reproductively active when scrotal. A female's vaginal condition (perforate or imperforate), pregnancy status (determined by palpation), and lactational status were used to assess reproductive condition.

Minimum number known alive in each enclosure was calculated by summing the number of unique individuals caught during a 3-day trapping session and all individuals that were caught before and after that session (Krebs 1966; Pollock et al. 1990). Estimates of the minimum number known alive were considered to be generally accurate because $\geq$87% of the cotton rats were caught during each trapping session (Hilborn et al. 1976). Estimates were converted to densities (cotton rats/ha), and females and males were analyzed separately and together. Sex ratios were calculated as proportions of females to males. Age-class ratios were calculated as proportions of juveniles, subadults, and adults. Survival rates were calculated as proportions of cotton rats captured during a trapping session that were recaptured during any subsequent session (Schetter et al. 1998). Therefore, survival rates were not calculated for the last trapping session of the experiment. Survival rates of females and males were calculated separately and together. Given that cotton rats could not immigrate into enclosures, recruitment was determined as the number of new juveniles divided by the number of mature females (subadults and adults pooled—Schetter et al. 1998). Breeding intensity was measured as proportions of mature males and females in enclosures that were reproductively active.

Statistical analyses.—The experimental design required confirmation that vegetative effects did not confound effects of supplementation. Vegetation was measured seasonally to confirm that enclosures did not differ among treatments (i.e., did not result in significantly different availabilities of native vegetation, and thus potential sources of food and methionine, that cotton rats could consume). Webb et al. (2003) reported that only 2 of 22 vegetative characteristics differed statistically among treatments, and those differences (i.e., magnitude of effect—Robinson and Wainer 2002) were biologically small relative to the overall plant community; they concluded that they did not affect availability of methionine in the enclosures. Therefore, any differences in demographic characteristics of cotton rats in the enclosures were assumed to be the result of supplementation.

Treatment effects and treatment-by-date interactions for density, sex ratio, age ratio, survival rate, per capita recruitment, and proportion of reproductively active cotton rats were assessed with repeated-measures analyses of variance (General Linear Models—SAS Institute Inc. 1996). When significant treatment-by-date interactions occurred, least-squares-means tests were used to determine how treatments differed by sampling date (SAS Institute Inc. 1996). If no treatment-by-date interactions occurred in the repeated-measures analyses, then only overall treatment means were compared with least-squares-means tests. One corner enclosure was removed from analyses because predation, presumably by raptors that were observed perching on the enclosure's boundary, eliminated cotton rats within weeks after stocking. Therefore, the control included 3, rather than 4, replicates.

Because of the clustered nature and relatively small size of the enclosures, climatic conditions were assumed to be the same in all enclosures. However, given seasonal changes in availabilities of methionine with, for example, the flush of new vegetation following spring rainfall, it was possible that demographic responses of cotton rats to climate, if they occurred at all, varied among treatments. That would suggest some synergy between ambient availabilities of naturally occurring methionine and our supplementations, compromising the experimental design. Average monthly temperature (°C), total monthly precipitation (cm), and total monthly snowfall (cm) from the National Oceanic and Atmospheric Administration (1997, 1998, 1999) were used as independent variables in multiple regression analyses to assess their relationship to density, survival, recruitment, and reproductive intensity of cotton rats; a P-value of 0.15 was set for inclusion of independent variables in those models (Cody and Smith 1997; Ott 1993). If no multivariable models were indicated, then simple linear regressions by treatment were conducted, and slopes of each relationship were compared among treatments using F-tests (Neter and Wasserman 1974; Ott 1993). Statistical significance was set at $P = 0.05$.

Results

Regardless of treatment, densities of cotton rats declined as the experiment progressed, although they were about twice as high in supplemented enclosures throughout most of the experiment (Fig. 1). Generally, densities of cotton rats in control enclosures decreased earliest and to the greatest extent, followed by mixed ration and then methionine-enhanced treatments. Treatment effects on overall density interacted with sampling date ($F = 1.86$, $d.f. = 28, 112$, $P = 0.012$; Fig. 1A). Densities of females were greater in the methionine ($P = 0.003$; Fig. 1B) and mixed-ration ($P = 0.015$) treatments than the control, but female density in mixed-ration and methionine treatments did not differ ($P = 0.301$). Male densities in mixed-ration ($P = 0.009$) and methionine ($P < 0.001$) treatments were greater than the control, but mixed-ration and methionine treatments did not differ ($P = 0.067$; Fig. 1C). Sex ratios did not differ among treatments ($F = 0.48$, $d.f. = 2, 8$, $P = 0.635$). Supplementation did not affect proportions of juveniles ($F = 1.84$, $d.f. = 2, 8$, $P = 0.220$), subadults ($F = 2.11$, $d.f. = 2, 8$, $P = 0.184$), or adults ($F = 0.24$, $d.f. = 2, 8$, $P = 0.790$; Table 1).

Overall survival rates interacted with treatment and sampling dates ($F = 1.76$, $d.f. = 28, 112$, $P = 0.021$), with positive effects of supplementation in October and November (Fig. 2A). Treatment and sampling date interacted with female survival ($F = 2.49$, $d.f. = 28, 112$, $P < 0.001$), with supplemented females experiencing higher survival from August through November than control females (Fig. 2B). Male survival rates did not differ among treatments ($F = 0.87$, $d.f. = 2, 8$, $P = 0.454$; Fig. 2F). Mean recruitment in the methionine treatment (0.49 new juveniles/mature female ± 0.12 SE) was greater than the control (0.25 ± 0.11, $P = 0.005$) and mixed-ration treatment

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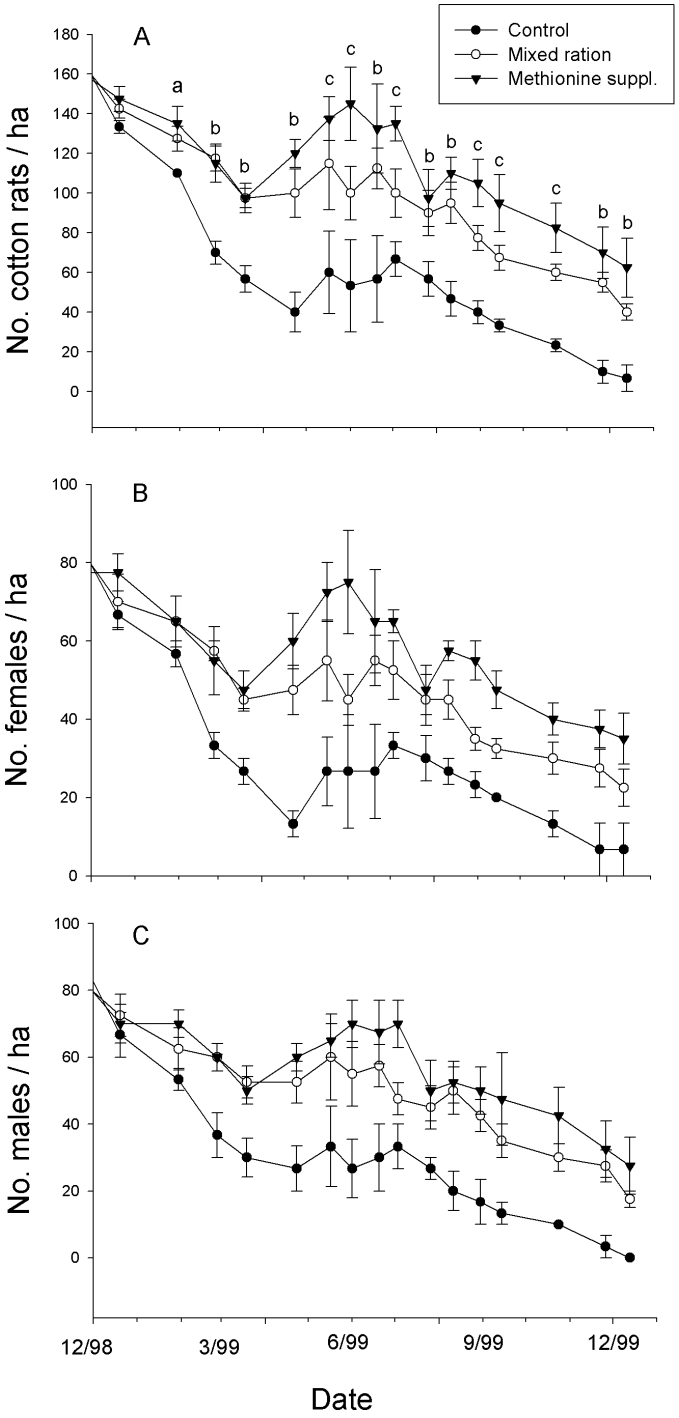


FIG. 1.—Mean (± *SE*) densities of wild cotton rats known to be alive for A) both sexes combined, B) females, and C) males in control, mixed-ration, and methionine enclosures. Differences among means, determined using least-squares-means tests when repeated-measures ANOVA indicated significant treatment-by-date interaction, are indicated as a = methionine > control, b = mixed-ration and methionine supplementation > control, and c = methionine supplementation > mixed-ration supplementation > control.

(0.23 ± 0.07, $P = 0.008$), but no differences were found between control and mixed-ration treatments ($P = 0.488$).

Effects of supplementation on proportions of cotton rats in reproductive condition varied between sexes (Fig. 3). Treatment effects on proportions of cotton rats in reproductive condition interacted with sampling date overall ($F = 2.17$, $d.f. = 32, 128$, $P = 0.001$; Fig. 3A) and for females ($F = 5.19$, $d.f. = 32, 128$, $P < 0.001$), with differences in March–July (Fig. 3B). In contrast, no treatment-by-date interactions occurred in the proportion of scrotal males, but scrotal males were more abundant in methionine treatments than the control ($P = 0.021$) and mixed-ration treatments ($P = 0.044$), which did not differ ($P = 0.522$). Patterns of change, overall and for both sexes, suggested earlier and longer reproductive activity with methionine supplementation (Fig. 3). For example, control females did not become reproductively active until after 19 March 1999, by which time a significantly higher proportion of methionine-enhanced females already were active (Fig. 3B). At the end of the breeding season, some methionine-enhanced females remained reproductively active after 26 July 1999, whereas control females were inactive by 3 July (Fig. 3B). Despite starting reproductive activities later, proportions of reproductively active females in control enclosures were higher during some sampling dates than proportions in supplemented or methionine-enhanced enclosures. The lengthened reproductive season for methionine-enhanced females was associated with a lower proportion of reproductively active individuals throughout the period (Fig. 3B).

No significant multivariable regression models were obtained from the assessment of climate with demographic parameters of cotton rats; however, some individual relationships existed by treatment. Only the relationship between precipitation and reproductive intensity was significant among all 3 treatments ($r = 0.473$–0.548, $P = 0.005$–0.011); temperature and recruitment were correlated in control ($r = 0.413$, $P = 0.045$) and methionine-enhanced ($r = 0.418$, $P = 0.038$) treatments; and precipitation and density were correlated in only the methionine treatment ($r = 0.454$, $P = 0.023$). Nevertheless, no differences in the slopes of the relationships of like-paired variables were detected among treatments ($F = 0.01$–0.45, $d.f. = 2, 16$, $P > 0.05$), suggesting that any interplay among climatic variables and supplementation was uniform among treatments.

DISCUSSION

The addition of methionine to the mixed ration effectively increased the overall crude protein in the ration from 9.5% to 10.5%, so it might be argued that methionine itself was not responsible for effects observed during our experiment. However, we contend that an increase of only 1% increase in overall crude protein would not cause significant alterations in the dominant demographic parameters that we measured. In support of our contention, Parsons (2001) found that survival rates of cotton rats were basically 100% when fed 6−18% dietary crude protein, and growth rates of young cotton rats did not differ with 12−22% dietary crude protein. Both parameters suggest that quality of the available protein, in our case enhanced by methionine, has a greater impact on population parameters of cotton rats than its overall percentage in the diet (Schetter et al. 1998). Assuming that optimal lactational requirements of laboratory rats for methionine

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Table 1.—Proportion of females, juveniles, subadults, and adults in populations of wild cotton rats (*Sigmodon hispidus*) with no supplementation (control), mixed-ration supplementation, and methionine supplementation in north-central Oklahoma, 1998–1999.

	Treatment								
	Control			Mixed ration			Methionine supplementation		
Class	*n*	$\bar{X}$	*SE*	*n*	$\bar{X}$	*SE*	*n*	$\bar{X}$	*SE*
Female	45	0.486	0.027	60	0.486	0.009	60	0.507	0.009
Juvenile	48	0.200	0.043	68	0.149	0.025	68	0.210	0.029
Subadult	48	0.354	0.051	68	0.283	0.033	68	0.252	0.033
Adult	48	0.446	0.049	68	0.568	0.032	68	0.538	0.033

(1.11−1.24%—Nelson and Evans 1958) approximate those of cotton rats, positive responses of recruitment and reproductive activity to methionine supplementation, particularly for females early and late in the breeding season and males overall, suggest that our design did elucidate a positive role of methionine in cotton rat nutrition.

Overall, female, and male densities, overall and female survival, and some proportions of reproductively active cotton rats were enhanced by supplementation (Table 2), which suggested that methionine had its greatest impact in late spring, early summer, and early autumn. Relative to mixed-ration treatments, methionine supplementation increased overall density of cotton rats. Only percentages of reproductively active males and recruitment were uniquely higher on methionine treatments relative to control and mixed-ration treatments (Table 2). It is apparent from our experiment that ad libitum supplementation with either increased quantity or quality did not permit populations to maintain a static density at any level. Consistent with previous conclusions (Boutin 1990; Doonan and Slade 1995), supplementation allowed cotton rat populations in mixed-ration and methionine treatments to maintain densities higher (up to twice) than the control during most sampling periods. Nevertheless, an overall pattern of decline occurred on all treatments—highlighting the interplay among limitation of food availability and quality and density-dependent factors such as sociality (Christian and Davis 1964) and density-independent factors such as weather (Doonan and Slade 1995).

Our experiments differed from those of Doonan and Slade (1995) in several ways. We set the initial density of cotton rats in our experiments at high levels (160 cotton rats/ha) and started supplementing experimental populations in November; they supplemented free-ranging populations at initial densities generally $<$10 cotton rats/ha in June. We provided 2 types of supplementation ad libitum; they provided a single source of supplementation at fixed amounts (Saitoh 1989) and in pulses. While both studies were conducted in the northern part of the geographic distribution of cotton rats (Cameron and Spencer 1981), our experiments occurred about 410 km southwest of their study. Doonan and Slade (1995) contended that cotton rat populations at the northern latitudes of their range can respond to food supplementation by increased densities, but populations are ''mediated'' by seasonality, climatic unpredictability, and suspected social interactions. There was some indication that climate interplayed with supplementation to influence population dynamics in our experiment (e.g., precipitation was correlated positively with reproductive activity in all treatments). We did not assess sociality but observed no outward signs of social stress (e.g., scars, injuries—Webb et al. 2003). It is possible that such mechanisms are most pronounced at the northern extent of the geographic range of cotton rats, but future research is required to elucidate any effects of latitude.

Differences in the experimental designs between Doonan and Slade (1995) and our study resulted in variation in population response. In both studies, overall density of cotton rats and recruitment were higher with supplementation; interestingly, only added methionine in our study was associated with increased recruitment and male reproductive activity (Table 2). Unlike in our study, Doonan and Slade (1995) did not observe any differences in overall survival or percentages of reproductively active males or females. Conversely, they were able to document increased percentages of subadults in their populations, whereas relative percentages of age classes did not vary among experimental treatments in our study. Apparently, our ad libitum supplementation and differences in the nutritional values of supplementation between studies allowed our experimental populations to experience some enhanced survival and male reproductive activity.

With either form of supplementation, we were able to maintain considerably higher mean densities of cotton rats (overall: 57.1 cotton rats/ha for control, 97.2 cotton rats/ha for mixed-ration treatments, and 115.0 cotton rats/ha for methionine-enhanced treatments) than occur in local wild populations. In habitats that provided high-quality protein, wild local populations averaged 23, 31, 78, and 37 cotton rats/ha in February, May, August, and November, respectively (Schetter et al. 1998). In contrast, average densities in low-quality habitats were about 7, 6, 2, and 4 cotton rats/ha in February, May, August, and November, respectively (Schetter et al. 1998). It is tempting to conclude that such differences in density of cotton rats are due exclusively to differences in availability of food, but other factors may be involved. Habitats in our study may have been of higher quality than those evaluated by Schetter et al. (1998); unfortunately, we did not conduct food-habit analyses to permit a comparison between studies. Nonvolant predators of cotton rats were excluded from our enclosures by design, but populations in the other studies (Doonan and Slade 1995) presumably experienced natural predation. Taitt and Krebs

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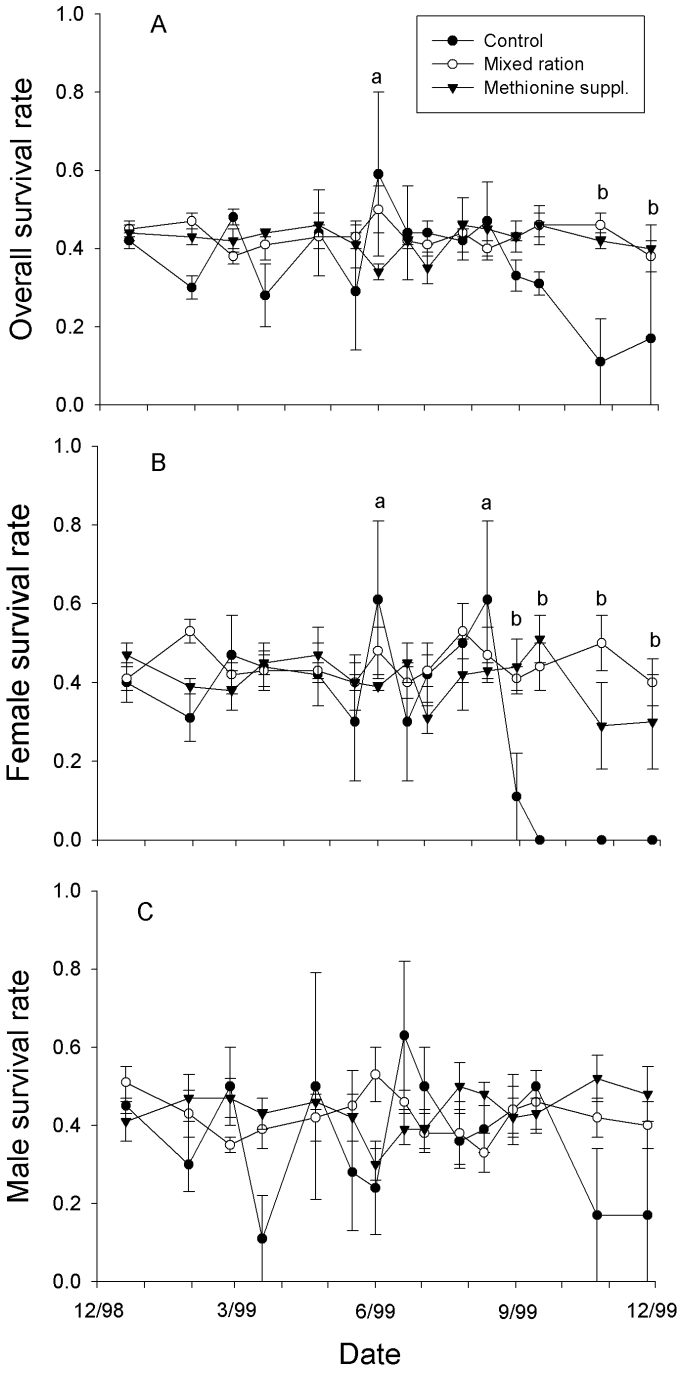


FIG. 2.—Mean (± *SE*) survival rates of cotton rats for A) both sexes combined, B) females, and C) males in control, mixed-ration, and methionine enclosures. Differences among means, determined using least-squares-means tests when repeated-measures ANOVA indicated significant treatment-by-date interaction, are indicated as a = control > mixed-ration and methionine supplementation and b = mixed-ration and methionine supplementation > control.

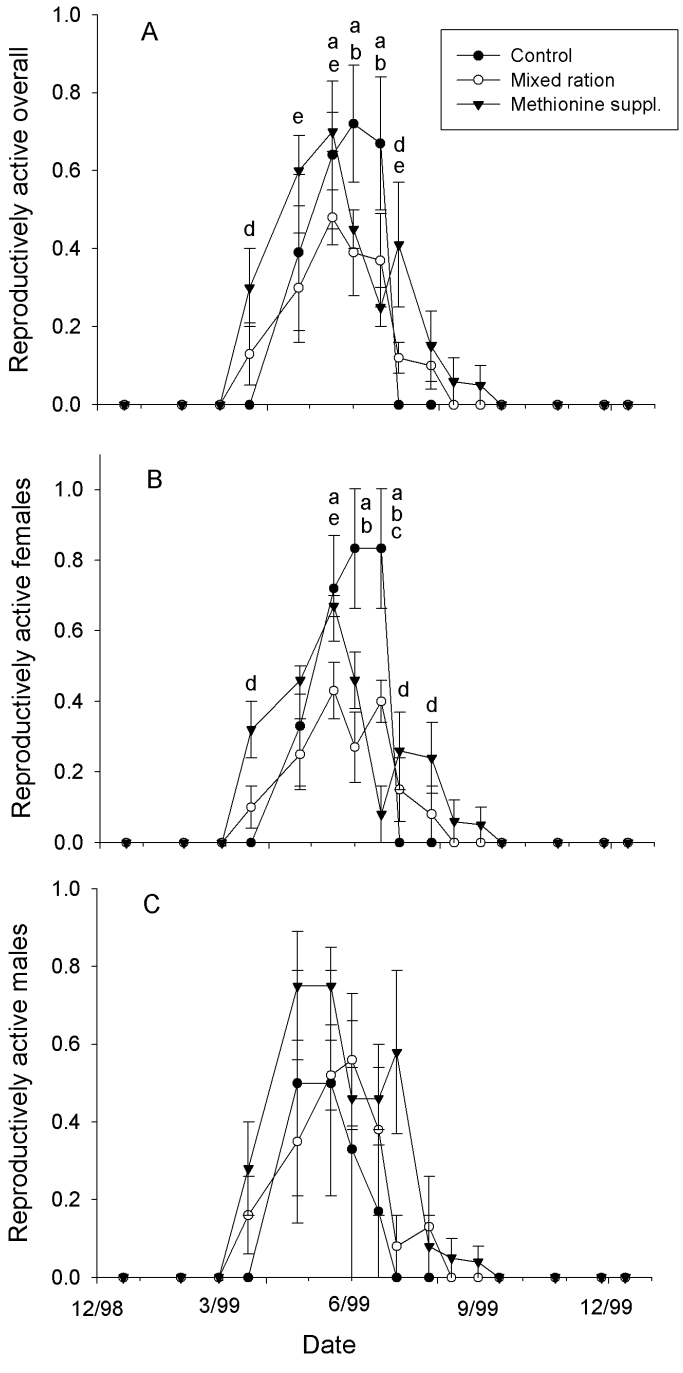


FIG. 3.—Mean (± *SE*) proportions of reproductively active cotton rats for A) both sexes combined, B) females, and C) males in control, mixed-ration, and methionine treatments. Differences among means, determined using least-squares-means tests when repeated-measures ANOVA indicated significant treatment-by-date interaction, are indicated as a = control > mixed-ration supplementation, b = control > methionine supplementation, c = mixed-ration supplementation > methionine supplementation, d = methionine supplementation > control, and e = methionine supplementation > mixed-ration supplementation.

(1983) observed increased densities of Townsend's voles (*Microtus townsendii*) when protected from predators and supplied with additional food. Populations of prairie voles (*M. ochrogaster*) that were protected from predators also reached higher densities than control populations (Desy and Batzli 1989), and when prairie voles were protected from predators and supplemented with additional food, densities were even higher (Desy and Thompson 1983). Finally, dispersal can play a major role in the population dynamics of cotton rats and is density dependent (Joule and Cameron 1975; Spencer and Cameron

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1983), but individuals in our experiments could not disperse, resulting in higher densities in treatments than would occur naturally.

Overall, cotton rats in mixed-ration and methionine treatments had higher survival rates than the control in autumn, presumably because of enhanced food quantity and quality. In particular, females provided with additional food had higher survival rates. When high-quality forage was available, life expectancy of prairie voles was increased (Cole and Batzli 1979). Townsend's voles (Taitt et al. 1981), northern flying squirrels (*Glaucomys sabrinus*—Ransome and Sullivan 2004), Douglas squirrels (*Tamiasciurus douglasii*—Sullivan and Sullivan 1982), and snowshoe hares (*Lepus americanus*—Boutin 1984) also experienced increased survival when supplemental food was provided. However, supplementation does not always affect overall survival (Doonan and Slade 1995; Duquette and Millar 1995; Pennycuik et al. 1987; Saitoh 1989; Sullivan 1990; Taitt and Krebs 1981), as was apparent in some months in our experiment.

Supplemented populations of cotton rats in our experiment were expected to achieve higher rates of recruitment compared with control populations, but recruitment under both conditions was expected to be constrained because of increased density and the elimination of dispersal in our design. Cotton rats supplemented with methionine had greater recruitment than those in control and mixed-ration treatments; however, our estimates of recruitment rates (range = 0.23–1.42 new juveniles/mature female) were lower than local populations of cotton rats (0.50–3.50 new juveniles/mature female—Schetter et al. 1998), likely because of constraints of density in the enclosures. Schetter et al. (1998) reported that total number of juvenile recruits that entered the trappable population was about 5 times greater in populations with access to high-quality protein than populations occupying low-quality habitat.

Nutritional requirements increase during reproduction, especially for females, and inadequate nutrition can inhibit reproduction (Eshelman 1991; Randolph et al. 1995; Robbins 1993). Supplemental food (especially methionine supplementation) resulted in earlier and longer reproductive seasons, suggesting that supplementation influenced reproduction. Yet only male cotton rats were consistently more reproductively active with enhanced methionine. Webb et al. (2003) found that male cotton rats supplemented with methionine in these experiments had enhanced platelet and total leukocyte counts, which may provide some advantages to overall health (e.g., improved macrophagic function during pathogenic exposure—McMurry et al. 1999) and thereby may have enhanced reproductive potential. The addition of high-quality food can influence temporal patterns of reproduction in mice and voles. White-footed mice (*Peromyscus leucopus*) experience an earlier breeding season with supplementation of high-quality food (Briggs 1986; Hansen and Batzli 1978, 1979). Populations of wood mice (*Apodemus sylvaticus*—Akbar and Gorman 1993) and house mice (*Mus musculus*—Bomford 1987; Bomford and Redhead 1987) breed earlier and longer with additional high-quality food. Supplementation of high-quality food also shortened the winter nonbreeding season in populations of Townsend's voles (Taitt and Krebs 1981).

Table 2.—Responses of demographic variables of cotton rats (*Sigmodon hispidus*) to quantity (mixed ration) and quality (methionine) supplementation relative to the control. Effects of supplementation are indicated as positive or negative if the overall treatment effect with no treatment-by-date interaction or ≥2 least-squares-means tests following a treatment-by-date interaction were significant ($P < 0.05$); no effect is indicated by a zero.

Demographic variable	Mixed ration versus control	Methionine versus control	Methionine versus mixed ration
Overall density	+	+	+
Female density	+	+	0
Male density	+	+	0
Sex ratio	0	0	0
% Juvenile	0	0	0
% Subadult	0	0	0
% Adult	0	0	0
Overall survival	+	+	0
Female survival	+	+	0
Male survival	0	0	0
Recruitment	0	+	+
% Reproductive females	−[a]	−[a], +[b]	0
% Reproductive males	0	+	+

[a] Negative effect in May and June.
[b] Positive effect in March and July.

In general, densities of cotton rats in our study were highest with supplementation. Methionine supplementation further enhanced various demographic characteristics in late spring, early summer, and early autumn. Overall survival rates increased with supplementation, particularly for females in autumn. Per capita recruitment and reproductive intensity of males were increased with methionine supplementation. Supplementation also appeared to result in an earlier and longer reproductive season. Methionine may be fundamentally involved in the population dynamics of wild cotton rats, but future studies are needed to assess the role of methionine and other essential amino acids in the nutrition of cotton rats and other herbivores. White (1993:95) described the work of Prestidge and McNeill (1983) as supporting the ''amino-acid-quality index'' whereby availabilities of groups of amino acids limit populations of herbivorous insects. Obviously, the role of amino acids in population dynamics of mammalian herbivores is more intricate than the effects of methionine alone, but our results tend to support White's (1993) tenet suggesting that individual essential amino acids can play important roles in limiting abundances of herbivores.

Resumen

Mucha investigación demestra que la cantidad y calidad de la comida limitan la densidad de las poblaciones de vertebrados. Evaluamos la hipótesis de que la disponibilidad de comida y del aminoácido esencial, metionina, está relacionada con el control del tamaño poblaciónal de la rata algodonera (*Sigmodon hispidus*). Se examinó el efecto del aporte adicional de comida y metionina en la densidad, supervivencia, y reproducción de la rata algodonera silvestre

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en la región central del norte de Oklahoma entre 1998 y 1999. Doce grupos encajonados, de 16 animales cada uno (8 machos, 8 hembras), fueron asignados al azar a uno de los siguientes grupos experimentales: el control (sin aporte adicional de comida/metionina), suplemento de comida con aporte de metionina un poco menos que el nivel de mantenimiento (0.20%) o suplemento de comida con alto aporte de metionina (1.20%). En general, las densidades de los grupos con suplemento alimenticio resultaron ser el doble respecto al grupo control, siendo el grupo con mayor aporte de metionina el de mayor densidad. El efecto del tratamiento en la tasa de supervivencia fue dependiente de la época del año, siendo mayor en los grupos con aporte adicional de comida/metionina en octubre y noviembre. La tasa de reclutamiento por individuo fue mayor en el grupo tratado con suplemento de comida con alto nivel de metionina. Los efectos del tratamiento en la población general, y en hembras de la rata algodonera en las proporciones reproductiva dependieron de la fecha de muestreo, sin embargo los machos fueron reproductivamente más activos con un suplemento de metionina. El aporte adicional de metionina adelantó y alargó la temporada de reproducción. Aunque se sabe que la dinámica de poblaciones de la rata algodonera está determinada por factores dependientes e independientes de la densidad, nuestros datos sugieren que la metionina juega un papel en la dinámica poblacional de estos roedores, aparentemente aumentando su densidad en general, el reclutamiento y la actividad reproductiva de los machos.

Acknowledgments

Funding and support was provided by McIntire-Stennis (Department of Forestry, Oklahoma State University), Department of Zoology, and Oklahoma Cooperative Fish and Wildlife Research Unit (Oklahoma State University, Oklahoma Department of Wildlife Conservation, United States Geological Survey, and Wildlife Management Institute cooperating). We thank E. C. Hellgren, S. S. Ditchkoff, and D. P. Rafferty for providing valuable comments during the course of the study and on earlier drafts of this manuscript, W. D. Walter and S. Leis for assistance with revisions to the figures, and Raùl Pastor Medall, Carrie M. Leslie, and S. F. Fox for translation of the abstract into Spanish. The late R. L. Lochmiller deserves credit for the genesis of this project. This publication was approved by the Director of the Oklahoma State University Agricultural Experiment Station.

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Submitted 16 December 2003. Accepted 6 September 2004.

Associate Editor was Ronald D. Gettinger.

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