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Research Article

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Dispersal of the Golden-mantled Ground Squirrel (*Callospermophilus lateralis*)

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Abstract

Dispersal is common in mammals and can have an important role in shaping demography, genetics, distribution, and social structure. Dispersal entails potential costs but also potential benefits, and the dispersal decision is thought to be conditional; the potential disperser assesses prospects for success at its current location and disperses to improve its fitness. However, the costs and benefits of dispersal, as well as factors influencing the dispersal decision, are not well known. We used trapping and observation to study dispersal in the Golden-mantled Ground Squirrel (*Callospermophilus lateralis*), a species for which dispersal is largely unknown. We characterized the dispersal process by evaluating dispersal timing and distance, assessed factors that might influence the dispersal decision, and analyzed the fitness cost of dispersal after settlement. We found that most dispersal occurred during the summer of birth, as is expected for a small-bodied sciurid. However, some squirrels delayed dispersal until early in their yearling summer. Dispersal was male-biased in dispersal tendency, and it was also male-biased in dispersal distance, but only over shorter dispersal distances. The dispersal decision for juvenile females appeared to originate as soon as 10 days after they emerged from the natal burrow, and the decision was not associated with body mass or several measures of competition. Instead, dispersal of juvenile females was associated with the number of littermate sisters, with each sister present increasing the likelihood of dispersal by 26%. Littermate sisters might be a cue foretelling the effects of kin competition the following year. We did not find a significant difference in lifetime reproductive success between philopatric and dispersing females after settlement, suggesting that for golden-mantled ground squirrels, any cost of dispersal is experienced primarily during the transience phase.

Key words: *Callospermophilus lateralis*, cause of dispersal, dispersal, golden-mantled ground squirrel, lifetime reproductive success.

Dispersal, the movement of an animal away from its current home range to a new home range (Lidicker 1975), is an important process that may influence the demography, genetics, distribution, and social structure of a population (Greenwood 1980; Waser and Jones 1983; Bowler and Benton 2005; Ronce 2007). Dispersal is a common feature in the life cycle of mammals (Nunes 2007), and it is often sex-biased, wherein males are more likely to disperse than females, or to disperse farther (Smale et al. 1997; Lawson Handley and Perrin 2007; Nunes 2007; Mabry et al. 2013).

Dispersal may incur several potential costs. After emigrating, a dispersing animal might face increased predation risk, exposure to harsh conditions, or energetic challenges due to the cost of movement and reduced feeding (Gaines and McClenahan 1980; Bonte et al. 2012; Waser et al. 2013; Maag et al. 2019). Dispersers that survive this "transience" phase might settle at locations with reduced prospects for survival or reproduction (Anderson 1989; Bonte et al. 2012; Martinig et al. 2020). Many studies have addressed the post-settlement consequences of dispersal by comparing the fitness of residents (philopatric individuals) and immigrants (dispersers that have settled), but most of these studies were short-term or utilized only 1 fitness measure, either survival or reproduction (Bélichon et al. 1996; Doligez and Pärt 2008). However, compensation can occur between different fitness components (Doligez and Pärt 2008; Waser et al. 2013). Lifetime reproductive success (LRS), which incorporates survival and reproduction over multiple years, has been evaluated in only a few studies that compared dispersing and philopatric individuals (Doligez and Pärt 2008; Bonte et al. 2012).

Dispersal has benefits as well as costs including improved access to resources or mates, and reduced chances of inbreeding (Greenwood 1980). For many species dispersal appears to be a plastic life-history strategy that is condition-dependent; the potential disperser assesses prospects for success at its current location and disperses to improve its fitness (Bowler and Benton 2005; Ronce 2007). Several proximate factors have been proposed as influences on the dispersal decision, and these factors might vary among species (Bowler and Benton 2005; Nunes 2007).

In ground-dwelling squirrels, dispersal is thought to be influenced by body-mass energetics (Armitage 1981). Larger species take longer to reach sexual maturity, leading to a delay in the age of dispersal and the formation of social groups through retention of offspring

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(Armitage 1981). On the other hand, smaller species reach maturity more quickly, disperse at an earlier age, and are less social (Armitage 1981). Dispersal in ground-dwelling squirrels is considered to be strongly male-biased, with males more likely to disperse, to move longer distances, or both (Holekamp 1984). The Golden-mantled Ground Squirrel (*Callospermophilus lateralis*; GMGS) is a small-bodied (130 to 240 g) species that is classified as asocial, and dispersal is thought to occur during the summer of birth, shortly after juveniles are weaned (Armitage 1981; Michener 1983). Dispersal is important in this species, as populations experience pronounced fluctuations in size, and immigration can result in demographic and genetic rescue of small populations (McEachern et al. 2011). Dispersal behavior in the GMGS is poorly known; the only paper published found that most juveniles—both males and females—dispersed before the end of their natal summer, although some squirrels apparently delayed dispersal until their yearling summer or remained philopatric, with no evidence of a sex bias in dispersal tendency or distance (Jesmer et al. 2011). Our objectives were to: (1) characterize the dispersal process of the GMGS by evaluating dispersal timing and distance, in the context of an expectation of a sex bias; (2) evaluate factors that might influence the decision to disperse; and (3) analyze the fitness cost of dispersal after settlement.

Materials and methods.

Study area and data collection.

The GMGS occurs in medium to high-elevation mountains in western North America and inhabits a variety of habitat types including conifer forest, chaparral, sagebrush, and mountain meadows (Bartels and Thompson 1993). We studied GMGS from 1995 to 2022 at the Rocky Mountain Biological Laboratory (2,900 m elevation), in the East River Valley, Gunnison County, Colorado, United States (38°58′N, 106°59′W). The 13-ha study area consisted mostly of subalpine dry meadow, with patches of wet meadow and stands of Quaking Aspen (*Populus tremuloides*), willow (*Salix* spp.), and Engelmann Spruce (*Picea engelmannii*).

The study area supported a discrete population of GMGS that was bounded by perennial streams on the west and south, and aspen woodlands on the north and east that were not inhabited by squirrels. GMGS in the East River Valley utilized mainly dry meadow habitat (Aliperti et al. 2022), and our study population was separated from the nearest localities that typically supported other GMGS by >1,000 m to the west, 1,875 m to the south, 300 m to the north, and 250 m to the east (McEachern et al. 2011). Our study population averaged 32 adult squirrels (≥1 year old), although numbers varied annually (Howland et al. 2024). Squirrels emerged from hibernation in late April or May and were active until entering hibernation in August or early September (Wells et al. 2017; Howland et al. 2024). Adult females mated shortly after emerging from hibernation (Wells et al. 2017), and after about 28 days gestation gave birth to a litter of 1 to 8 pups ($\bar{x}$ = 4.8; Kneip et al. 2011). Juveniles were nursed underground for 26 to 33 days until they emerged from their natal burrow (Bartels and Thompson 1993); presumably, juveniles were weaned upon emergence. In our study area, most litters emerged during late June to mid-July.

Data collection typically began in late May or early June each year and continued until late August or sometimes early September. We studied dispersal using a combination of trapping and visual observation of squirrels. At the beginning of each field season, we conducted an annual census in which we livetrapped all squirrels in the study area using traps (Tomahawk Model 201; Hazelhurst, Wisconsin) baited with black-oil sunflower seeds and peanut butter. We used uniquely numbered ear tags to permanently identify all squirrels. For visual identification of individual squirrels, we applied a unique pattern of black dye (Nyanzol D; Greenville Colorants, Greenville, South Carolina) on the dorsal pelage of the animal. We recorded mass (measured with a spring scale accurate to 1 g), sex (based on anogenital distance), trap location, and reproductive status for females (based on color and swelling of nipples). We continued early-season trapping and visual searches until all squirrels in the study area had been identified. Most squirrels were re-trapped multiple times during summer to renew dye marks and obtain body mass and reproductive status. Females considered to be reproductive were monitored closely by searching their home ranges several times per day for newly emerged juveniles. The emergence date for a litter was recorded as the day on which the first juvenile was seen aboveground, and juveniles in the litter were trapped usually within 1 to 2 days of emergence from the natal burrow. Trapping and observation of a newly emerged litter continued until all unmarked juveniles had been trapped. Because all squirrels in the study area were identified, newly arrived, unmarked squirrels were considered immigrants and were trapped and marked. All trapping procedures were approved by the institutional animal care and use committees of the University of California at Davis and the Rocky Mountain Biological Laboratory, and met guidelines set by the American Society of Mammalogists (Sikes et al. 2016).

We conducted visual observations of squirrels daily using binoculars and identified individuals based on their dye marks. Squirrels were diurnal and readily observable when aboveground. Only a portion of our study area was in view from a given location, so we rotated among different portions of the study area at varying times of the day to promote an even distribution of sampling effort. We observed all portions of the study area at least twice per day, once during morning and once during afternoon. When 1 or more squirrels were in view and identified, we used instantaneous scan sampling, recording the identity and location of each squirrel at 1-min intervals. A given sampling bout continued until squirrels left the area or entered a burrow (usually <10 min), whereupon we moved to a new location. Squirrel locations were determined using a grid map of the study area with 7 m × 7 m cells.

Characterization of the dispersal process.

Dispersal in GMGS is thought to occur shortly after weaning (Armitage 1981; Michener 1983), and we described this process in 2 ways, by determining distance from the natal burrow over time and by date of disappearance after weaning. We calculated mean distance from the natal burrow of male and female juveniles in 5-day intervals, beginning on the date of emergence, which we assumed was the date of weaning. For each observation, we measured the Euclidian distance between the center of the grid square in which the squirrel was observed and the center of the grid square containing the natal burrow. For juveniles with multiple distance observations during a given interval, we chose the distance observation closest to the midpoint to calculate the mean distance for that interval. Some juveniles remained as residents or dispersed to a location within our study site, but most disappeared by the end of their first summer. To estimate the timing of dispersal, we used the date of disappearance for each juvenile (Wiggett and Boag 1989), defined as the last date on which the juvenile was trapped or observed. Disappearance is only an estimate of dispersal because juveniles might disappear due to either dispersal or death. To further elucidate dispersal timing, we compared distance from the natal burrow for juvenile females whose dispersal status was known, using a retrospective approach. About 30% of juvenile females remained in our study area the following year (Kneip et al. 2011); some were philopatric and some had dispersed within the study area (see

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below). We compared distance from the natal burrow over time for these known-status females the year before, when they were juveniles. Too few males were present as yearlings for analysis.

Additional information on dispersal timing was obtained from the date on which each immigrant squirrel first appeared in our study area. Early in the active season, adults (≥1 year old) and juveniles can be distinguished reliably by body mass. By August, however, some early-emerging juveniles approached the mass of small-bodied adults. We classified late-season immigrants as juvenile, adult, or age unknown based on analysis of masses and growth rates of known-age squirrels (Nguyen 2023).

We measured distance for dispersal movements within the study area and also beyond the study area. Resident GMGS were spatially clumped across our study area, occurring at 6 discrete localities of dry meadow habitat that were occupied long-term (Wells and Van Vuren 2017). Home ranges of adult females within each locality overlapped about 30%, with related females overlapping more than unrelated females (Aliperti 2020). Juveniles that remained as residents the following summer were classified as philopatric if they remained at their locality of birth, or as a disperser if they settled at a different locality. We measured dispersal distance as the Euclidian distance between the center of the grid square containing the natal burrow and the centroid of the centers of all grid-square locations recorded during the yearling summer. To assess distances for dispersers that moved beyond our study area, we opportunistically searched for marked squirrels at 7 other locations in the East River Valley inhabited by GMGS. We searched each location 1 to 9 times during the course of the study. Marked squirrels were trapped and identified, and the Euclidian distance from their current capture location to the center of the grid square containing their natal burrow was recorded. We compared dispersal distances of males and females using a t-test for unequal variances; because dispersal distance distributions are often skewed, we also used a Mann–Whitney *U* test.

Factors influencing dispersal.

Several factors are thought to play a role in dispersal decisions including competition for resources such as space, the presence or absence of relatives, and body mass of the potential disperser (Bowler and Benton 2005; Armitage et al. 2011; Hoogland 2013). To determine factors that influence dispersal, we modeled dispersal status (0 = philopatric, 1 = dispersed) using logistic regression; we considered a suite of predictors (below) as fixed effects and included birth year as a random effect to account for unobserved variation in the environment among years. In this analysis we included only females that were philopatric and females that we knew had dispersed as juveniles. Males were too few for analysis; throughout the study, only 7 juvenile males remained philopatric at their birth locality.

We included several factors as predictors that might reflect competition for space. Some litters emerge later in the season, in late July or early August, and juvenile females in these litters might perceive an abundance of larger, older juveniles as potential competitors. Hence, we included the date of natal emergence in our analysis. Density of adults might influence the dispersal decision, so we included the number of adult females at each locality. The reproductive status of adult females might also be important (Wiggett and Boag 1989), so we considered the number of reproductive and nonreproductive adult females at the locality. The presence of relatives can influence spatial organization, reproduction, and survival in golden-mantled ground squirrels (Wells and Van Vuren 2017, 2018; Aliperti 2020; Kanaziz et al. 2022), so we distinguished between the number of related and unrelated females at the locality. Related females were defined as those with coefficient of relatedness ≥ 0.125, with relatedness based on matrilineal relationships of adult females and their offspring (Wells and Van Vuren 2017). Because juvenile females might consider other juvenile females in their litter or their natal locality as competitors, we included the number of littermate sisters and the number of other juvenile females at the locality. Body mass might have either of 2 effects; heavy squirrels might disperse because they have the fat reserves needed for the energetic cost of dispersal, or light squirrels might disperse because they are competitively subordinate (Nunes et al. 1998; Bowler and Benton 2005). Because the dispersal decision might be made as early as 10 days after emergence (see Results), we used mass of the juvenile at 10 days. For juveniles not weighed on that date, we used the mass closest in time and adjusted to day 10 using a mean growth rate of 3 g/day (Wells and Van Vuren 2018). We analyzed collinearity among our variables and found that the number of adult females, the number of breeding and nonbreeding females, and the number of related and nonrelated females in the area showed strong collinearity. As a result, we did not include those 3 groups of variables in the same model with each other (Supplementary Data SD1).

We used Akaike's information criterion, corrected for small sample size (AIC_c), to determine the combination of predictor variables that best explained the variation in our response variable (Burnham and Anderson 1998, 2002). Since there is little information on factors that might influence dispersal in this species, we performed a comparison between various combinations of fixed effects. We used the cutoff value of $\Delta AIC_c < 2$ to select the models that best predicted the probability of juvenile dispersal in female GMGS (Richards 2005; Burnham et al. 2011). When there were multiple possible models chosen by this cutoff, we used model averaging across the entire model set to assess the averaged weight of each predictor that appeared in the top models. We performed natural model averaging, using only models containing the variable of interest to calculate the averaged estimate. We considered a variable to have a strong effect if the 95% confidence intervals (CIs) for the coefficient estimate of the averaged model did not include 0.

Fitness consequences of dispersal.

We were unable to determine the fitness cost of dispersal during the transient phase, so we focused on the fitness consequences after settlement, using LRS of adult females considered in 3 groups: philopatric residents, dispersers that left their locality of birth and settled within the study area, and immigrants that settled in the study area after dispersing from an unknown location elsewhere. To calculate LRS, we summed the number of offspring that emerged at the natal burrow for a female throughout her lifetime, beginning at age 1 year. We censored any females that experienced human-caused mortality (e.g., vehicle collision). In addition to LRS, we calculated length of lifespan and frequency of reproduction at age 1 year for each female. Age was known for females born on the study area, and age of most late-season immigrants was estimated based on body mass (Nguyen 2023). We assumed that females immigrating as adults early in the season were 1 year old; breeding dispersal, defined as dispersal after breeding (Greenwood 1980), is rare in our study area (see Results). We compared LRS among groups of females using a Kruskal–Wallis *H* test, and frequency of reproduction using a Chi-square test of independence.

All statistical analyses were conducted in Python (Van Rossum and Drake 2009) and R (R Core Team 2022). We performed logistic regression using the "lme4" package in R (Bates et al. 2015). We used the R package "AICcmodavg" (Mazerolle 2023) to calculate the ΔAIC_c

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value of our models and to perform model averaging. Statistical significance was considered to be $P \leq 0.05$.

Results

Characterization of the dispersal process.

We recorded locations of 365 male and 413 female juveniles; of those 778 juveniles, 40 males (11.0% of total males) and 132 females (32.0% of total females) emerged from hibernation the next year as yearlings and were recorded in the annual census. Some of those 172 yearlings soon disappeared, and the disappearance was male-biased; 25 males (62.5%) and 28 females (21.1%) were not trapped or observed after 30 June of their yearling summer. Immigrants frequently were trapped in our study area, and immigration was also male-biased; we recorded a total of 207 juvenile immigrants (152 male, 55 female) and 171 adult immigrants (128 male, 43 female). The age of 14 male and 3 female immigrants during late season could not be determined, and these immigrants were excluded from further analysis. Many squirrels trapped as immigrants did not become residents in our study area, suggesting that they were still in the transience phase of dispersal.

The mean date of litter emergence was 8 July (median date = 7 July), with a range of 8 June to 11 August. Analysis of juvenile locations revealed that juveniles of both sexes began moving progressively farther away from the natal burrow within a few days of emergence (Fig. 1). By 21 to 25 days postemergence the sexes diverged, with mean distances for males continuing to increase but those for females stabilizing at about 60 to 70 m from the natal burrow. Analysis of the date of last known residency for juveniles showed that disappearance rate peaked at 11 to 30 days after emergence, and that disappearance of males was more pronounced than that of females (Fig. 2). Retrospective analysis of mean distance from the natal burrow for females of known dispersal status indicated that by 11 to 15 days after emergence, dispersing juveniles were moving farther away than philopatric juveniles, with distance stabilizing at about 50 m for the latter (Fig. 3).

Immigrant juveniles appeared in our study area in substantial numbers beginning mid-July, with a peak during August (Fig. 4). Immigrant adults appeared throughout the active season, with a pronounced peak during June (Fig. 4). For both juveniles and adults, the timing of immigration was generally similar for males and females.

We recorded 34 squirrels (25 females and 9 males) that dispersed within our study area. The mean dispersal distance within the study area was 293 m for males (median = 292 m, range = 163 to 419 m) and 142 m for females (median = 136 m, range = 73 to 241 m; Supplementary Data SD2). We found a significant difference between the sexes in dispersal distance within the study area (*t*-test for unequal variances, $t = -5.2373$, $P < 0.005$; Mann–Whitney *U* test, $W = 16$, $P < 0.005$). We identified 17 squirrels (11 males, 6 females) that dispersed beyond our study area. Dispersal distances beyond the study area were a mean of 1,150 m for males (median = 640 m, range = 260 to 3,480 m) and a mean of 1,333 m for females (median = 1,330 m, range = 270 to 2,380 m). We did not find a significant difference in dispersal distance between males and females that moved beyond the study area (*t*-test for unequal variances, $t = 0.375$, $P = 0.715$; Mann–Whitney *U* test, $W = 96$, $P = 0.802$).

Almost all dispersals by females, both within and beyond the study area, were natal dispersals (Greenwood 1980), occurring as juveniles or as yearlings before breeding. We documented only 3 breeding dispersals throughout the study, involving females that dispersed after they had reproduced. We did not detect any breeding dispersals by males, but such events would have been difficult to detect because we did not know the breeding status of most males in the study.

Factors influencing dispersal.

We identified 25 females that dispersed to a new locality within our study area, and 74 that remained philopatric at their locality of birth. In addition, we included 4 females that vanished during their juvenile summer and were subsequently trapped and identified outside the study area as yearlings; hence, we knew that they

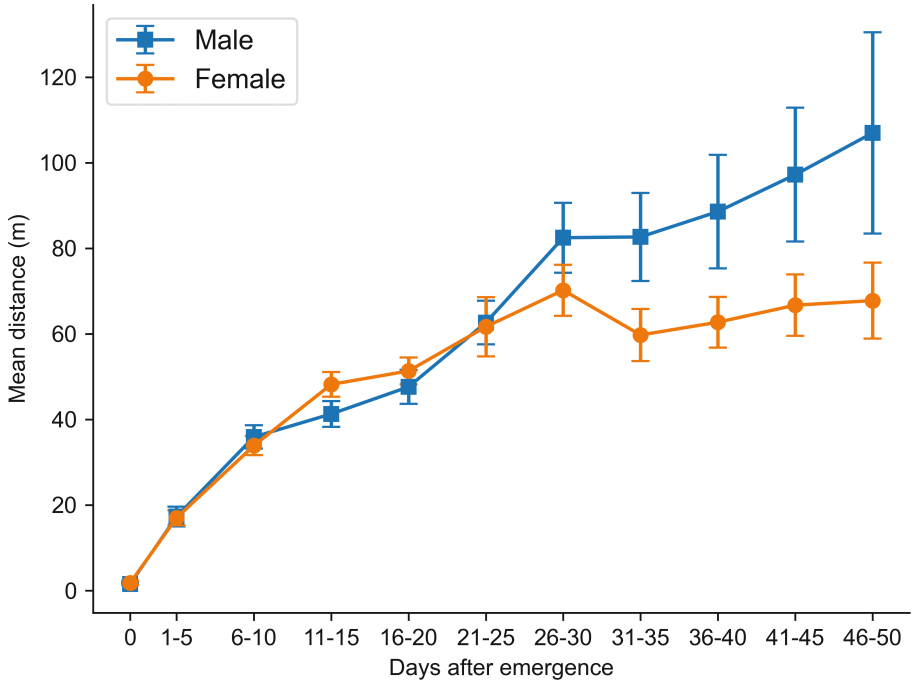


Fig. 1. Mean (±SE) distance from the natal burrow after emergence date, in 5-day intervals, for male ($n = 365$) and female ($n = 413$) juvenile golden-mantled ground squirrels at the Rocky Mountain Biological Laboratory, Colorado, 1995 to 2022.

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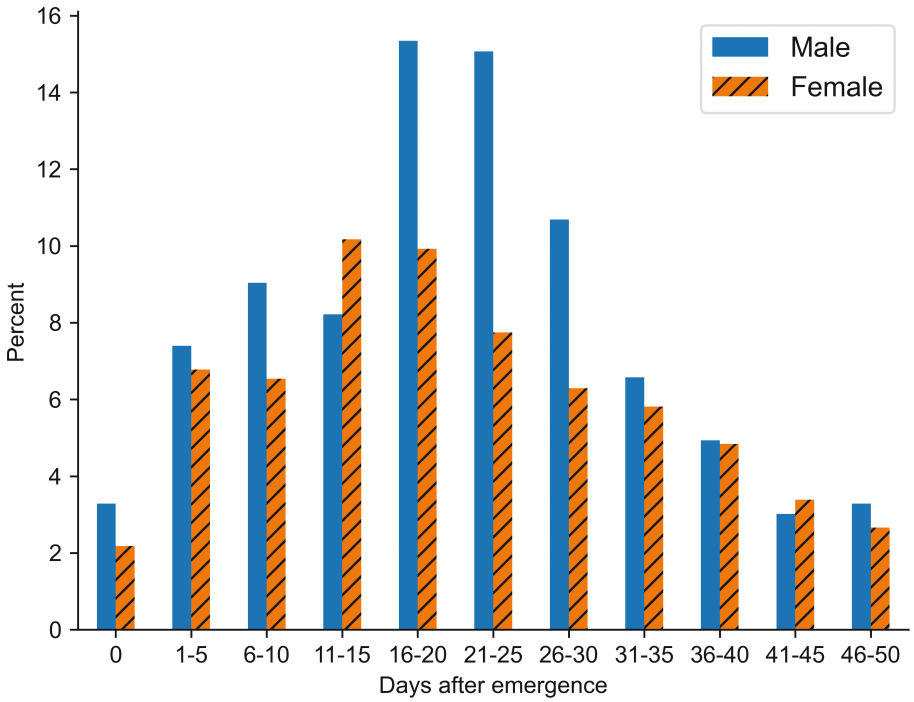


Fig. 2. Date of last known residency, in 5-day intervals after natal emergence date, of male (n = 365) and female (n = 413) juvenile golden-mantled ground squirrels at the Rocky Mountain Biological Laboratory, 1995 to 2022.

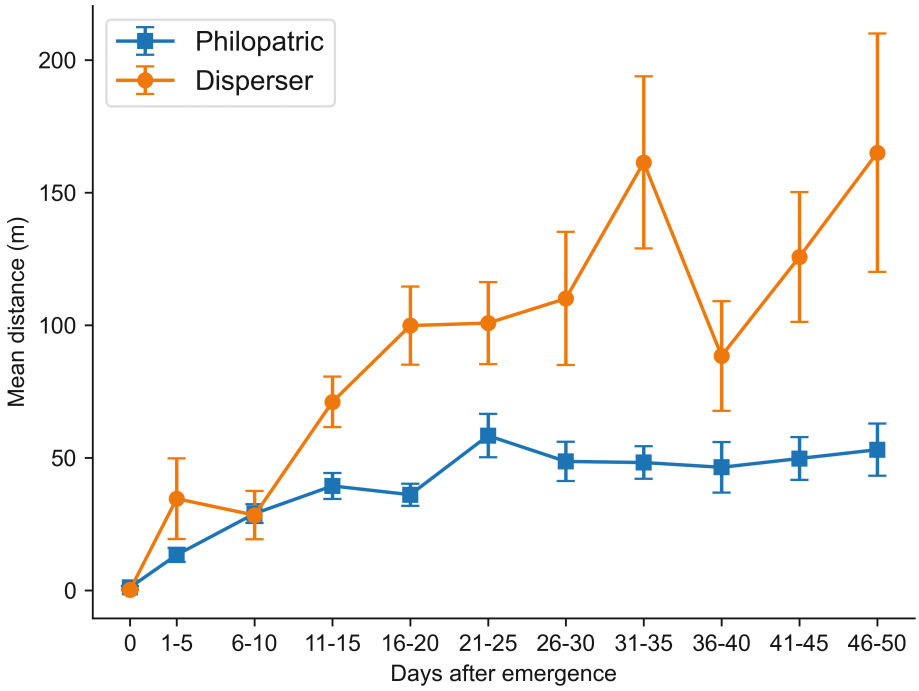


Fig. 3. Mean (±SE) distance from the natal burrow after emergence date, in 5-day intervals, for philopatric (n = 74) and dispersing (n = 25) female juvenile golden-mantled ground squirrels at the Rocky Mountain Biological Laboratory, 1995 to 2022.

had dispersed as juveniles. When analyzing the logistic regression global model, we found that none of the variance was contributed from the random effect (year) and thus it was removed from the rest of the model selection. Of all possible combinations of models, 6 models ranked within 2 ΔAIC_c units of the top model, including the null model "1," which represents a baseline model in which all factors considered in the analysis have no effect on dispersal (Table 1). We used model averaging to assess the averaged weight of the 4 predictors that appeared in the top-ranked models: number of nonbreeding females, number of unrelated females, number of breeding females, and number of littermate sisters. The 95% CI for the estimates of coefficients for nonbreeding females, number of unrelated females, number of breeding females, and number of littermate sisters all overlapped with 0, indicating that none had a consistently strong effect (Fig. 5). However, the 95% CI for number of littermate sisters barely included 0, indicating that this variable generally had

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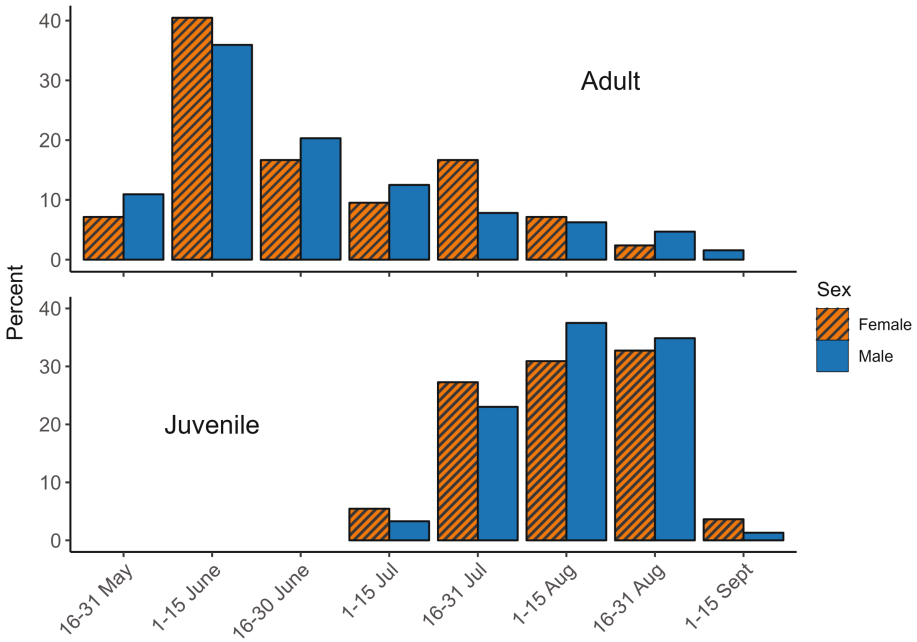


Fig. 4. Relative frequency distribution of date of appearance for adult (males, n = 128; females, n = 43) and juvenile (males, n = 152; females, n=55) immigrant golden-mantled ground squirrels during the summer active season at the Rocky Mountain Biological Laboratory, 1995 to 2022.

Table 1. Logistic models assessing factors associated with dispersal in juvenile female golden-mantled ground squirrels at the Rocky Mountain Biological Laboratory, Colorado, 1995 to 2022. All models with ΔAICc < 2 and the null model are shown. Variables: num_sis = number of littermate sisters; dens_nbf = number of adult nonbreeding females in the same locality with the focal squirrel; dens_bf = number of adult breeding females in the same locality with the focal squirrel; dens_nonrel = number of nonrelated adult females in the same locality with the focal squirrel. The null model "1" represents a baseline model that predicts dispersal in an environment where none of the considered factors would have any effect on the decision of a squirrel.

Model	df	AIC_c	ΔAIC_c	LogLik	Wi
num_sis	2	123.6206	0	−59.7503	0.0588
dens_nbf	2	124.1898	0.5692	−60.0349	0.0442
num_sis + dens_nbf	3	124.3236	0.7030	−59.0406	0.0414
1	1	124.4890	0.8684	−61.2247	0.0380
num_sis + dens_nonrel	3	125.0441	1.4235	−59.4008	0.0288
num_sis + dens_bf	3	125.6016	1.9810	−59.6796	0.0218

a positive effect on dispersal. Moreover, the effect was substantial; converting the estimate to log-odds revealed a 26% increase in the likelihood of dispersal for each littermate sister present.

Fitness consequences of dispersal.

We recorded LRS for 104 adult females—62 that remained philopatric, 17 that dispersed and settled within the study area, and 25 that had dispersed from elsewhere and settled in the study area. The mean number of offspring was 5.6 for philopatric females (SD = ±6.1, median = 4, range = 0 to 23), 5.6 for dispersing females (SD = ±4.1, median = 5, range = 0 to 13), and 7.9 for immigrant females (SD = ±9.7, median = 5, range = 0 to 31). The distribution was right-skewed for the number of offspring. We did not find a significant difference in the number of offspring among the 3 groups (Kruskal–Wallis H test, χ^2 = 0.606, P = 0.739). The mean lifespan was 2.0 years for philopatric females (SD = ±6.1, median = 2, range = 1 to 6), 1.9 years for dispersing females (SD = ±4.1, median = 2, range = 1 to 3), and 2.5 years for immigrant females (SD = ±9.7, median = 2 years, range = 1 to 7). We did not find a significant difference in lifespan among the 3 groups (Kruskal–Wallis H test, χ^2 = 0.368, P = 0.832). Frequency of reproduction at age 1 year was 42% for philopatric females, 53% for dispersing females, and 28% for immigrant females. Frequency of reproduction at age 1 year was independent of dispersal status (Chi-square test of independence, χ^2 = 2.768, P = 0.251), although there was some evidence of a lower frequency among immigrant females.

Discussion

The GMGS is a small-bodied sciurid considered to be asocial; hence, dispersal is expected to occur during the summer of birth, shortly after weaning, and to be male-biased (Armitage 1981; Michener 1983; Holekamp 1984). Our results are consistent with that expectation, although some juveniles appeared to delay dispersal until early in their yearling summer. Almost all juvenile males and most juvenile females born in our study area disappeared before age 1, and most of these losses probably resulted from either dispersal during summer or overwinter mortality. Overwinter survival of juvenile females that hibernated in our study area was 54% (Howland et al. 2024); overwinter survival of juvenile males has not been evaluated, but assuming a survival rate similar to that for juvenile females, an estimated 80% of juvenile males and 41% of juvenile females vanished by the end of their first summer. Some active-season disappearances were due to pre-hibernation mortality; we observed 21 predations on juveniles by red foxes (*Vulpes vulpes*) and weasels (*Mustela* spp.). Most disappearances, however, likely were due to dispersal. Juveniles began moving away from their natal burrow soon after emergence, with mean distances stabilizing at about 60 to 70 m for females by about 3 weeks after emergence but continuing to increase for males. Home ranges of adult females in our study area average 1.7 ha (Aliperti 2020). Assuming a circular shape with the natal burrow at the center, the radius would be about 75 m, suggesting that juvenile females moved to the periphery of the home range of their mother, perhaps to escape interactions with their mother. In golden-mantled ground squirrels, adult interactions

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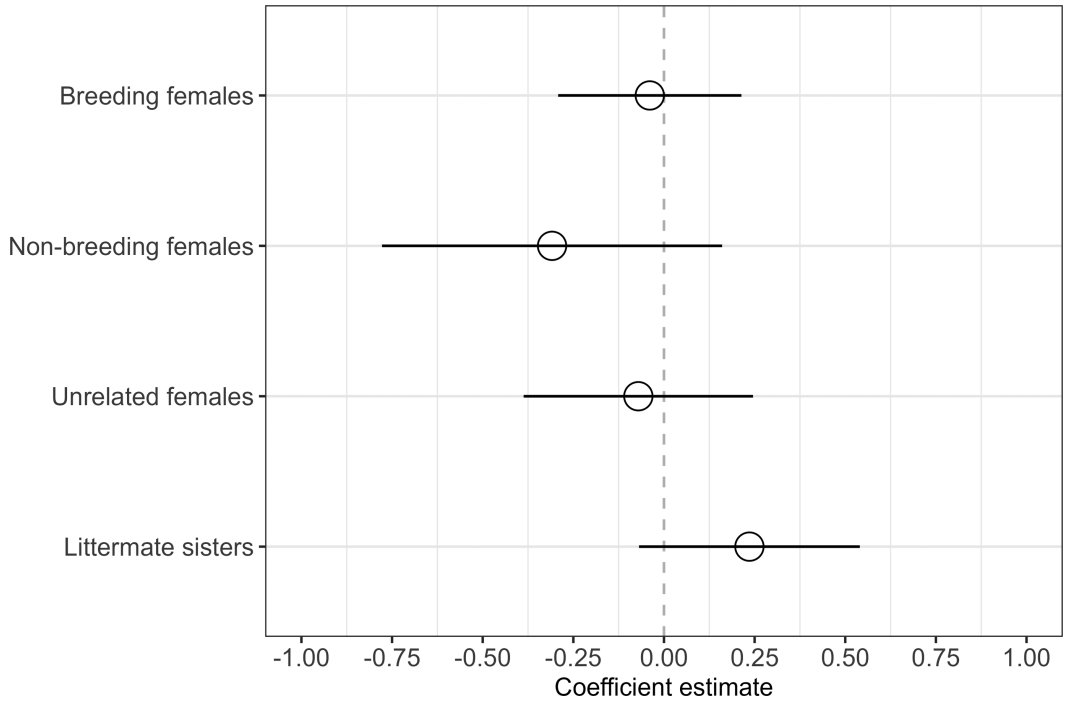


Fig. 5. Plot of coefficients for the 4 predictors that appeared in the best models used to predict factors used in a dispersal decision in juvenile female golden-mantled ground squirrels at the Rocky Mountain Biological Laboratory, Colorado, 1995 to 2022. These models were selected using Akaike's information criterion method. Circles represent point estimates and lines represent 95% CI (2 SE). Positive values indicate an increase in dispersal as the predictor's value increases; negative values indicate a decrease in dispersal as the predictor's value increases.

with juveniles are generally agonistic, including those between mothers and their offspring (Ferron 1985). Adult females appear to be territorial in the central part of their home range, with the 50% "core area" of each female showing minimal overlap with those of other females (Jesmer et al. 2011; Aliperti 2020). Adult male home ranges are much larger than those of adult females (Aliperti 2020), and avoidance of interactions with adult males might explain the increasing distance shown by juvenile males after 3 weeks postemergence. Alternatively, increased male distance could result from a male-biased dispersal tendency, with more males than females in the process of dispersing.

Juveniles began disappearing soon after emergence, with a peak in disappearance of both males and females occurring about 2 to 4 weeks after emergence, especially for males. Some disappearances were due to mortality, especially predation. Also, some late-season disappearances likely resulted from causes other than dispersal or mortality; early-emerging juveniles might have entered hibernation, and termination of fieldwork might have truncated observations of late-emerging juveniles. Nonetheless, our results suggest that dispersal peaks about 2 to 4 weeks after emergence from the natal burrow. Given a mean emergence date of 8 July, dispersal would peak in late July to early August. Dates of appearance in our study area of immigrants born elsewhere are generally consistent with this timing.

Retrospective analysis of distance from the natal burrow for juvenile females of known status revealed that mean distance of eventual dispersers and philopatric residents diverged soon after emergence. Mean distance for eventual philopatric females stabilized at about 50 m, which is equivalent to a location away from the natal burrow and toward the periphery of the home range of their mother, while mean distance of eventual dispersers continued to increase to about 100 to 175 m. Moreover, the timing of the divergence in distance was distinct and occurred at about 11 to 15 days postemergence, suggesting that the dispersal decision originates at about that time.

Some juveniles that successfully hibernated in the study area vanished shortly after emergence the following spring, and we found a strong male bias in these early-season disappearances. Some of the disappearances could have resulted from mortality, but most probably represented dispersal. Appearance of adult immigrants in the study area showed a similar timing, with a peak during June. Hence, our results are consistent with those of Jesmer et al. (2011), who studied dispersal of golden-mantled ground squirrels in California using radiotelemetry and reported that although most dispersal occurred during the juvenile summer, some squirrels might have delayed dispersal until at least age 1.

Jesmer et al. (2011) found no evidence of a sex bias in dispersal distance in golden-mantled ground squirrels. Our data are consistent with that finding, but only for longer dispersal distances; we found a strong male bias for shorter dispersal distances, with males dispersing more than twice as far as females. Home ranges of adult males in our study area are about 4 times as large as those of females (Aliperti 2020); dispersing males might move farther than females to avoid interactions with adult males.

Our characterization of dispersal in golden-mantled ground squirrels is generally consistent with those of other asocial species of ground-dwelling squirrels. For Franklin's ground squirrels (*Poliocitellus franklinii*), dispersal appears to occur during the natal summer, with males more likely to disperse than females and moving longer distances (Martin and Heske 2005). For woodchucks (*Marmota monax*), many juveniles disperse before their first hibernation, but half or more delay dispersal until at least age 1 year, and dispersal tendency is male-biased (Maher 2006, 2009).

Breeding dispersal by females was rare in our population. Although breeding dispersal has been reported in other species of ground-dwelling squirrels, it is strongly male-biased (Holekamp

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1984), suggesting that female breeding dispersal is uncommon in other ground squirrel species.

For our analysis of factors influencing the dispersal decision, we focused on factors potentially discernable to a juvenile female shortly after emergence from her natal burrow. Although larger individuals might be better competitors for space near the natal burrow, or better equipped to survive dispersal away from the natal burrow (Nunes et al. 1998; Bowler and Benton 2005), our findings are consistent with those of other studies that failed to find an effect of body mass on the dispersal decision (Armitage et al. 2011; Rutherford et al. 2023). High density of conspecifics has been proposed as a factor promoting dispersal; in the case of golden-mantled ground squirrels, juvenile females might view other juvenile or adult females as competitors for space, especially if a juvenile female emerges from the natal burrow later than other juvenile females. However, even though numbers of squirrels varied greatly over the course of the study—including within localities (Wells and Van Vuren 2017)—and date of natal emergence varied as well, we did not detect an effect of number of adult females, number of breeding females, number of other juvenile females, or date of emergence on the dispersal decision. While some studies have found a positive effect of density on dispersal in other species, most studies have not (Nunes 2007; Armitage et al. 2011; Rutherford et al. 2023).

Kinship plays an important role in social ground-dwelling squirrels such as large-bodied ground squirrels, prairie dogs (*Cynomys* spp.), and some marmots (*Marmota* spp.), in which slow development and delayed dispersal result in recruitment of daughters to form social groups (Armitage 1981; Michener 1983). Golden-mantled ground squirrels are considered solitary (Armitage 1981; Michener 1983), but even in solitary species, female philopatry can lead to spatial clusters of kin (McEachern et al. 2007; Maher 2009). In our population, related females often live in close proximity and share space more than do unrelated females (Aliperti 2020), and proximity of relatives can influence the mating system, survival, reproduction, and offspring sex ratio (Wells et al. 2017; Wells and Van Vuren 2017, 2018; Kanaziz et al. 2022). Although we did not find an effect of number of adult female relatives on the dispersal decision, the number of littermate sisters was included in the top model and had a reliably positive effect on the dispersal decision, with a large effect size. Because the number of other juvenile females at the locality did not have an influence on the dispersal decision, the number of littermate sisters might have reflected competition for space in the immediate vicinity of the natal burrow. However, the number of littermate sisters also might be a cue foretelling prospects for reproduction the next year; yearling females in our study area were 78% less likely to breed when in the presence of littermate sisters (Wells and Van Vuren 2018). Because kin within the natal home range compete for resources, Hamilton and May (1977) proposed that the presence of nearby kin should promote dispersal, and our results are consistent with that expectation. Contrasting results were reported for yellow-bellied marmots (*M. flaviventris*) and 3 species of prairie dogs, in which the presence of kin promoted philopatry (Armitage et al. 2011; Hoogland 2013). However, yellow-bellied marmots and prairie dogs are social species in which the benefits of kin cooperation might exceed the benefits of kin competition (Armitage 1989; Nunes 2007; Hoogland 2013). It is worth noting that the null model was ranked very highly in the chosen model set, suggesting there could be other factors contributing to the dispersal decision of female juveniles.

Dispersers that survive transience might still face costs after settlement (Bonte et al. 2012). For example, immigrant Columbian ground squirrels (*Urocitellus columbianus*) and black-tailed prairie dogs (*C. ludovicianus*) settled at the colony periphery and experienced higher mortality (Garrett and Franklin 1988; Wiggett and Boag 1993), and recently immigrated Utah prairie dogs (*C. parvidens*) were more vulnerable to predation than were established residents (Hoogland et al. 2006). Those studies that have compared LRS of immigrants and philopatric residents have produced inconsistent results. For example, immigrant female North American red squirrels (*Tamiasciurus hudsonicus*) had a 23% lower LRS than residents (Martinig et al. 2020), whereas immigrant female Eurasian red squirrels (*Sciurus vulgaris*) showed no difference with residents in LRS (Wauters et al. 1994). Similarly, we did not find a significant difference in LRS among immigrants from outside the study area, immigrants from elsewhere within our study area, and philopatric residents. Our results suggest that for golden-mantled ground squirrels, any cost of dispersal is experienced primarily during the transience phase. However, we found a nonsignificant effect on age of first reproduction that might be biologically significant; only 28% of immigrant females reproduced at age 1 year, substantially less than a combined 42% for females born in the study area. Perhaps some immigrant females failed to breed because of the energetic cost of dispersal, or because of the time needed to establish familiarity with resources and the social environment in a new location. Similarly, immigrant males in our population showed very low reproductive success during their first year (Wells et al. 2017). Evidence of compensation, although not statistically significant, was suggested by immigrant females being less likely to breed at age 1 year but living longer. Moore et al. (2016) reported that female golden-mantled ground squirrels who delayed reproduction past age 1 year lived longer.

In summary, dispersal in golden-mantled ground squirrels generally follows expectations based on their classification as an asocial ground squirrel (Armitage 1981; Michener 1983); dispersal begins soon after emergence from the natal burrow, although some squirrels delayed dispersal until the following summer. Consistent with other ground-dwelling squirrels (Holekamp 1984), dispersal in golden-mantled ground squirrels is male-biased in dispersal tendency, and it is also male-biased in dispersal distance, but only over shorter dispersal distances. The dispersal decision, which occurs soon after emergence from the natal burrow, appears to be influenced by the number of littermate sisters, either because of competition for resources that year or as a cue for future competition the next year. Finally, we found little evidence of lower fitness for immigrants, suggesting that for the GMGS, any cost of dispersal is primarily during the transience phase.

Supplementary data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1. Logistic models assessing factors associated with dispersal in juvenile female Golden-mantled Ground Squirrel at the Rocky Mountain Biological Laboratory, Colorado, 1995 to 2022. A total of 128 combinations of models were tested for the effect of 9 different variables: emergence date; mass at 10 days postemergence; number of adult females at the locality of birth; number of reproductive adult females at locality of birth; number of nonreproductive adult females at locality of birth; number of adult females related to the focal juvenile at the locality of birth; number of adult females unrelated to the focal juvenile at the locality of birth; number of littermate sisters; and number of other juvenile females at the locality of birth. The 3 variable groups—number of adult females, number of breeding and nonbreeding females, and number of related and nonrelated females—showed strong collinearity, so they were not included in the same models with each other.

Supplementary Data SD2. Frequency distribution of the distance between the natal burrow and the centroid of all locations recorded

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during the yearling summer for philopatric (defined as resident in their locality of birth, $n = 74$) and dispersing females (defined as settled in a different locality than the one in which they were born, $n = 25$).

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Author contributions

NTTN: conceptualization, data curation, formal analysis, investigation, methodology, software, resources, visualization, writing original draft, reviewing and editing drafts. DHVV: conceptualization, funding acquisition, data curation, formal analysis, investigation, methodology, project administration, supervision, software, resources, writing original draft, reviewing and editing drafts. CPW: conceptualization, data curation, funding acquisition, investigation, project administration, supervision, resources, reviewing and editing drafts.

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Conflict of interest

None declared.

Data availability

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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