EFFECTS OF FOOD ABUNDANCE ON INDIVIDUALS AND POPULATIONS OF THE ROCK MOUSE (*PEROMYSCUS DIFFICILIS*)

C. GALINDO-LEAL AND C. J. KREBS

Centre for Conservation Biology, Department of Biological Sciences, Stanford University, Stanford, CA 94305-5020 (CG-L)
Department of Zoology, University of British Columbia, Vancouver, Canada, V6T-2A9 (CJK)

We examined individual and population responses of the rock mouse, *Peromyscus difficilis,* to experimental changes in food abundance. Two food addition experiments lasting 4 months were carried out during breeding and non-breeding seasons to test the hypothesis that females are more responsive to food resources than are males, especially during reproduction. On two grids, we added food on relatively widely spaced point sources to compare effects within grids on fed and unfed mice. We also compared populations on two treatment grids and a control grid. Food addition resulted in increased immigration, earlier breeding, and increased reproduction in contrast to the control grid. Improvement of summer survival was evident only when analysis was undertaken at a fine scale; fed individuals showed longer residence times. Females gained weight and had improved reproduction, and improved survival, during both wet and dry seasons. Males responded less consistently than did females.

Key words: *Peromyscus difficilis,* rock mouse, demography, food supplementation, Durango, Mexico

Dispersion, abundance, renewability, and seasonality of resources can influence social interactions and spatial distribution of individuals (Clutton-Brock and Harvey, 1978; Davies and Lundberg, 1984; Jarman, 1974; Ostfeld, 1985; Rubenstein, 1981). Social systems and social interactions, in turn, may affect demographic characteristics of populations (Dunbar, 1985).

Populations of *Peromyscus* species, like many other insectivorous and granivorous rodents, are relatively more stable than those of herbivorous rodents (Kaufman and Kaufman, 1989; Montgomery, 1989). Population stability seems to be influenced greatly by social interactions (Halpin 1981; Harland et al., 1979; Healey, 1967; Lusk and Millar, 1989; Sadleir, 1965; Taitt, 1981; Terman, 1968). For example, spacing behavior of adult males and females affects the distribution of individuals (Galindo-Leal, 1991), limits recruitment of new individuals into the population (Fairbairn, 1977; Galindo and Krebs, 1987; Hansen and Batzli, 1978; Harland et al., 1979; Healey, 1967; Metzgar, 1971; Mihok, 1979; Nadeau et al., 1981; Sadleir, 1965; Taitt, 1981), and inhibits maturation of young females (Lusk and Millar, 1989).

Dispersion and individual interactions of *Peromyscus* vary seasonally (Lusk and Millar, 1989; Sadleir, 1965; Wolff, 1989). In the breeding season, resources are most abundant, but behavioral interactions increase with reproductive activity (Sadleir, 1965). In the non-breeding season, breeding stops as resources decrease. Several authors have suggested that breeding females should be more responsive to environmental conditions than males (Anderson, 1989; Boonstra, 1977; Fordham, 1971; Ostfeld, 1985; Schiebe and O'Farrell, 1995; Taitt, 1981). Lactation requires an increase of from 74 to 147% over energy requirements of non-lactating individuals for *Peromyscus* (Glazier, 1985; Millar, 1989); therefore, the behavior of breeding females should reflect their requirements for food resources.

We investigated the effect of supplementary food on individuals and populations of *P. difficilis* to test the hypothesis that females are more responsive to food availability than males and that these differences are more pronounced during the breeding season than the non-breeding season. The following predictions were tested. Supplemented food should affect most strongly body weight, residence time, and reproduction of resident adult females compared with adult males. These changes should be particularly evident in the breeding season.

MATERIALS AND METHODS

Study area.—Our study took place from May 1987 to July 1988 in southwestern Durango on the eastern slopes of the western Sierra Madre, Mexico (23°25′N; 104°15′W), at 2,400 m above mean sea level. Annual precipitation ranged from 50 to 70 cm and was concentrated in 5 months between June and October. Mean monthly temperatures fluctuated from 17.4 to 20.4°C. The dominant forest type was dry-temperate oak-pine with dominant tree species including several species of oaks (*Quercus durifolia, Q. sideroxyla, Q. eduardii, Q. chihuahuensis, Q. convalata, Q. potosina, Q. rugosa*), and pines (*Pinus arizonica, P. chihuahuana, P. engelmani, P. leiophylla, P. teocote*). Point-leaf manzanita (*Arctostaphylos pungens*) and guazapol (*Ceanothus buxifolius*) were the main components of the shrub stratum.

Experimental design.—We used two different experimental designs to analyze individual and population responses to food provisioning. To analyze individual responses, we used two grids (I, II). Unlike most food addition experiments that provide food near every other trap station (Briggs, 1986; Duquette and Millar, 1995*a*, 1995*b*; Gilbert and Krebs, 1981; Taitt, 1981; Wolff, 1985), food was placed at stations near the most used trap station in home ranges of one-half of the individuals on each grid. Food stations consisted of two 2-l cans containing a mixture of sunflower seeds and whole-grained oats, nailed (0.5–2 m high) next to each other on the tree nearest to a trap station. Each can had a small entrance to prevent birds from taking food. Two cans were provided to insure a constant food supply. They were refilled every 2 weeks and were rarely emptied before refilling. Experiments were carried out during both wet and dry seasons on both grids.

In this design, individuals were considered experimental units. Individuals were chosen randomly with the restriction that food stations should not be in contiguous home ranges. Therefore, most food stations were spaced widely. We considered experimental individuals fed to be those that used the closest trap to each food station; control individuals were non-fed mice that were never caught in these traps. Only one of 51 fed individuals survived from the wet to the dry season and was considered experimental in both seasons. The objective of this design was to eliminate pseudoreplication by interspersing experimental and control units and increase replication (Hurlbert, 1984). Grids were analyzed individually, because the duration of experimental manipulations and their population dynamics differed (Galindo-Leal, 1991, 1997; Galindo-Leal and Krebs, 1997).

To analyze population responses, we considered grids as experimental units. The control grid (grid III) was situated between experimental grid I and II, 600 m and 1 km from them, respectively. No movements between grids were documented. This design achieved neither replication nor interspersion and suffered from pseudoreplication. Consequently we opted for a conservative approach and used no inferential statistics in comparisons (Hurlbert, 1984). Instead we searched for consistent differences between both pretreatment and treatment periods within and between experimental grids. Accurate population estimates were provided by the complete enumeration technique because both maximum and minimum trappabilities (Hilborn et al., 1976; Krebs and Boonstra, 1984) were > 64% for all areas.

Trapping on grids I, II, and III (control) began in May 1987 and continued through July 1988. Each grid had 136 Longworth traps set in a 8- by 17-point grid with 20-m intervals, covering 5.4 ha. Traps were baited with whole oats and were placed on the ground or fixed with wide elastic bands 1–2 m high on the closest trees. Trapping sessions lasted 2 nights and were scheduled at 2–4-week intervals. Traps were opened in the afternoon, checked for the next 2 consecutive mornings, and left locked open between trapping sessions (Galindo-Leal, 1996; Galindo-Leal and Krebs 1997). Trapped individuals were ear-tagged, and their sex, reproductive condition, weight (to 1.0 g), and location of capture were recorded. Breeding condition in males was determined by recording visible cauda epydidimis, and that of females was determined by presence of perforated or non-perforated vaginas. Size of nipples was scored as large, medium, or small, and evident pregnancies were recorded. Individuals were assigned to one of three age categories: adults (sexual maturity or >22 g), subadults (molting, brown pelage and/or >19 and <23 g), and juveniles (gray pelage and <20 g). Individuals trapped for two or more sessions were considered residents, while those trapped only once were considered as transients. We analyzed these two categories separately. Recruitment included resident individuals only.

Wet season.—The pretreatment period lasted from May to 27 July 1987. Food stations were filled from then until 5 December on grid I, but only until 20 November on grid II due to heavy disturbance of trap stations. There were 13 food stations on grid I and 8 food stations on grid II.

Dry season.—The dry season lasted from December through May. The pretreatment period lasted from January to 7 April 1988. Food stations were filled from then until 13 July on both grids. To avoid familiarity with locations from previous treatment, we moved all food stations one trap station away. In this period, there were 13 food stations on grid I and 11 on grid II.

Sex ratios are shown as the proportion of females to the total population. We used contingency tables and log- likelihood tests (*G*) to compare sex, age and residency of control and experimental individuals. We used ANOVA to analyze differences in residence time of experimental and control individuals (Sokal and Rohlf, 1981).

RESULTS

Wet Season

Density and seasonal patterns.—Populations of rock mice were usually low at the end of the dry season in April–June and during the first one-half of the wet season in June–August (Galindo-Leal, 1991; Galindo-Leal and Krebs, 1997). Populations increased during the second one-half of the wet season (September–October) and continued increasing steadily throughout the first one-half of the dry season (November–January). Food addition began at the end of July before populations began to increase and lasted until December when they begin to decline (Galindo-Leal and Krebs, 1997).

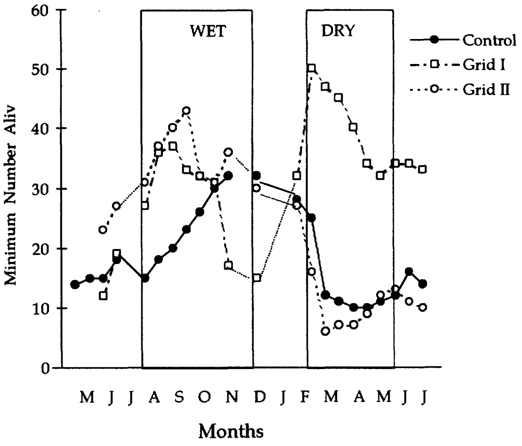

FIG. 1.—Population trends of experimental (I, open circle; II, open square) and control areas (closed circle) for suppmental food studies of *Peromyscus difficilis*. Rectangles indicate periods of food addition in the wet and dry seasons.

Pretreatment numbers in populations were similar on grid II and the control grid but were 1.6× higher on grid I. After treatment, numbers of individuals on both experimental grids increased at a higher rate than on the control, doubling the numbers on the control grid during September. Populations on both experimental grids began declining in October (Fig. 1). In contrast, the population on the control grid did not begin increasing until September and reached high numbers at the end of October and November. At this point, all three populations had similar numbers. The annual fluctuation of the control population was similar to that of unmanipulated grids in the previous year (Galindo-Leal and Krebs, 1997). On grid II, an excessive number of traps was disturbed by predators in November causing a decline in the population. The experiment was terminated on this grid at this time.

Sex ratios on both experimental grids did not deviate significantly from 1:1 both during the pretreatment period (I, II, $\bar{X} = 0.5$) and after food addition (I, $\bar{X} = 0.47$; II, $\bar{X}$

= 0.52). The sex ratio on the control grid was biased towards males both during pretreatment ($\bar{X} = 0.41$) and treatment periods ($\bar{X} = 0.44$).

The number of fed individuals was 35 on grid I and 16 on grid II of 196 (17.9%) and 97 (16.5%) individuals caught on each grid, respectively, during the treatment period. Age and sex composition of fed individuals on both grids did not differ from the whole population (grid I, $G = 0.58$, *d.f.* = 3, $P > 0.05$; grid II, $G = 3.72$, *d.f.* = 3, $P > 0.05$). However, there were clear sex differences in the temporal response. Whereas pretreatment sex ratios on both grids were close to 1:1, the sex ratio of fed individuals became highly skewed toward females soon after food was provided. Males began to use food stations more readily on grid I by the end of September, and the sex ratio fluctuated from close to 1:2. On grid II, sample sizes of fed individuals were too small to obtain reliable sex ratios, but the trend was similar (Fig. 2). Most fed individuals on both grids were residents (I, 77%; II, 81%). On both grids, there were slightly more residents than expected by the composition of the population, but differences were not significant (G's < 2.5, *d.f.* = 1, $P > 0.05$).

Changes in body weight.—Fed and unfed females had similar weights at the beginning of the treatment on grid I. By mid-September, fed females were heavier than were unfed females and continued to be heavier throughout the treatment period. On grid II, fed females were heavier from the beginning of treatment, but by October, the difference between fed and unfed females diminished (Fig. 3). On both grids unfed males were slightly heavier than fed males at the beginning of the experiment. The trend reversed after mid-September, and fed males were heavier than unfed males throughout the rest of the treatment period. The difference in weight was particularly evident in October and November (Fig. 3).

Differences in recruitment.—Pretreatment recruitment was similar on grids II and the control but slightly low on grid I. After food addition, recruitment increased on both experimental grids, but this response was evident only during the first one-half of the treatment period. In August and September, there were 24 recruits on each experimental grid but 13 on the control grid. Sex composition of recruits was similar between grids, but age composition differed substantially. Experimental grids recruited 7 (I) and 2.4 (II) times more adults than subadults and juveniles. In contrast, the control grid recruited 2.3 times more juveniles and subadults than adults. During October and November there was little difference in recruitment between the three grids (15 and 14 recruits on experimental grids and 18 on the control grid).

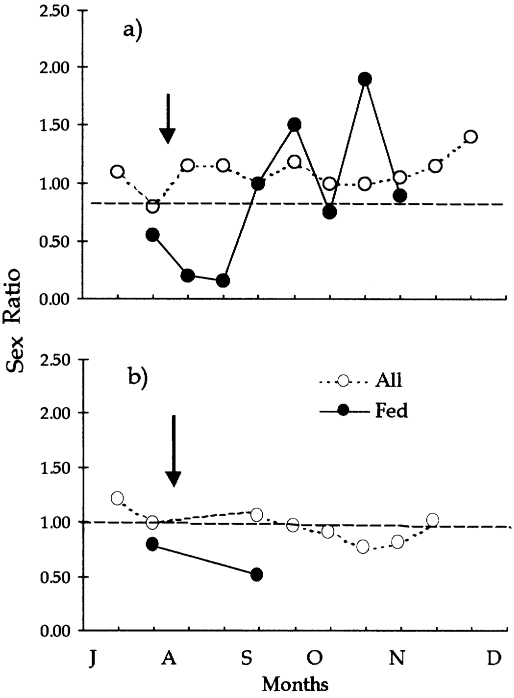

FIG. 2.—Sex ratio (males/females) of all individuals (open symbols) and among fed individuals (closed symbols), in a) grid I and b) grid II in the wet season. Arrows indicate the beginning of experiments. Sampling periods with five or less individuals were eliminated.

Before food addition, there were few transients on any of the three grids. After food addition the number of transients in-

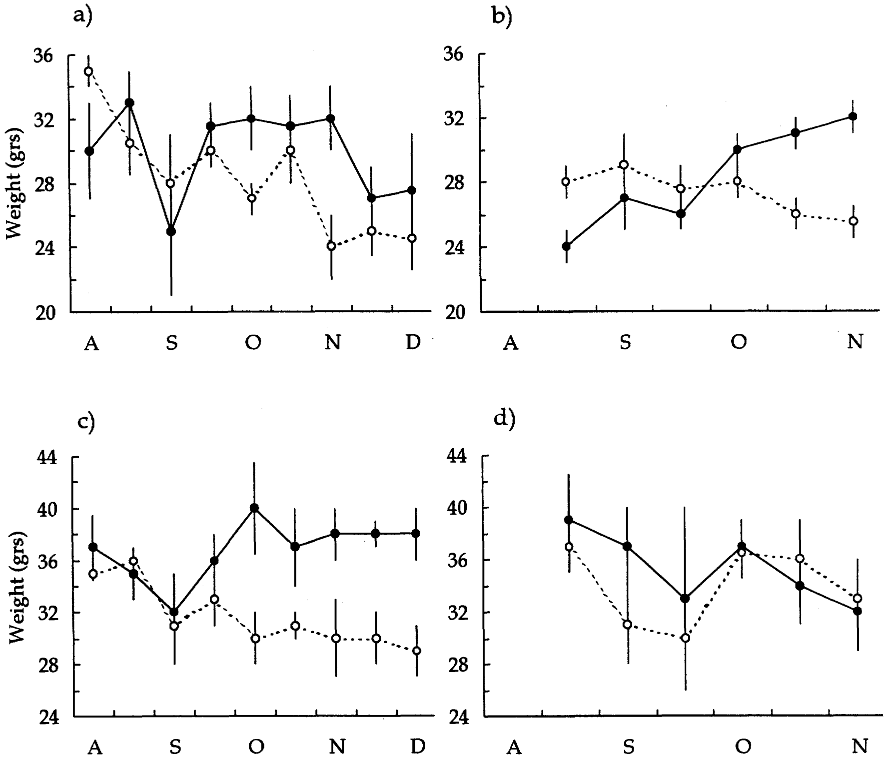

FIG. 3.—Changes in body weight of fed (closed circles) and unfed (open circles) males and females in the wet season. Bars represent ± 1 *SE*.

creased on all grids, including the control. However, more transients were caught on both experimental grids, and their age composition differed from those on the control. On the experimental grids, 72% (I) and 41% (II) of transients were adults, but only 15% of the transient individuals were adults on the control grid.

Changes in survival.—Females on all three grids had high survival during the pretreatment period. During the treatment period, female survival was slightly lower on all grids due to a slowly declining general trend through the fall. Considerable reductions in survival occurred in September and October on grid I and in November on both experimental grids. Mean 2-week survival of females during the treatment period was slightly higher on the control ($\bar{X}$ = 0.87) than on the experimental grids (I, $\bar{X}$ = 0.85; II, 0.79).

Males also had high survival on all three grids in the pretreatment period. There was also a slowly declining trend in survival in the autumn. During the treatment period, survival of males also declined in September and October on all three grids. It continued to decline in November on both experimental grids, but not on the control grid. Mean 2-week survival of males during the treatment period was higher on the control grid ($\bar{X}$ = 0.93) than on experimental grids (I, $\bar{X}$ = 0.86, II, 0.74). In summary, food addition had no apparent effect on survival of either males or females during the wet season.

Average residence times of both fed males and fed females were 1.5 times longer than those of unfed individuals on grid I (two-way ANOVA, $F = 4.95$, *d.f.* = 1,59, $P < 0.05$). On grid II, fed females stayed 1.6 times longer than unfed females, but the difference was not statistically significant (ANOVA, $F = 1.82$, *d.f.* = 1,24, $P > 0.05$).

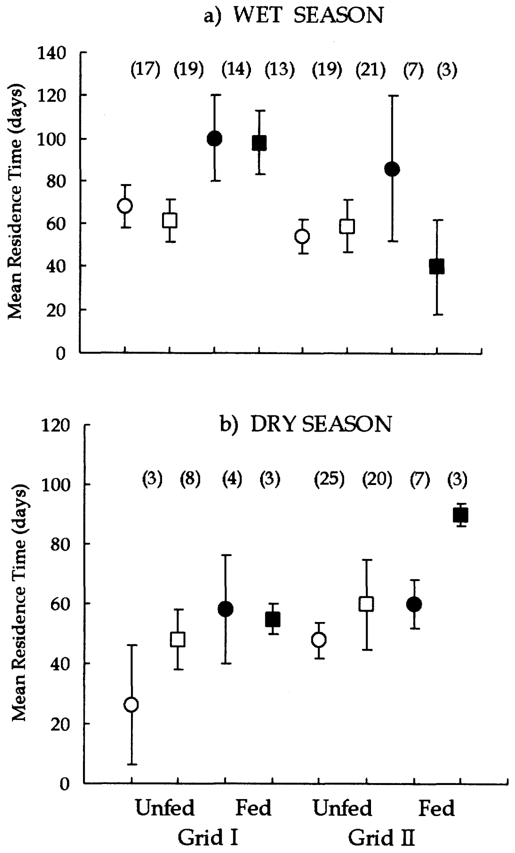

FIG. 4.—Average residence time (days) of fed (closed) and unfed (open) individuals in a) grids I and b) grid II in the wet and dry season. Circles represent females and squares represent males. Bars indicate one standard error. Sample sizes in parentheses.

Average residence time of fed males on grid II was slightly lower than that of unfed males. No statistical test was performed because only three resident males used food stations (Fig. 4).

Effects on reproduction.—During pretreatment, >50% of the females were breeding on all three grids. After food addition, a high percentage of females continued breeding on both experimental grids but not on the control grid. In this period <50% of the females were in breeding condition in only one and two of the eight trapping sessions on grids I and II, respectively. In contrast, <50% of the females were breeding in five sessions on the control grid. During the pretreatment period, five females were breeding on the control grid, whereas only two were breeding on both experimental grids. Most females were recorded as pregnant only once during this period. One female on the control grid was pregnant two times. After food addition, there was a reversal in the trend. The number of females breeding on the experimental grids (I, 20; II, 23) was twice that on the control grid (10). During this time, some females had from one to three pregnancies. The average number of pregnancies in 4 months of treatment was slightly larger on grid I ($\bar{X} = 1.7$) than on grid II ($\bar{X} = 1.3$) and on the control grid ($\bar{X} = 1.4$).

During the pretreatment period, >50% of the males were breeding on all three grids. More males were breeding on experimental grids during most sessions of the treatment period. During this period, <50% of the males were in breeding condition in only two and three of the eight trapping sessions on grids I and II, respectively. In contrast, <50% of the males were breeding in five sessions on the control grid.

More fed (I, 86%; II, 89%) than unfed females (I, 71%; II, 79%) on both grids were pregnant. The average number of pregnancies per female also was higher among fed females on both grids than on the control. On grid I, fed females had an average of 1.86 pregnancies in 4 months ($SE = 0.312$, $n = 14$), and on grid II, the average was 1.3 in 4 months ($SE = 0.289$, $n = 9$). Unfed females had an average of 1.1 pregnancies on grid I ($SE = 0.2$, $n = 17$) and 1.2 on grid II ($SE = 0.175$, $n = 19$). The difference was statistically significant only on grid I ($F = 4.95$, $d.f. = 1,29$, $P < 0.05$). The proportion of males breeding was similar among fed and unfed individuals on grid II ($G = 0.02$, $d.f. = 1$, $P > 0.05$). There were too few fed males on grid II to assess differences.

Dry Season

Density and seasonal patterns.—Populations of rock mouse usually decline from

December to March and have low densities during late spring and early summer (Galindo-Leal and Krebs, 1997). When the treatment began population trends and densities differed markedly among grids. Populations on experimental grid I and the control grid were low during the pretreatment period (Fig. 1). Numbers did not change after food addition but followed a similar pattern on both grids, increasing slightly in the summer. In contrast, the population on experimental grid II was 4.5 times higher than control densities and gradually declined from peak numbers in February. After food addition, numbers continued declining slowly throughout April and stabilized in May at about three times those of the other two grids.

On both experimental grids, average sex ratios were biased slightly toward females before food addition (I, $\bar{X} = 0.60$, II, $\bar{X} = 0.63$). After food was added, average sex ratios became more biased toward males (I, $\bar{X} = 0.38$) or were more even (II, $\bar{X} = 0.55$). The sex ratio on the control grid was more biased towards males both during pretreatment ($\bar{X} = 0.34$), and treatment ($\bar{X} = 0.33$).

There were nine fed individuals on grid I and 12 on grid II of 37 and 72 individuals caught on each grid, respectively, during the treatment period. No juveniles were caught on grid I during the dry season. In terms of age and sex, there was no difference between composition of fed individuals and that of the whole population on grid I ($G = 0.01$, $d.f. = 1$, $P > 0.05$). On grid II, juveniles and adults were caught. Age and sex composition of fed individuals did not differ from that of the whole population ($G = 0.61$, $d.f. = 13$, $P > 0.05$). Most fed individuals on grid I (78 %) and all on grid II (100 %) were residents. These proportions were similar to those in the whole population (I, $G = 3.15$, $d.f. = 1$, $P > 0.05$; II, $G = 1.49$, $d.f. = 1$, $P > 0.05$).

Changes in body weight.—There were too few individuals on grid I to assess differences in body weight between fed and unfed individuals. On grid II, unfed and fed females had similar weights. On grid II fed males were slightly heavier than unfed males after 1.5 months. Sample sizes were small and variability was high.

Differences in recruitment.—Pretreatment recruitment was similar on grids I and control and higher on grid II. Recruitment during the treatment period was higher on both experimental grids. The response, however, was evident only during the first 2 months of the experiment. In April and May, there were 12 and nine recruits on grids I and II, respectively, but only four on the control grid. In June and July, there were three and eight recruits on grids I and II, respectively, but 11 on the control grid. No juveniles and few subadults were recruited during April and May, and, therefore, only differences in sex composition were analyzed. Most individuals recruited on the experimental grids were males (proportion of females—I, $\bar{X} = 0.25$, II, 0.33). In contrast, female recruits outnumbered males in ratio in the control grid (0.75).

The number of transients during pretreatment was low on grid II and the control grid, and higher on grid I. At this time most transient individuals were adults. During treatment, the number of transients decreased on the control grid and grid II but increased on grid I. During this period, all transients were adults. There was no evident sex-bias among adults.

Changes in survival.—Female survival during the pretreatment period was lower on both experimental grids than on the control grid. During the treatment period, average 2-week survival of females increased on both experimental grids, but was slightly higher on the control grid ($\bar{X} = 0.92$) than on experimental grids (I, $\bar{X} = 0.71$, II, 0.88). This difference was due, however, to a decline in June. Males also had low 2-week survival during pretreatment on grids I and control grid. After the addition of food, male survival improved on grid II. Male survival on grid I was already high and continued to be so. Both experimental grids had higher survival than did the control until June, when survival decreased to the level of the control. Average survival of males during the treatment period was slightly higher on both experimental grids (I and II, 0.90) than on the control grid (0.84).

On grid I, average residence times of fed and unfed males were similar, but fed females stayed 2.1 times longer than unfed females. Sample sizes, however, were too small for statistical analysis. Average residence times of fed and unfed males on this grid were similar. On grid II, fed females stayed 1.2 times than unfed females. Fed males on this grid had longer residence time (1.5 times) than did control males, but the difference was not statistically significant (ANOVA, $F = 1.823$, $d.f. = 1,24$, $P > 0.05$, Fig. 4).

Effects on reproduction.—No females were breeding during the pretreatment period on any of the three grids. Breeding began in early June on grid II and in the second half of June on grid I and the control grid. On all three grids, <50% of the females were breeding in June and July, and only one pregnancy occurred on any grid. Males in breeding condition were recorded in late May on grid I and in June on the other two grids. During July, >50% of the males were breeding on all three grids.

The treatment period began at the end of the dry season, before breeding usually occurs (Galindo-Leal and Krebs, 1997). Only one female on each grid, both of them fed individuals, showed signs of pregnancy on 21 and 22 June. No unfed females showed signs of pregnancy until mid July. There were no obvious differences in the breeding conditions of fed and unfed males; however, the low numbers of fed males in both categories precluded statistical analysis.

DISCUSSION

Several authors have suggested that females should be more responsive to food resources than males, particularly during the breeding season (Anderson, 1989; Boonstra, 1977; Fordham, 1971; Galindo and Krebs, 1987; Ims, 1987*a,* 1987*b*; Ostfeld, 1986; Taitt, 1981). Our results support this idea. Females responded more intensely to food additions than males. Females who used food stations gained weight after food addition and had improved reproduction and improved survival during both wet and dry seasons. Males used food stations less than females. They gained weight and had improved survival, but less consistently than females. Although male reproductive activity appeared less affected than that of females, reproductive performance is more difficult to quantify in males.

Most previous food addition studies of populations (Boonstra, 1977; Fordham, 1971; Hansen and Batzli, 1978; Taitt, 1981) and more detailed studies of individuals (Ims, 1987*a,* 1987*b*; Ostfeld, 1986; this study) have shown that distribution and abundance of artificial food might affect differentially spatial distribution, reproduction, and survival of sexes. Recently, in a natural addition experiment, Glendinning and Brower (1990) monitored populations of *Peromyscus melanotis* inside and outside overwintering aggregations of monarch butterflies (*Danaus plexippus*). Monarch butterflies represent a natural high protein food for this rodent that is adapted to their high cardenolide content. Mouse populations of *P. melanotis* inside aggregations were denser and had a higher proportion of adult females and breeding females than those outside. These results substantiate previous studies that have provided artificial supplementary food.

In our study, effects of food addition during the breeding season were biased toward adults for recruits and transients. Glennding and Brower (1990) also found that juvenile residency was lower on the sites with butterflies where populations of *P. melanotis* were dense and female-biased.

Boutin (1990) underscored two consistent responses of populations to experimental food additions; there is often an increase in numbers of 1.5–2.5 times, but the population also declines in the presence of food. In this study, we expected few changes at the population level, because food was provided in widely spaced and highly clumped food sources. Food stations were located at only 10% of the traps on grids I and 8% of traps on grid II on 5.4 ha. In contrast, most food addition studies provide many food stations, often one at every other trap station (Briggs, 1986; Duquette and Millar, 1995*a,* 1995*b*; Gilbert and Krebs, 1981; Taitt, 1981; Wolff, 1985). The addition of food in the wet season surprisingly produced strong effects in the population dynamics of rock mice, consistent with Boutin's first general response. Populations on both experimental grids increased as a result of the food addition, and reproduction and adult recruitment improved.

Higher recruitment of adults on experimental grids than control grids suggests that the response on experimental grids was due more to immigration than local recruitment of juveniles. Results from the wet season also support Boutin's second general response because both experimental grids reached higher densities than the control and then declined to control levels despite the added food.

Experiments in the dry season are more difficult to interpret than those from the wet season. Food was added when populations on the control grid and experimental grid I were already low after a decline during winter. In contrast, the population on grid II had undergone an increase during the dry season in winter prior to addition of food and was higher in numbers. This population also declined somewhat during the addition of food but remained about three times higher than the other two populations and also was three times higher than its previous density in early summer. It is difficult to know if the moderate decline and high summer density were due to the addition of food because the control population was already low. However, both increased recruitment and survival on this grid after addition of food indicate a possible effect of the supplementary food.

The unexpected increase throughout the dry season in our study resulted from high recruitment. All three grids had similar trends during the previous dry season and early wet season. All previously documented populations of rock mice in the study area declined during the dry season (winter-spring—Galindo-Leal and Krebs, 1997). Recruits may have been juveniles which resulted from higher breeding intensity during the food-addition experiment in the wet season. In turn, they might have been individuals that immigrated to the grid because of the accidental removal of a substantial fraction of the resident population. In mid-November, the population declined sharply after traps were disturbed. This observation suggests that factors other than food prevent further increases (Boutin, 1990), and thus, food-addition experiments coupled with removal experiments might be particularly useful (Klenner, 1991).

Most food supplementation experiments with terrestrial vertebrates have focused on the population level to assess effects of food addition (Boutin, 1990). Supplemental food provided evenly over large areas often results in home-range reductions by both sexes (Mares et al., 1982; Sullivan et al., 1983; Taitt, 1981; Taitt and Krebs, 1981) or females only (Ostfeld, 1986; Taitt et al., 1981). However, individuals may monopolize food resources, especially when they are clumped, and, therefore, benefits of the food provided may not be distributed evenly in the population (Boutin, 1990).

In this study, we analyzed responses of individuals and the population that were likely to have received the benefits of the addition of food. As in other studies, we documented increased densities through immigration, earlier breeding, and increased reproduction after addition of food (Boutin, 1990). Similarly, we detected no effect on summer survival (Boutin, 1990), although fed individuals did show longer residence times than unfed individuals during this period. This suggests that effects of food provisioning might not be obvious at the population level, even when some individuals responded. This is likely to occur if the food is not shared equally by the population but monopolized by some individuals (Boutin, 1990).

Because individuals are most likely to respond to local abundance and distribution of food resources by altering their movements and other behavior (Clutton-Brock and Harvey, 1978; Davies and Lundberg, 1984; Ostfeld, 1985), spatial distribution of food addition is of major interest. Most studies, however, largely have ignored distribution of supplementary food. Recent studies have examined behavioral responses of small mammals to spatial patterns of food distribution (Ims, 1987*a*, 1987*b*; Ostfeld, 1986). Ostfeld (1986) monitored movements of California voles (*Microtus californicus*) before and after adding fresh carrots evenly to one 100-m^2 patch during 10 days on each of 2-years. Ims (1987*a*, 1987*b*) investigated effects of distribution of food on dispersion and dominance in *Clethrionomys rufocanus*. In both studies, females with additional food had reduced home ranges and increased overlap. Despite of the highly clumped food distribution, females did not behave territorially as predicted (Ostfeld, 1985). Further experiments should compare the effect of food distribution (Noyes et al., 1982; Stueck and Barrett, 1978), preferably using foods similar to the natural food and over longer periods to document consequences to the population.

The majority of food-addition studies have not incorporated replicated treatments (Boutin, 1990). Appropriate replication is particularly difficult for small mammal studies that are highly dependent on live-trapping grids to obtain demographic information. Experimental manipulations of small mammals using highly-spaced individuals as experimental units, as in our study, overcome the problem of pseudoreplication and increase the limited number of replicates provided by live-trapping grids.

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