FEMALES DELAY DISPERSAL AND BREEDING IN A SOLITARY GERBIL, *MERIONES TAMARISCINUS*

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We studied dispersal and breeding patterns in a solitary gerbil, *Meriones tamariscinus*, from 1995 to 1999 in Kalmykia, southern Russia. The females of this species delay breeding far beyond the age of maturation. We suggest that delayed breeding in young females is associated with delayed emigration from the natal site. Most young female *M. tamariscinus* showed strong natal philopatry that resulted in female kin clustering. Proximity to adult females suppressed their maturation and restricted breeding opportunities. Breeding rate of young females correlated negatively with the survival rate of adult females. Therefore, dispersal and breeding patterns in this solitary species appear similar to those in social (group living) species of gerbils. Results are discussed in terms of ecological, demographic, and life-history traits of this species that set constraints on dispersal and breeding in young females.

Key words: delayed breeding, delayed dispersal, Kalmykia, *Meriones tamariscinus*, natal philopatry

Social systems and processes of dispersal are interrelated in a cycle of causation; social behavior affects dispersal, which in turn affects social behavior (Brandt 1992). Therefore, studying dispersal is essential for understanding both evolutionary and ecological factors responsible for intraspecific and interspecific variation of social systems. Delay of dispersal beyond the minimum age of maturation results in group living in many rodents with various degrees of sociality, e.g., voles (Getz 1997), ground squirrels (Waterman 1995), and naked mole rats (Bennett et al. 1994). Reproduction of nondispersing young may or may not be suppressed, resulting in extended families with singular or plural breeders (reviewed by Solomon and Getz 1997).

Numerous hypotheses have been suggested to explain delayed dispersal and breeding in communal-living species (see recent reviews by Hatchwell and Komdeur 2000; Hayes 2000; Solomon and Getz 1997). One set focuses on the ecological and demographic constraints on dispersal and stems from the ''habitat saturation hypothesis.'' Shortage of breeding sites when the population density is near habitat carrying capacity limits the opportunities for immediate independent breeding and increases the costs of dispersal through saturated habitat. Other hypotheses stress the benefits of natal philopatry associated with familiarity with the ecological and social

environment within or near the natal home range. Species-specific life-history traits, e.g., longevity, may also determine the choice in the stay-or-go alternative. High adult survival results in habitat saturation and restricts opportunities for dispersal and immediate independent breeding of the young (Hatchwell and Komdeur 2000). On the other hand, high adult mortality or short length of tenure of parents may also favor nondispersal (Waser and Jones 1983; Wolff 1993). From this viewpoint, the young do not need to disperse since the low survival rate or desertion of parents increases availability of breeding sites, minimizes intrasexual competition, and excludes incest within the natal site. Thus, ecological, demographic, and life-history constraints appear to be interlinked, codetermining the rate of turnover of breeding sites and/or mates (Hatchwell and Komdeur 2000).

If young delay dispersal and breeding they can increase their direct or indirect fitness through the benefits of communal living or breeding (reviewed by Hayes 2000; Solomon and Getz 1997). However, many solitary species that do not perform any group activities also delay dispersal and show strong natal philopatry. Therefore, natal philopatry appears to be a necessary but not sufficient prerequisite for communal living (Waser and Jones 1983). To understand evolution of delayed dispersal and breeding, it seems reasonable to focus on conditions favoring and mechanisms underlying nondispersal in solitary species. In this study we try to apply some of the explanatory models of delayed dispersal and breeding in communally living species to explain delayed dispersal and breeding in the solitary tamarisk gerbil, *Meriones tamariscinus*.

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The tamarisk gerbil is a relatively large (100–140 g adult mass), nocturnal, and strictly solitary gerbil showing strong preferences for habitats with dense grass or shrub cover (Gromov and Tchabovsky 1995; Pavlinov et al. 1990). Interactions between individuals are rare and mainly agonistic, regardless of the sex and age of the individuals (Popov and Tchabovsky 1998). Adult females occupy nonoverlapping home ranges; home ranges of males are larger in size and overlap among themselves and with females (Gromov and Tchabovsky 1995). The breeding season lasts from March to October; 2 to 3 litters are produced (Pavlov 1962). Young of the 1st spring cohort appear on the surface from the end of May to the beginning of June. Soon after emergence from the burrow, young disperse over the mother's home range; they move and forage alone and rarely are in contact with each other or with their mothers (Popov and Tchabovsky 1998). Young males usually do not reproduce during their 1st year. Sexual maturation in females is estimated at 70 days, and they are ready to reproduce by mid-July (Kim 1960). However, only 4% to 40% of females breed during their 1st year, while the rest delay breeding until the following spring (Prokopov 1979).

We suggest that delayed breeding in young females is associated with delayed emigration from the natal site.

MATERIALS AND METHODS

Study area and field procedures.—Our study was conducted from 1995 to 1999 in southern Kalmykia, northwestern Cis-Caspian region, Russia (45°29′N 45°26′E). The area represents subboreal semidesert with discontinuous vegetation of grasses, herbs, and shrubs on sandy or loamy soils. Tamarisk gerbils inhabit sandy patches with tall and relatively dense grass and shrubs of *Tamarix* (Neronov et al. 1997). The climate is continental with hot dry summers (40–45°C in July) and cold (−20–30°C in January) winters characterized by little or no snow.

The data were collected in May–June (spring session) and September–October (autumn session) each year from 1995 to 1999 by means of capture–marking–recapture method. Gerbils were trapped during 14-day periods in wire laboratory-made live traps (100 × 100 × 300 mm) baited with sunflower seeds and located within 10 × 10 m squares of stationary 1-ha grids. Traps were set every evening just after sunset and checked after 2 to 2.5 h. For each trapped gerbil, sex, age, and mass were recorded and the animal was marked by toe clipping. Vagina and nipples in females were examined visually to determine breeding status. Females with opened vagina and/or enlarged nipples that had obviously been used to nurse young were classified as breeding. Juveniles were trapped and marked during the first few days after their emergence from the natal burrow. Due to the asynchronous breeding and restricted movements of juveniles, only a portion of them was marked in spring.

Four age classes were identified: overwintered (all adults in spring or males with body mass >120 g and females with body mass >100 g in autumn) and young of the 1st (spring), 2nd (summer), and 3rd (autumn) cohorts. Young females were assigned to the 1st cohort if they were marked as juveniles in spring or if they had body mass of 70–100 g in autumn. Young females with body mass of 50–70 g in autumn were assumed to belong to the 2nd cohort, while females with body mass less than 50 g or marked as juveniles in autumn were assigned to the 3rd cohort of the young. This age classification was based on a preliminary analysis of body mass change in individuals marked as juveniles and with known life histories.

Trapping was conducted on 3 grids. One grid (hereafter referred to as the main grid) was surveyed every year, yielding 10 successive trapping sessions. Data from successive sessions provided information on population and cohort turnover, as well as on life and breeding histories of individuals. Additional trapping was performed on 2 more grids in 1998 to get more data on spacing patterns of the young.

Data analysis.—To assess the rate of turnover of adult males and females, we estimated the proportions of animals that appeared and disappeared between or within trapping sessions on the main grid. Additionally, we calculated time of residence within the grid for adult animals as the difference between dates of the last and the 1st capture as adults. If individuals disappeared from the grid during the trapping session or between successive sessions, we could not discriminate between long-distance dispersal and death; however, a gerbil that stayed within a grid (natal habitat) until the following trap session obviously did not perform a long-distance dispersal between sessions. Thus, we estimated the proportion of non-dispersers among the young females. For resident young females that remained within the grid until the next session, we assessed short-distance (or locational) dispersal as shift of the center of activity (i.e., the trap location with maximal number of recordings of the individual). We considered young females not to have left the natal home range if the shift of center of activity was less than the average radius of the home range of an adult female. We considered young females to delay dispersal if they stayed within their natal home range and/or within natal grid until autumn (for females of the 1st cohort that are ready to reproduce by mid-July) or the following spring (for all females born the previous year).

Proximity to an adult female was estimated for young females as the distance of their center of activity to that of the nearest overwintered female, assumed to be their mother. Increase of this distance between successive sessions was assumed to reflect the process of social dispersal, i.e., leaving familiar conspecifics (Isbell and Van Vuren 1996). Spacing patterns of young females (data from all 3 grids) were tested for correlation with the proximity to an overwintered female. Maximal distance between locations, number of traps visited, coefficient of exclusiveness of use of space in relation to adult females (Alho 1979), and extent of overlap with adult male home range (OLMHR) were used to describe spacing patterns in young resident females trapped 5 times or more. Index of OLMHR was based on Alho's coefficient of exclusiveness of use of space (Alho 1979) and was calculated as

$$OLMHR = 1 - Alho's\ coefficient.$$

Since grid structure with fixed trap stations can provide only discontinuous fixed distance measures, we used the number of trap stations that separate locations of individuals as an index of distance for all distance measures. An index of 0 corresponded to captures in the same trap; an index of 1 corresponded to capture in 1 of the nearest trap stations; a value of 2 meant capture in 1 of the next nearest trap stations, etc. Analysis of 50 randomly selected distances indicated strong correlation between metric distance measure and trap-station distance index ($r_s = 0.98$, $P < 0.0001$). Data on dispersal and spacing patterns from different years were pooled separately for the spring and autumn sessions; thus, no between-year variation was analyzed.

Females of the 1st (spring) cohort were assumed to delay breeding if they were classified as nonbreeding in autumn. All young females that survived the winter bred the following spring. Thus, delayed breeding was analyzed only for the females of the 1st cohort during their 1st year. Breeding versus nonbreeding young females were compared with regard to the distance of their locational and social dispersal. The population density varied across years, ranging from 17 individuals/ha

in 1999 to 71 individuals/ha in 1997, thus providing an opportunity to test the effect of habitat saturation on breeding of young females. Breeding rates were estimated for each year as the portion of breeding young females of the 1st cohort among the total number of females of the 1st cohort present in autumn. To assess between-year variation in success of breeding site establishment by young females at the population level, we measured the percentage of grid squares occupied in autumn by all the young breeding females collectively.

We defined close kin as littermates; that is, individuals that were marked as juveniles within the home range of the same adult female soon after their emergence from the burrow. For each adult female we estimated the number of close kin (sisters) that lived within the same study grid to assess kin structure of local populations.

Variables analyzed did not conform to the assumptions of normality (Kolmogorov–Smirnov $D_{max} = 0.24$–0.44, $P < 0.01$) and could not be transformed to normal distribution. Thus, nonparametric statistical analyses were used. Spacing and dispersal characteristics of breeding and nonbreeding young females were compared using the Mann–Whitney U-test and were tested for correlation with the proximity to overwintered females by Spearman's rank order correlation. Rates of turnover and demographic structure were compared by chi-square test. In general, all statistical tests follow Zar (1984). We used the significance level of $P \leq 0.05$.

RESULTS

Turnover of adult population.—The population of adult females was much more stable during spring than that of males; males were significantly more likely to appear (14 of 42, 33% of newcomers; Table 1) and to disappear (11 of 39, 28%) than were females (3 of 42 in both cases, 7%, $\chi^2 = 8.92$, $d.f. = 1$, $P = 0.003$ and $\chi^2 = 6.27$, $d.f. = 1$, $P = 0.012$, respectively). A considerable fraction of both males (47 of 53, 87%) and females (31 of 45, 69%) disappeared during the summer; however, females were more likely to stay than were males ($\chi^2 = 5.87$, $d.f. = 1$, $P = 0.015$). Few new overwintered males and females appeared during the summer. Nevertheless, there were more newcomers among males (5 of 11, 45% of the resident male population in autumn) than among females (2 of 16, 13%, $\chi^2 = 3.69$, $d.f. = 1$, $P = 0.055$). Male-biased immigration did not compensate for male-biased disappearance. The sex ratio among overwintered animals was female biased in autumn (11:16) in contrast to male biased in spring (53:45). Only 30% (3 of 10) of males and 13% (2 of 16) of females of the autumn population on the grid survived their 2nd winter and stayed within the grid until the following spring ($\chi^2 = 1.21$, $d.f. = 1$, $P = 0.271$). On the whole, length of tenure of overwintered males was significantly shorter than that of females (38.2 ± 10.5 days, $n = 53$ and 59.1 ± 11.0, $n = 45$; Mann–Whitney $U = 731.5$, $P = 0.002$; Fig. 1).

Unlike females, the male population in spring consisted mostly of newcomers (29 of 37, 78% compared to 6 of 34, 18%, $\chi^2 = 26.15$, $d.f. = 1$, $P < 0.0001$), while the major part of the female population comprised females born within the grid during the previous year (26 of 34, 76% in contrast to only 5 of 37, 14% in males, $\chi^2 = 29.34$, $d.f. = 1$, $P = 0.0001$). As a result, half of the overwintered females in spring were known to have at least 1 close female kin among resident females: 31% of females had 1 close female kin, and 19% were known to

TABLE 1.—Turnover of overwintered male and female *Meriones tamariscinus* within the main study grid in southern Kalmykia, northwestern Cis-Caspian region, Russia.

	During spring[a]		From spring to autumn[b]		From autumn to the next spring[c]	
	Males	Females	Males	Females	Males	Females
Disappeared	11	3	47	31	7	14
Stayed	28	39	6	14	3	2
Immigrants	14	3	5	2	29	6
Recruited					5	26

[a] Changes in population between the 1st and the 2nd halves of the trapping session (pooled data for 5 spring sessions).
[b] Pooled data for 5 periods between spring 1995 and autumn 1999.
[c] Pooled data for 4 periods between autumn 1995 and spring 1999.

have 2 close female kin ($n = 32$). Almost all female kin (88%) occupied neighboring home ranges.

Dispersal and spacing patterns of young females.—Of 18 young females of the 1st generation born in spring and marked as juveniles within the main grid that were ready to reproduce by mid-July, 14 (78%) still lived within the grid in autumn, while only 4 (22%) disappeared. Of 67 young females comprising all 3 generations born in spring, summer, and autumn, 26 (39%) successfully overwintered and remained within the natal habitat until the following spring.

Nondispersing females that stayed within the grid until autumn or the following spring moved very short distances, so that the shift of the center of activity of the majority of young females (62% in spring and 48% in autumn) did not exceed the average radius of the home range of adult females (Fig. 2). Thus, most young females stayed within their natal home ranges, while others settled next to their natal site.

Distance to the nearest overwintered female significantly increased from spring to autumn in young females of the 1st cohort (Mann–Whitney $U = 508.5$, $P = 0.002$). However, many of them (36%) stayed within the average radius of the adult female home range until autumn (Fig. 3), i.e., maintained close spatial ties with adult females of the previous generation (presumed to be their mothers).

Distance to older females did not correlate with body mass of resident young females of the 1st cohort in autumn ($r_s = 0.20$, $n = 21$, $P = 0.394$) but related positively to the maximal distance between captures ($r_s = 0.43$, $n = 31$, $P = 0.015$), number of entered traps ($r_s = 0.40$, $n = 31$, $P = 0.027$), and extent of overlap with the home ranges of breeding males ($r_s = 0.38$, $n = 31$, $P = 0.035$). Thus, close proximity to mothers did not affect growth but restricted movements and breeding opportunities of young females.

Recruitment.—Only 22 of 74 (30%) young females of the 1st spring cohort captured in autumn on all 3 grids and 14 of 50 (28%) captured in autumn on the main grid were classified as breeders. Four of fourteen (29%) young females marked as juveniles in spring that remained within the main grid until autumn had reproduced. Thus, about 70% of young females of the 1st cohort delayed breeding until the next spring. Of 39 overwintered females with known breeding history, 69% bred
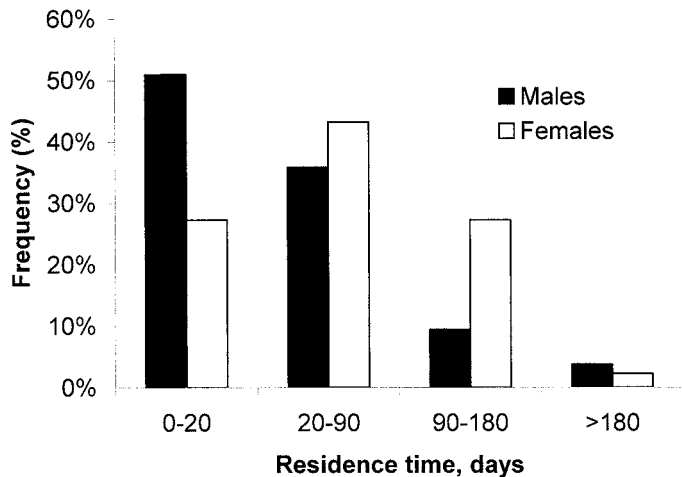
FIG. 1.—Frequency of residence times for overwintered male and female *Meriones tamariscinus* within the main grid, assessed as the difference between dates of 1st and last captures within the grid.
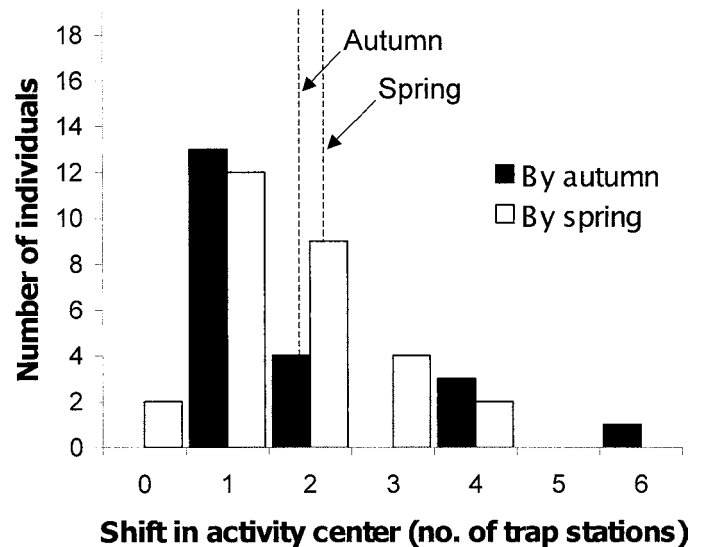

FIG. 2.—Shift of centers of activity of young female *Meriones tamariscinus* born in spring by autumn and by the following spring, measured as number of trap stations (distance between trap stations equals 10–14.1 m). Dashed lines indicate average radius of home range of overwintered females in the respective season.

in spring for the 1st time, 18% for the 2nd time, and 13% for the 3rd time.

Female recruitment was associated with social but not locational dispersal, as indicated by a significant increase in distance to the nearest overwintered female (Fig. 4, Mann–Whitney $U = 117.5$, $P = 0.0002$) and lack of significant difference in distance of home range shift between breeding and nonbreeding young females (Mann–Whitney $U = 48.5$, $P = 0.647$). Breeding females ranged significantly more widely (Fig. 5, Mann–Whitney $U = 166.0$, $P = 0.028$ for maximal distance between locations) and had larger and more isolated home ranges than nonbreeding young females (Mann–Whitney $U = 146.0$, $P = 0.009$ for Alho's coefficient in relation to other adult females).

Analysis of between-year variation in breeding activity of young females on the main grid (Table 2) revealed a significant negative relationship between number of overwintered females that survived to autumn on the one hand and breeding rate and area occupied by young breeding females on the other ($r_s = -0.95$, $P = 0.014$ and $r_s = -0.89$, $P = 0.042$, respectively; Fig. 6). Survival and immigration rate of overwintered males was low, did not vary strongly from year to year, and was not correlated with breeding activity of young females.

DISCUSSION

Our results clearly indicate that most young female *M. tamariscinus* show strong natal philopatry and delay dispersal far beyond the minimum age of maturation, waiting for a chance to breed within their natal area. As a result, close spatial associations of female kin emerge and the breeding population of females consists mainly of locally born females of the previous year. However, staying within the natal home range in close proximity to mothers restricts breeding opportunities and suppresses maturation of young females. Breeding opportunities of female nondispersers thus depend on survival rate of old females and vary from year to year. When

survival rate is high and the habitat is saturated, most young females have no chance to breed within the natal area during their 1st year and delay reproduction until the following spring. Nevertheless, on average, only a few old females stay within the habitat throughout the breeding season and still fewer survive the 2nd winter. Thus, the short length of tenure of overwintered females provides high turnover of breeding sites within the natal habitat. Disappearance of old females stimulates reproduction in young females. Turnover of over-wintered males during the breeding season is even higher than that of old females: most of them have disappeared by the time of 1st reproduction of young females. At the same time, new males establish themselves within the habitat. By the beginning of the next breeding season almost the entire population of resident males consists of strangers.

In many mammalian and bird species, delayed dispersal and reproduction is assumed to be associated with intrinsic benefits of group living, such as enhanced foraging efficiency, reduced susceptibility to predation, communal breeding, and care of offspring (Hatchwell and Komdeur 2000; Hayes 2000; Koenig et al. 1992; Solomon and Getz 1997). This seemed to be also true for some gerbil species.

While they are a relatively homogenous taxonomic group (Pavlinov et al. 1990), gerbils vary strongly in degree of sociality, from highly social (*Meriones unguiculatus, Rhombomys opimus*) to solitary species (*M. meridianus, Psammomys obesus;* Agren et al. 1989; Daly and Daly 1975; Goltsman et al. 1994; Naumov et al. 1972; Tchabovsky et al. 1990). This variation corresponds to their patterns of dispersal: in the former species, young of the year stay in natal groups as nonbreeders until the next breeding season, while in the latter species, the young disperse in the shortest possible time around or soon after maturation.
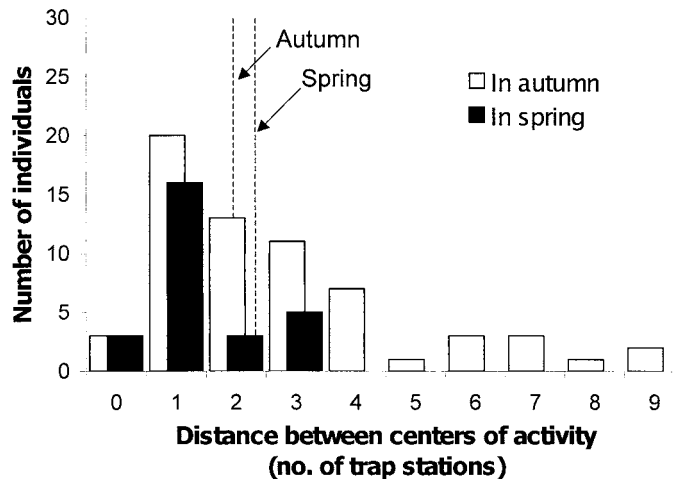
FIG. 3.—Distance between the centers of activity of young female *Meriones tamariscinus* and the nearest overwintered female in autumn and in spring, measured as number of trap stations (10–14.1 m between stations). Dashed lines indicate the average radius of the home range of overwintered females in the respective season.
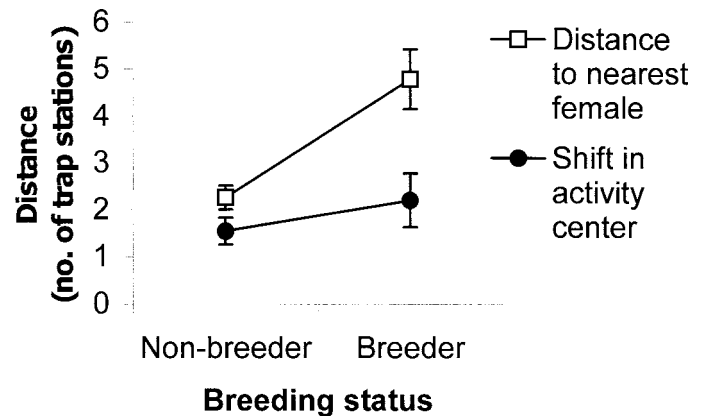

FIG. 4.—Distance to the nearest overwintered female and shift of center of activity between spring and autumn sessions in breeding versus nonbreeding young female *Meriones tamariscinus*. Breeding young females find themselves at greater distances from adult females than do nonbreeding females, although there is no significant difference in the distance of the shift of their ranges. This shows that initiation of breeding is associated with a major social dispersal but only a small locational dispersal.

Tamarisk gerbils show a dispersal and breeding pattern similar to that of social gerbils. However, they do not form social groups, avoid contacts, and do not perform any type of group activity (Popov and Tchabovsky 1998). Thus, spatial matrilines are likely to be a byproduct of strong natal site fidelity. Taking into account nocturnal activity and preference for habitats with dense visually occlusive cover (Pavlinov et al. 1990), it is unlikely that delayed dispersal and breeding in this species can be attributed to benefits of group living.

Alternatively, staying close to the natal site can be associated with benefits of living in a familiar social and ecological environment, in particular, increased tolerance of familiar or related individuals and ready access to resources of known quality (Brandt 1992; Jacquot and Solomon 1997; Lidicker 1975; Waser and Jones 1983). Familiarity with space may be crucial for efficient foraging specifically in tamarisk gerbils, one of the most herbivorous and mesophilic species within the family (Pavlinov et al. 1990). Unlike many other gerbils, this species requires high water intake, whereas like other gerbil species, it is poorly adapted for digestion of cellulose (Abaturov and Khasheva 1995; Magomedov and Akhtayev 1993). As a result, tamarisk gerbils show high levels of food selectivity; food items consumed must include young leaves and generative parts of plants. Because of its ephemeral nature, such a resource must require constant monitoring. Costs of dispersal by gerbils to unfamiliar habitats may be extremely high.

Moreover, females staying within their natal habitat may avoid costs of dispersing in an unfamiliar social environment. Females of tamarisk gerbils are territorial (Gromov and Tchabovsky 1995) and, thus, may suppress immigration and establishment of breeding territories by young females. However, experimental dyadic encounters indicated that adult females show more amicable and less aggressive behavior toward kin than nonkin neighbors (Tchabovsky and Kolmanovsky, pers. comm.). Thus, costs of encountering strangers in an unfamiliar environment associated with increased aggression from territorial nonrelatives may be extremely high, especially in saturated habitats. Optimization of foraging may be ultimately responsible for strong natal site fidelity in female *M. tamariscinus*, while increased tolerance among kin and territoriality may be proximate causes or simply consequences of nondispersal (Waser and Jones 1983; Wolff 1994).

Nondispersing females, however, face a problem of habitat saturation; shortage of breeding sites within natal area sets limits on immediate reproduction by nondispersers. Reproductive suppression of young females by adult females is balanced by relatively short length of tenure of the latter, resulting in high overall turnover of breeding sites. At the same time, high turnover of breeding males increases the probability of securing unfamiliar mates within the natal habitat. These data support the view that low survival or short length of tenure of adults favors nondispersal of young animals by reducing both competition and probability of simultaneous breeding of parents and their young (Waser and Jones 1983; Wolff 1993).

Delayed breeding of nondispersing individuals has been explained in terms of either intrasexual competition for resources or inbreeding avoidance (Dobson et al. 1997; Gerlach 1996; Viitala et al. 1994; Waser and Jones 1983; Wolff 1994, 1997). The resource-competition hypothesis predicts that young should delay breeding in the presence of same-sex parents to reduce competition for resources or mates. In contrast, the inbreeding-avoidance hypothesis attributes suppression of maturation to the presence of the opposite-sex parents. Our data conform more closely to the resource-competition hypothesis. Indeed, in the absence of fathers
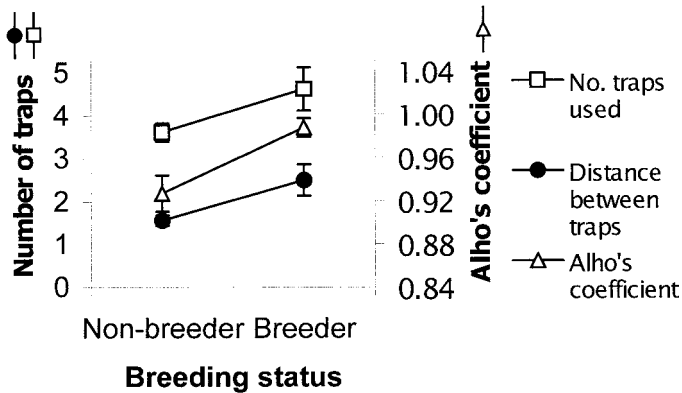
Fig. 5.—Relation between characteristics of ranges of breeding and nonbreeding young female *Meriones tamariscinus*, as shown by number of traps used by females, maximal distance between locations at which trapped, and Alho's coefficient (exclusiveness of use of space) in relation to adult females.

(length of male tenure was very short, males ranged widely and did not form stable bonds with females), breeding in young females was suppressed by the presence of and close proximity to adult females. Suppression of maturation by same-sex adults is known to occur in numerous species of rodents including communal-living gerbils (Payman and Swanson 1980; Sokolov et al. 1983; Solomon and Getz 1997; Swanson and Lockley 1978). High turnover of males must considerably reduce probability of mating with familiar males, and young females are unlikely to face a problem of inbreeding avoidance when they start to reproduce. Thus, we conclude that intrasexual competition rather than inbreeding avoidance is responsible for delayed breeding in young female tamarisk gerbils.

To conclude, females of solitary tamarisk gerbils show strong natal philopatry and delayed breeding, i.e., a dispersal pattern common for many group-living species. Species specifics of nutrition and foraging determine extremely high costs of dispersal for young females. Ready access to familiar resources, rather than benefits of group living, may be crucial ultimate factors responsible for nondispersal in this solitary

species. Social tolerance within close-kin clusters in combination with increased aggression from strange territorial females may serve as proximate causes suppressing dispersal and immigration. Proximity of female nondispersers to adult females suppresses reproduction, especially at high densities. Reproductive suppression may function to reduce competition for breeding sites among females. Short length of tenure of adult females and males, however, provides high turnover of breeding sites and mates, thus increasing the probability of establishing breeding territory and of finding an unfamiliar mate within the natal habitat.

Delayed dispersal and reproductive suppression are not solely attributes of social species and thus cannot be explained in terms of benefits of communal living or cooperative breeding. Dispersal and breeding patterns may evolve under ecological, demographic, and life history constraints regardless of species sociality. However, in solitary species with no or low level of social cooperation, nondispersal may increase population viscosity (sensu Gadgil et al. 1983), which may in turn favor evolution of sociality and set further constraints on dispersal (Brandt 1992; Gadgil et al. 1983). Such solitary, but kin-clustered, species as *M. tamariscinus* may be near the threshold of this positive feedback viscosity-cooperation system and may evolve to either increased or decreased social dependence.

TABLE 2.—Turnover of overwintered (adult) *Meriones tamariscinus* and number of breeding young females on the main grid from 1995 to 1999.

	Caught in spring[a]		Remained until autumn[b]		Newcomers in autumn[c]		Total[d]		Young females of the 1st cohort in autumn		
Year	Females	Males	Females	Males	Females	Males	Females	Males	Total	Breeders	% breeding
1995	10	16	0	0	1	2	1	2	6	5	83
1996	10	9	6	1	0	0	6	1	13	1	8
1997	13	11	6	1	1	1	7	2	20	1	5
1998	6	9	2	3	0	1	2	4	6	3	50
1999	6	8	0	1	0	1	0	2	5	4	80
Total	45	53	14	6	2	5	16	11	50	14	28

[a] Overwintered individuals captured during the spring session.
[b] Overwintered individuals captured in spring and again in autumn.
[c] Adult overwintered individuals captured during the autumn session that had not been captured during the previous spring session.
[d] Overwintered individuals captured in autumn, including both those that were and those that were not captured the previous spring.
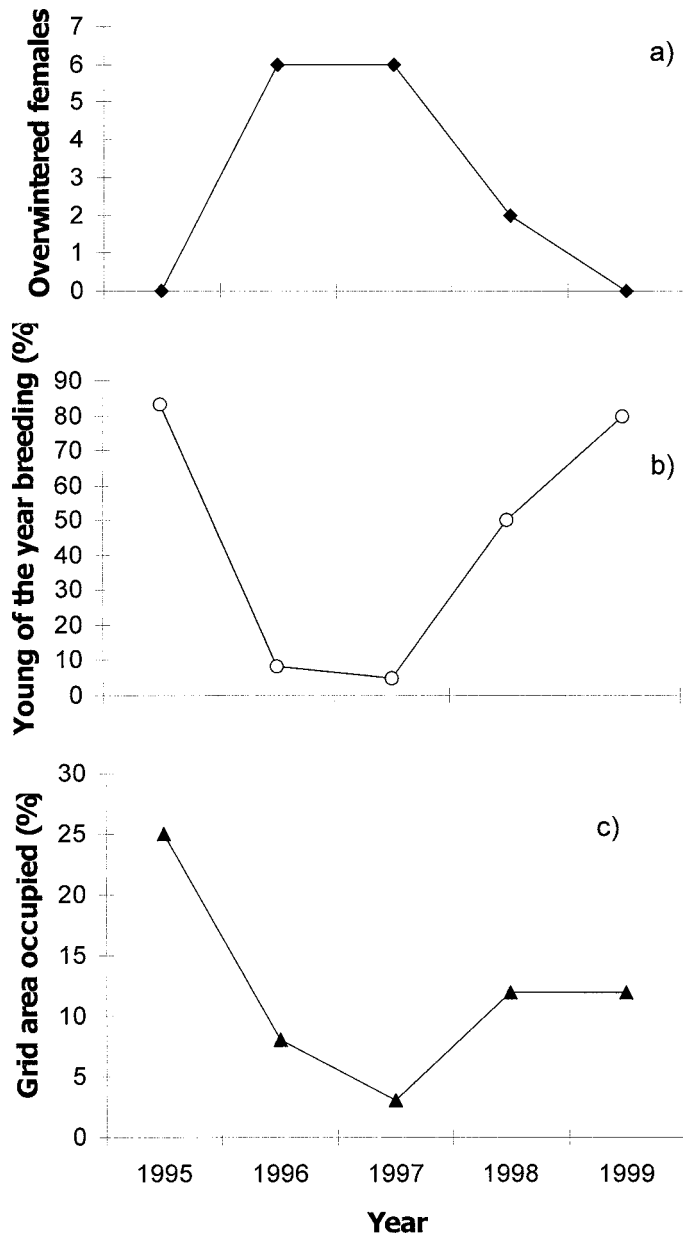
FIG. 6.—Relation between density of old females and breeding opportunities of young females of *Meriones tamariscinus*, as shown by a) the number of overwintered females that stayed within grid until autumn, b) the percentage of the young of the year of the 1st cohort that started breeding by autumn, and c) the percentage of the grid area occupied collectively by the young of the year of the 1st cohort that were breeding in autumn.

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