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Dispersal of the Golden-mantled Ground Squirrel

By

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ABSTRACT

Dispersal, the permanent movement of an animal away from its location of birth, 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.

INTRODUCTION

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 of the life cycle of mammals (Nunes 2007), and it is often sex-biased; in mammals, males are more likely to disperse than females, or disperse farther (Dobson 1982; Smale et al. 1997; Lawson Handley and Perrin 2007; Nunes 2007).

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 were short-term or utilized only one fitness measure, 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; benefits include 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 (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)* is a small-bodied (130-240 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 behavior in the Golden-mantled Ground Squirrel 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 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 Golden-mantled Ground Squirrel 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 Golden-mantled Ground Squirrel (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 (2900 m elevation), in the East River Valley, Gunnison County, Colorado, USA. (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*). GMGS mainly utilized dry meadow habitat (Aliperti et al. 2022). 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. Our study population was separated from the nearest localities that regularly supported other GMGS by >1000 m to the west, 1875 m to the south, 300 m to the north, and 250 m to the east (McEachern et al. 2011). Squirrels in our study area 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. in press). Adult females mated shortly after emerging from hibernation (Wells et al. 2017), and after about 28 days gestation gave birth to a litter of 1-8 pups (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 live-trapped all squirrels in the study area using traps (Tomahawk Model 201, Hazelhurst, Wisconsin, USA) baited with black-oil sunflower seeds and peanut butter. We used uniquely numbered eartags 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, USA) on the dorsal pelage of the animal. We recorded mass (measured with a spring scale accurate to 1 g), sex (based on ano-genital 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 1-2 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 above ground. 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 one or more squirrels were in view and identified, we used instantaneous scan sampling, recording the identity and location of each squirrel at 1-minute intervals. A given sampling bout continued until squirrels left the area or entered a burrow (usually <10 minutes), whereupon we moved to a new location. Squirrel locations were determined using a grid map of the study area with 7-m x 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 two 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 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. 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 of these were philopatric and some had dispersed within the study area (see 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 (Appendix I).

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 six 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 natal burrow and the centroid of all locations recorded during the yearling summer. To assess distances for dispersers that moved beyond our study area, we opportunistically searched for marked squirrels at seven other locations in the East River Valley inhabited by GMGS. We searched each location one to nine times during the course of the study. Marked squirrels were trapped and identified, and distance from their current location to 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. We considered only females whose dispersal status was known; males were too few for analysis. We included several factors as predictors that might reflect competition for space. Some litters emerge late 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 non-reproductive adult females at the locality. The presence of relatives can influence both spatial organization and reproduction in Golden-mantled Ground Squirrels (Wells and Van Vuren 2017, 2018; Aliperti 2020), 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 (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 two 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 non-breeding females, and the number of related and non-related females in the area showed strong collinearity. As a result, we did not include those three groups of variables in the same model with each other (Appendix III).

We used Akaike's information criterion, corrected for small sample size (AICc), 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 cut off, 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 zero.

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 lifetime reproductive success (LRS) of adult females considered in three groups: philopatric residents, local dispersers 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. We were unable to determine litter size for four litters (of 142 total litters); for three of these we were not certain that we had trapped and identified all juveniles in the litter, and one litter experienced human-caused mortality before it could be counted. For these four litters, we assigned the mean litter size of 4.3 (see Results). 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 (Appendix I). 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 lme4 package in R (Bates et. al 2015). We used the R package AICcmodavg (Mazerolle 2023) to calculate the ΔAIC_c value of our models and to perform model averaging.

RESULTS

Characterization of the dispersal process.—We recorded 365 male and 413 female juveniles in 181 litters, for a mean litter size of 4.3. 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 adults). 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 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 21-25 days post-emergence the sexes diverged, with mean distances for males continuing to increase but those for females stabilizing at about 60-70 m from the natal burrow. Analysis of the date of last known residency for juveniles showed that disappearance rate peaked at 11-30 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 11-15 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. 5). 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

= 163-419 m) and 142 m for females (median = 136 m, range = 73-241 m; Appendix II). We found a significant difference between the sexes in dispersal distance (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 1150 m for males (median = 640 m, range = 260-3480 m) and a mean of 1333 m for females (median = 1330 m, range = 270-2380 m). We did not find a significant difference between males and females moving beyond the study area in dispersal distance (t-test for unequal variances, $t = 0.375$, $P = 0.715$; Mann-Whitney U test, $W = 96$, $P = 0.802$).

Almost all dispersal 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 three breeding dispersals throughout the study, involving females that dispersed after they had reproduced.

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 augmented our sample size of dispersing females with four females that vanished during their juvenile summer and were subsequently trapped and identified outside the study area as yearlings. When analyzing the logistic regression global model, we found none of the variances 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, six models ranked within 2 ΔAIC_c units of the top model, including the null model (Table 1). We used model averaging to assess the averaged weight of the four predictors that appeared in the top ranked models: number of non-breeding females, number of unrelated females, number of breeding females, and number of littermate sisters. The 95% CI for the estimates of coefficients for non-breeding females (β = -0.31, 95% CI = -0.78-0.16), number of unrelated females (β = -0.07, 95% CI = -0.39-0.25), number of breeding females (β = -0.04, 95% CI = -0.29-0.21), and number of littermate sisters (β = 0.24; 95% CI = -0.07-0.54) all overlapped with zero, indicating that none had a strong effect. However, the 95% CI for number of littermate sisters barely included zero, indicating this variable had a reliably 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 108 adult females – 64 that remained philopatric, 17 that dispersed and settled within the study area, and 27 that had dispersed from elsewhere and settled in the study area. The mean number of offspring was 5.8 for philopatric females (median = 4), 5.6 for dispersing females (median = 5), and 8.3 for immigrant females (median = 5). The distribution was right skewed for the number of offspring. We did not find a significant difference in the number of offspring among the three groups (Kruskal-Wallis H Test, χ^2 = 0.905, P = 0.636). The mean life span was 2.0 years for philopatric females (median = 2 years), 1.9 years for dispersing females (median = 2 years), and 2.6 years for immigrant females (median = 2 years). There was no significant difference in life span among the three tested groups (Kruskal-Wallis H Test, χ^2 = 0.951, P = 0.622). Frequency of reproduction at age 1 year was 44% for philopatric females, 53% for dispersing females, and 30% for immigrant females. Frequency of reproduction at age 1 year was independent of dispersal status (Chi-squared test of independence, χ^2 = 2.613, P = 0.271), although there was some evidence of a lower frequency among immigrant females.

DISCUSSION

The Golden-mantled Ground Squirrel 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. in press); assuming a similar survival rate for juvenile males, 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 several 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 60-70 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 their mother's home range, perhaps to escape interactions with their mother. In GMGS, adult interactions 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 post-emergence. 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 2-4 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 field work might have truncated observations of late-emerging juveniles. Nonetheless, our results suggest that dispersal peaks about 2-4 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 their mother's home range, while mean distance of eventual dispersers continued to increase to about 100-175 m. Moreover, the timing of the divergence in distance was distinct and occurred at about 11-15 days post-emergence, 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 GMGS 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 GMGS. 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 four 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 Squirrel (*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 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 2011). 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 an effect of density in other species, other studies have not (Nunes 2007; Armitage et al. 2011).

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 results 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, reproduction, and offspring sex ratio (Wells et al. 2017; Wells and Van Vuren 2017, 2018). 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 three 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 dispersal decision of female juveniles.

Dispersers that survive transience might still face costs after settlement (Bonte et al. 2012). For example, the offspring of immigrant female Columbian Ground Squirrels (*Urocitellus columbianus*) apparently suffered higher mortality because they lived at the periphery of the colony (Wiggett and Boag 1993); similarly, immigrant Black-tailed Prairie Dogs (*C. ludovicianus*) settled at the colony periphery because of aggression from residents and experienced higher mortality (Garrett and Franklin 1988). 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 30% of immigrant females reproduced at age 1 year, substantially less than a combined 46% for females born in the study area. Perhaps some immigrant females failed to breed because they were establishing 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 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 also is 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 Golden-mantled Ground Squirrel, any cost of dispersal is primarily during the transience phase.

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TABLES AND FIGURES

Table 1: Logistic models assessing factors associated with dispersal in juvenile female Golden-mantled Ground Squirrels at the Rocky Mountain Biological Laboratory, Colorado, 1995-2022. All models with Δ AICc < 2 and the null model are shown. Variables: num_sis = number of littermate sisters, dens_nbf = number of adult non-breeding 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 non-related adult females in the same locality with the focal squirrel.

Model	df	AIC_c	ΔAIC_c	logLik	W_i
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

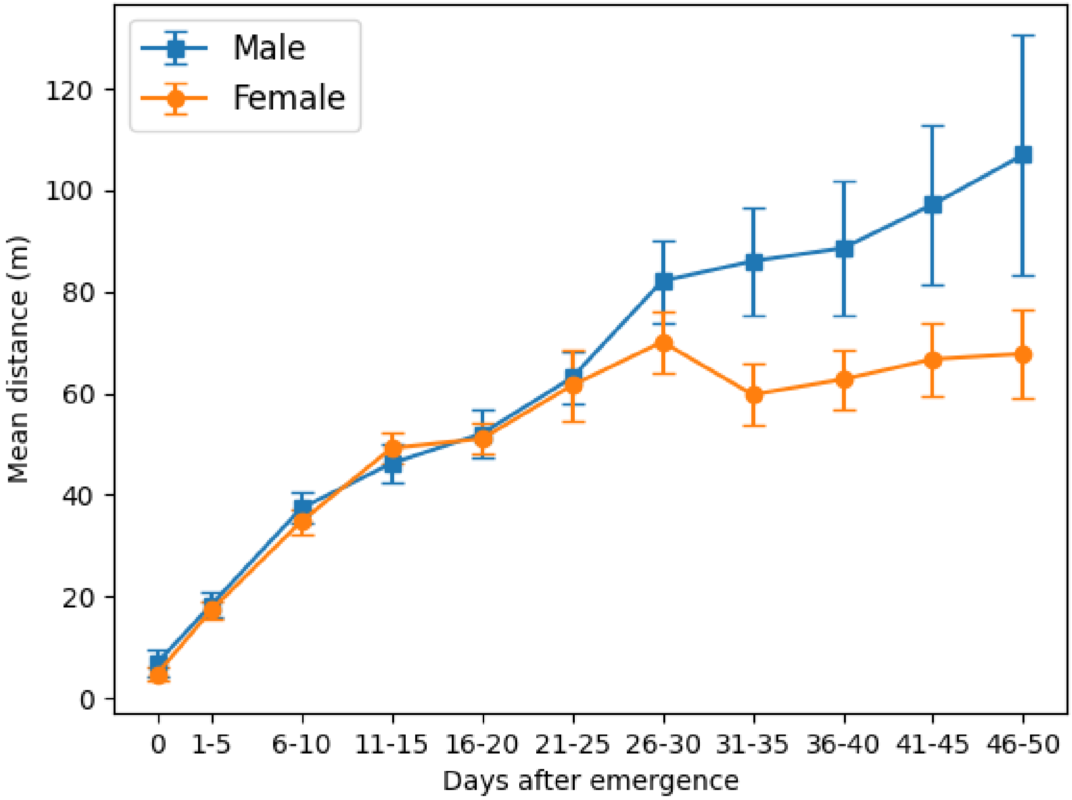


Fig.1—Mean (± *SE*) distance from the natal burrow after emergence date, in 5-day intervals, for male (*n*=365) and female (*n*=413) juvenile Golden-mantled Ground Squirrels at the Rocky Mountain Biological Laboratory, Colorado, 1995 to 2022.

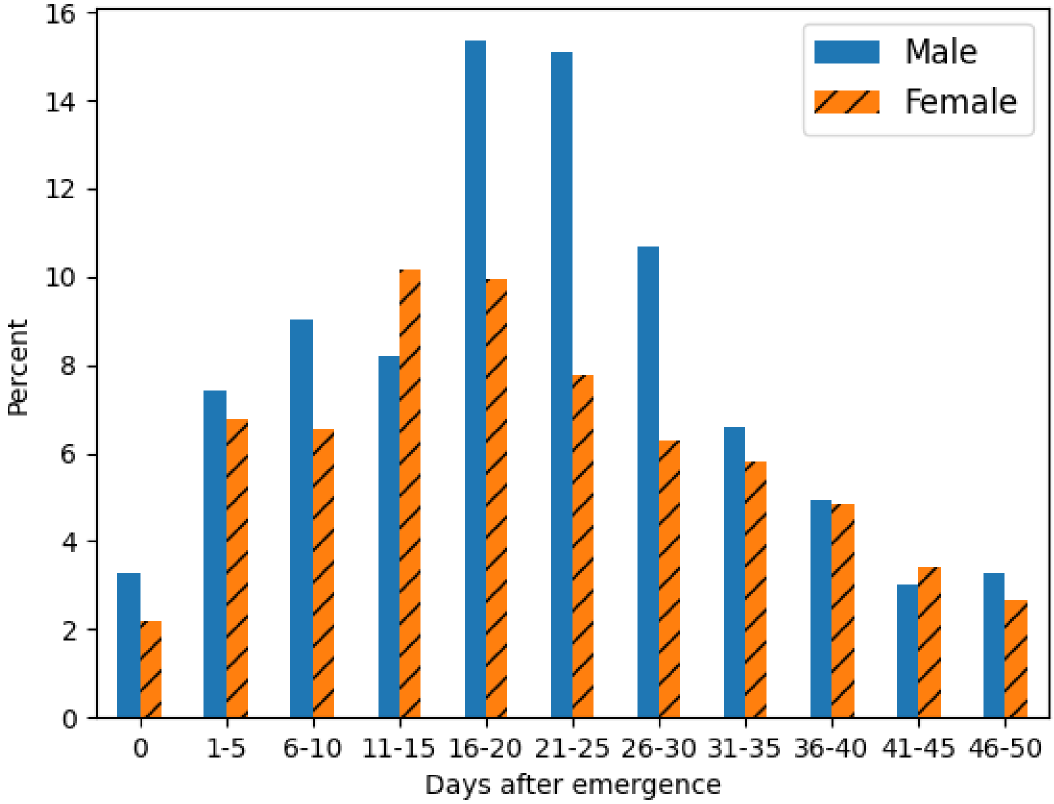


Fig. 2—Date of last known residency, in 5-day intervals after natal emergence date, of male (*n*= 413*)* and female (*n*=365) juvenile Golden-mantled Ground Squirrels at the Rocky Mountain Biological Laboratory, 1995 to 2022.

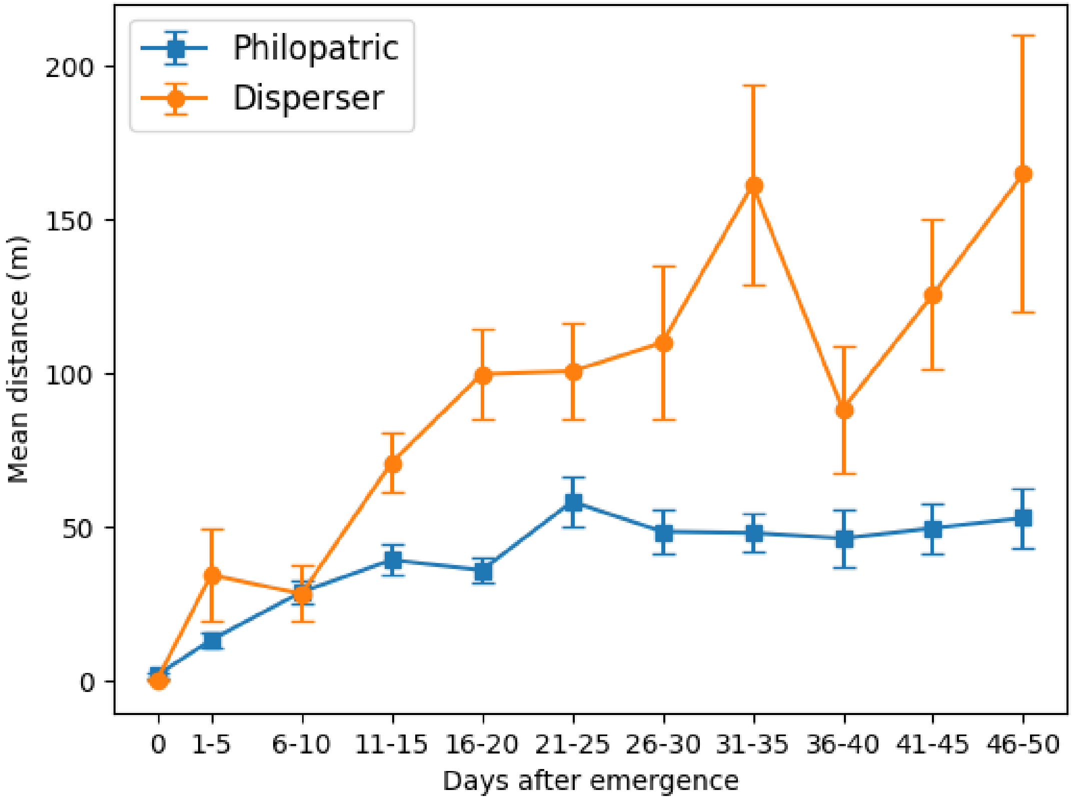


Fig.3—Mean (± SE) distance from the natal burrow after emergence date, in 5-day intervals, for philopatric (*n*=74) and dispersing (*n*=25) female juvenile Golden-mantled Ground Squirrels at the Rocky Mountain Biological Laboratory, 1995 to 2022.

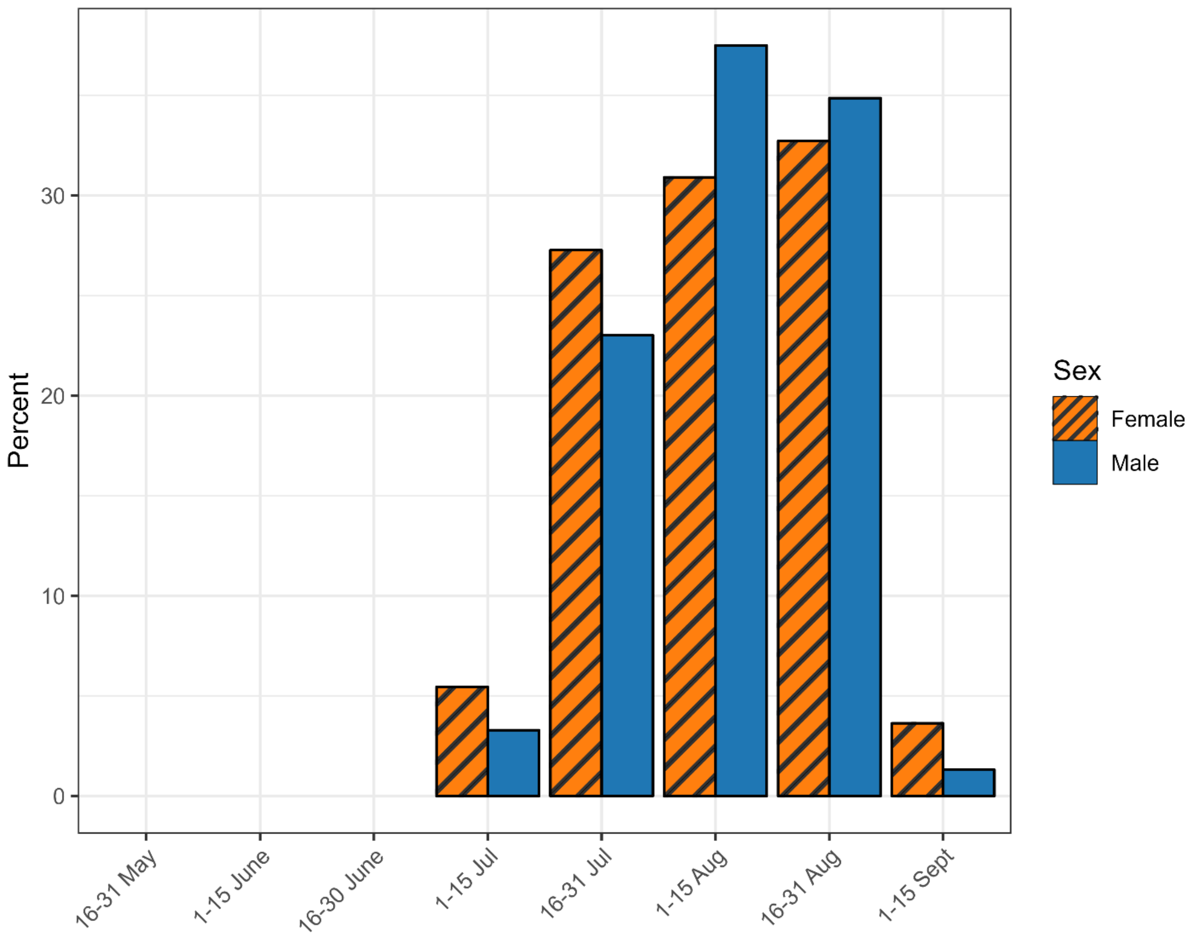


Fig. 4—Frequency distribution of date of appearance for juvenile male (*n*=152) and juvenile female (*n*=55) immigrant Golden-mantled Ground Squirrels during the summer active season at the Rocky Mountain Biological Laboratory, 1995 to 2022.

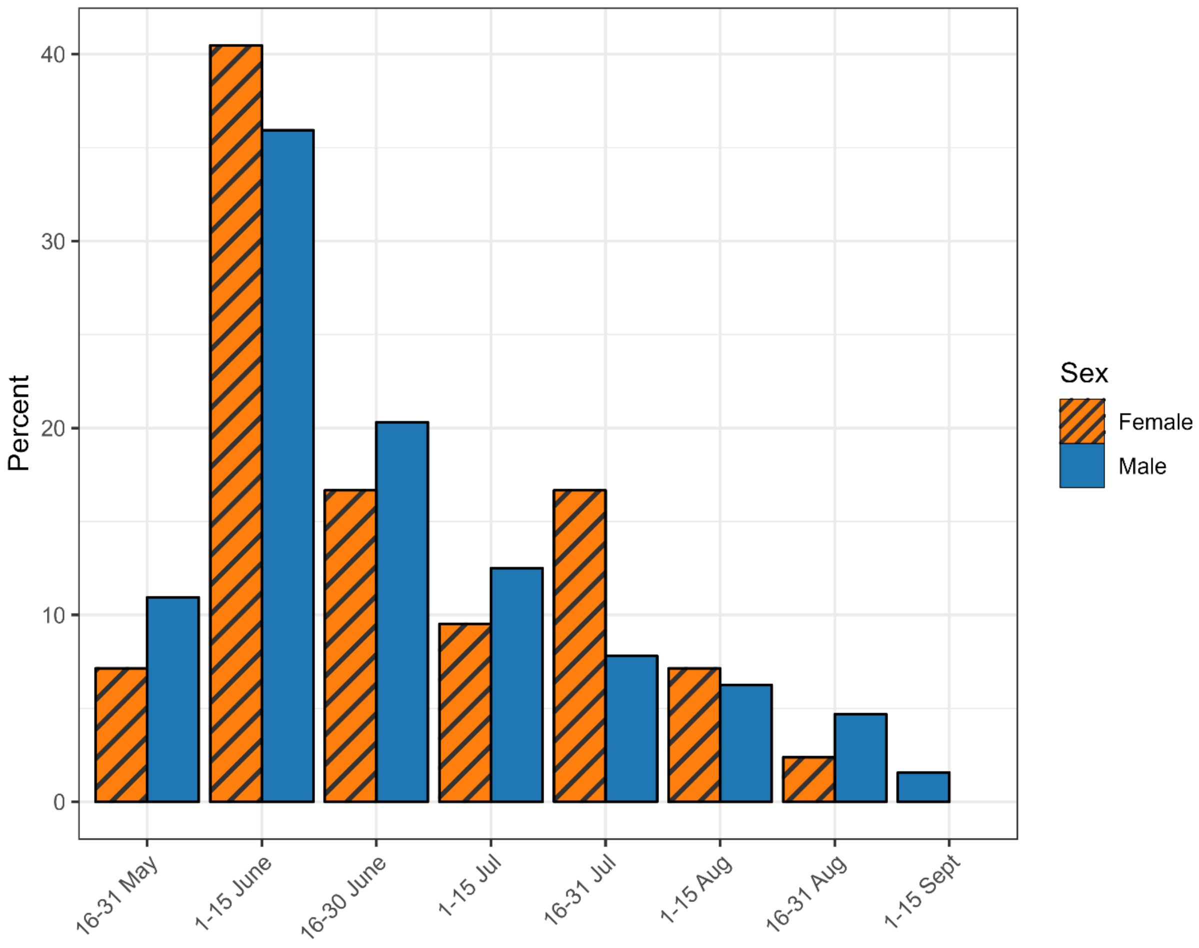


Fig. 5—Frequency distribution of date of appearance for adult male (*n*=128) and adult female (*n*=43) immigrant Golden-mantled Ground Squirrels during the summer active season at the Rocky Mountain Biological Laboratory, 1995 to 2022.

APPENDIX I: Age classification of late-summer immigrants

Immigrants that are first trapped in August are of unknown age, so we used body masses of known-age squirrels in August to estimate the age of immigrants.

For females, Howland et al. (in press) reported that growth rates of known-age yearling females during August averaged 2.2 g/day. Using this growth rate, and mass values of yearling females obtained during August, they adjusted the mass of each female to 15 August and calculated a mean mass on 15 August of 260 g (N = 54, range = 179-366). Using the same method, the mean growth rate was 2.3 g/day for juvenile females, and the mass of juvenile females adjusted to 15 August was a mean of 166 g (range = 59-298). Hence, slopes of mass versus time for juvenile and yearling females during August were nearly identical, but the y-intercept was 96 g greater for yearling females.

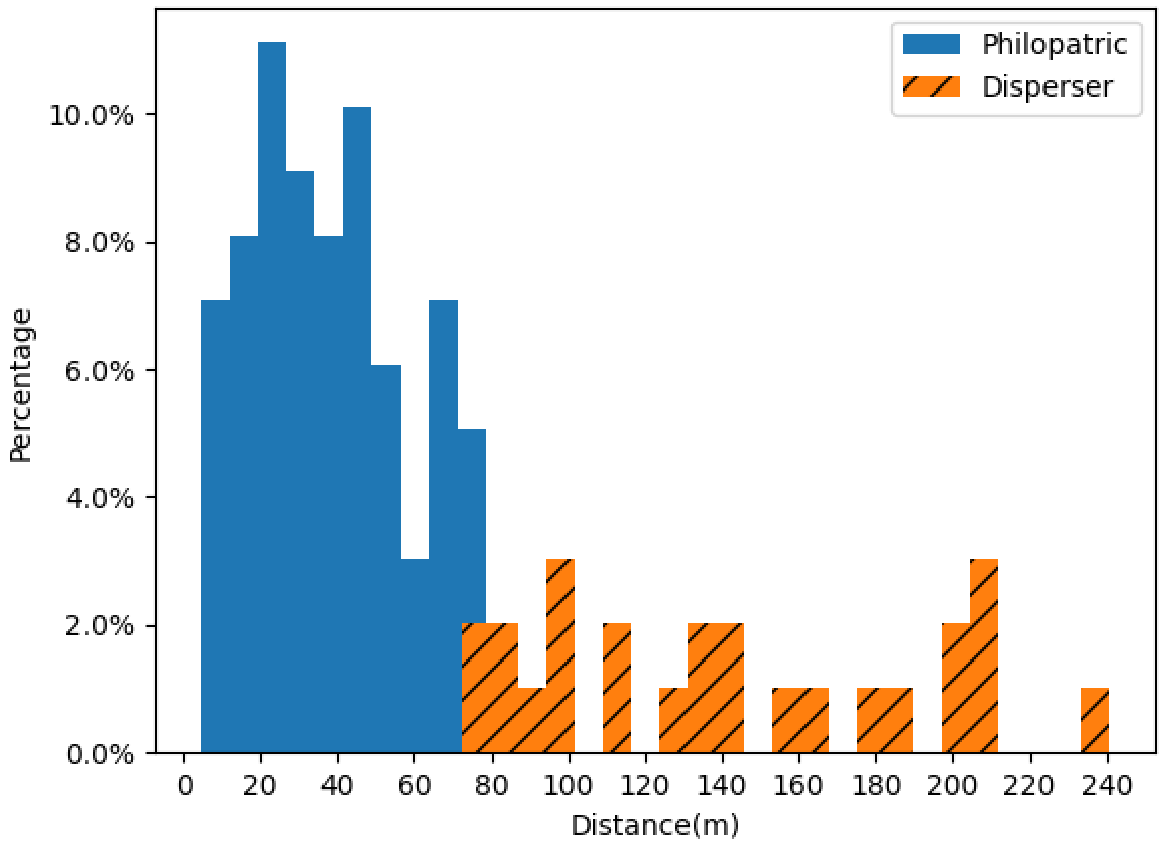
On August 15, 52 of 54 female yearlings (96%) weighed more than 190 g. Hence, any female immigrant that weighed less than 190 g, adjusted for number of days before or after 15 August at the rate of 2.3 g/day, was classified as a juvenile. All others were classified as age unknown.

For males, we searched our trap data 1995-2022 for records of known-age yearling males trapped during August. Using the method of Howland et al. (in press) for calculating mass gain for each male (2 masses, 5 days or more apart), we determined a mean mass gain for yearling males during August of 0.3 g/day (N = 11, range = -2.4-1.6 g/day). We used this growth rate to adjust masses of yearling males weighed in August to 15 August, and obtained a mean of 204 g (N = 25, range = 169-285). We then searched through our trap data 1995-2022 for records of juvenile males trapped within 2.5 days of 15 August (hence, 13-17 August); they averaged 169 g

(N = 48, range = 95-261). Hence, yearling males changed little in mass during August, with mass stable at about 200 g. In contrast, juvenile males gained mass continuously during August; we did not measure this, but the rate probably was similar to that of juvenile females (2.3 g/day).

During August, 24 of 25 yearling males (96%) weighed more than 170 g, and 24 of 25 (96%) weighed less than 225 g. Hence, any immigrant male that weighed less than 170 g or more than 225 g during August was classified as a juvenile. Also, any immigrant with multiple captures during August that gained weight appreciably was classified as a juvenile. All others were classified as age unknown.

Appendix II: Frequency distribution of the distance between the natal burrow and the centroid of all locations recorded during the yearling summer for philopatric (*n=74*) and dispersing females (*n=25*).



APPENDIX III: Logistic models assessing factors associated with dispersal in juvenile female Golden-mantled Ground Squirrels at the Rocky Mountain Biological Laboratory, Colorado, 1995-2022. A total of 128 combinations of models were tested for the effect of nine different variables: emergence date, mass at 10 days post-emergence, number of adult females at the locality of birth, number of reproductive adult females at locality of birth, number of non-repro 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, number of other juvenile females at the locality of birth. The three variable groups, number of adult females, number of breeding and non-breeding females, and number of related and non-related females, showed strong collinearity, so they were not included in the same models with each other. Variables: emerge_day = emergence date, mass_10 = mass at 10 days, fem_dens = number of adult females at the locality of birth, dens_bf = number of reproductive adult females at the locality of birth, dens_nbf = number of non-reproductive adult females at the locality of birth, dens_rel = number of adult females related to the focal juvenile at the locality of birth, dens_nonrel = number of adult females unrelated to the focal juvenile at the locality of birth, num_sis = number of littermate sisters, dens_fem_juv = number of other juvenile females at the locality of birth.

Number	Model	df	AIC_C	ΔAIC_c	logLike	W_i
1	num_sis	2	123.6206	0.0000	-59.7503	0.0588
2	dens_nb	2	124.1898	0.5692	-60.0349	0.0442
3	num_sis + dens_nbf	3	124.3236	0.7030	-59.0406	0.0414
4	1	1	124.4890	0.8684	-61.2247	0.0381
5	num_sis + dens_nonrel	3	125.0441	1.4235	-59.4008	0.0288

6	num_sis + dens_bf	3	125.6016	1.9810	-59.6796	0.0218
7	fem_dens + num_sis	3	125.6742	2.0536	-59.7159	0.0210
8	emerge_day + num_sis	3	125.6844	2.0638	-59.7210	0.0209
9	num_sis + dens_rel	3	125.7119	2.0913	-59.7347	0.0207
10	dens_fem_juv + dens_nbf	3	125.7139	2.0933	-59.7357	0.0206
11	mass_10 + num_sis	3	125.7387	2.1181	-59.7481	0.0204
12	dens_fem_juv + num_sis	3	125.7405	2.1199	-59.7490	0.0204
13	dens_fem_juv	2	125.8027	2.1821	-60.8414	0.0197
14	dens_rel	2	126.1072	2.4866	-60.9936	0.0170
15	emerge_day + dens_nbf	3	126.2272	2.6066	-59.9924	0.0160
16	dens_nonrel	2	126.2591	2.6385	-61.0696	0.0157
17	dens_bf + dens_nbf	3	126.3096	2.6890	-60.0336	0.0153
18	mass_10 + dens_nbf	3	126.3122	2.6916	-60.0349	0.0153
19	emerge_day + num_sis + dens_nbf	4	126.4265	2.8059	-59.0092	0.0144
20	dens_fem_juv + num_sis + dens_nbf	4	126.4737	2.8531	-59.0328	0.0141
21	fem_dens	2	126.4743	2.8537	-61.1771	0.0141
22	dens_bf	2	126.4774	2.8568	-61.1787	0.0141
23	mass_10 + num_sis + dens_nbf	4	126.4814	2.8608	-59.0366	0.0141
24	emerge_day	2	126.4851	2.8645	-61.1825	0.0140
25	num_sis + dens_bf + dens_nbf	4	126.4853	2.8647	-59.0386	0.0140
26	mass_10	2	126.5684	2.9478	-61.2242	0.0135

27	dens_fem_juv + dens_nonrel	3	126.9293	3.3087	-60.3434	0.0112
28	dens_fem_juv + num_sis + dens_nonrel	4	127.0418	3.4212	-59.3168	0.0106
29	emerge_day + num_sis + dens_nonrel	4	127.1629	3.5423	-59.3773	0.0100
30	num_sis + dens_rel + dens_nonrel	4	127.1797	3.5591	-59.3858	0.0099
31	mass_10 + num_sis + dens_nonrel	4	127.2098	3.5892	-59.4008	0.0098
32	dens_fem_juv + dens_bf	3	127.2258	3.6052	-60.4917	0.0097
33	fem_dens + dens_fem_juv	3	127.2653	3.6447	-60.5115	0.0095
34	dens_fem_juv + dens_rel	3	127.3933	3.7727	-60.5754	0.0089
35	dens_fem_juv + num_sis + dens_bf	4	127.6778	4.0572	-59.6348	0.0077
36	emerge_day + num_sis + dens_bf	4	127.6815	4.0609	-59.6367	0.0077
37	dens_fem_juv + dens_bf + dens_nbf	4	127.7287	4.1081	-59.6602	0.0075
38	emerge_day + dens_fem_juv + dens_nbf	4	127.7606	4.1400	-59.6762	0.0074
39	mass_10 + num_sis + dens_bf	4	127.7626	4.1420	-59.6772	0.0074
40	emerge_day + fem_dens + num_sis	4	127.7769	4.1563	-59.6844	0.0074

41	fem_dens + dens_fem_juv + num_sis	4	127.7858	4.1652	-59.6888	0.0073
42	emerge_day + num_sis + dens_rel	4	127.7934	4.1728	-59.6926	0.0073
43	emerge_day + dens_fem_juv	3	127.7965	4.1759	-60.7770	0.0073
44	mass_10 + fem_dens + num_sis	4	127.8345	4.2139	-59.7132	0.0071
45	emerge_day + mass_10 + num_sis	4	127.8423	4.2217	-59.7171	0.0071
46	emerge_day + dens_fem_juv + num_sis	4	127.8450	4.2244	-59.7184	0.0071
47	dens_fem_juv + num_sis + dens_rel	4	127.8685	4.2479	-59.7302	0.0070
48	mass_10 + num_sis + dens_rel	4	127.8698	4.2492	-59.7308	0.0070
49	mass_10 + dens_fem_juv + dens_nbf	4	127.8768	4.2562	-59.7343	0.0070
50	dens_rel + dens_nonrel	3	127.8821	4.2615	-60.8198	0.0070
51	mass_10 + dens_fem_juv + num_sis	4	127.9016	4.2810	-59.7467	0.0069
52	mass_10 + dens_fem_juv	3	127.9239	4.3033	-60.8407	0.0068
53	emerge_day + dens_rel	3	128.0361	4.4155	-60.8968	0.0065
54	mass_10 + dens_rel	3	128.2277	4.6071	-60.9926	0.0059
55	emerge_day + dens_nonrel	3	128.3122	4.6916	-61.0349	0.0056
56	mass_10 + dens_nonrel	3	128.3751	4.7545	-61.0663	0.0055

57	emerge_day + mass_10 + dens_nbf	4	128.3915	4.7709	-59.9917	0.0054
58	emerge_day + dens_bf + dens_nbf	4	128.3927	4.7721	-59.9923	0.0054
59	dens_fem_juv + dens_rel + dens_nonrel	4	128.4386	4.8180	-60.0152	0.0053
60	mass_10 + dens_bf + dens_nbf	4	128.4753	4.8547	-60.0336	0.0052
61	emerge_day + dens_bf	3	128.4934	4.8728	-61.1255	0.0051
62	emerge_day + fem_dens	3	128.5097	4.8891	-61.1336	0.0051
63	mass_10 + fem_dens	3	128.5959	4.9753	-61.1767	0.0049
64	mass_10 + dens_bf	3	128.5988	4.9782	-61.1782	0.0049
65	emerge_day + mass_10	3	128.6075	4.9869	-61.1825	0.0049
66	emerge_day + dens_fem_juv + num_sis + dens_nbf	5	128.6158	4.9952	-58.9986	0.0048
67	emerge_day + mass_10 + num_sis + dens_nbf	5	128.6232	5.0026	-59.0023	0.0048
68	emerge_day + num_sis + dens_bf + dens_nbf	5	128.6270	5.0064	-59.0042	0.0048
69	dens_fem_juv + num_sis + dens_bf + dens_nbf	5	128.6611	5.0405	-59.0213	0.0047
70	mass_10 + dens_fem_juv + num_sis + dens_nbf	5	128.6755	5.0549	-59.0285	0.0047

71	mass_10 + num_sis + dens_bf + dens_nbf	5	128.6878	5.0672	-59.0346	0.0047
72	emerge_day + dens_fem_juv + dens_nonrel	4	128.9852	5.3646	-60.2885	0.0040
73	mass_10 + dens_fem_juv + dens_nonrel	4	129.0923	5.4717	-60.3421	0.0038
74	emerge_day + dens_fem_juv + dens_bf	4	129.1428	5.5222	-60.3673	0.0037
75	dens_fem_juv + num_sis + dens_rel + dens_nonrel	5	129.1686	5.5480	-59.2750	0.0037
76	emerge_day + dens_fem_juv + num_sis + dens_nonrel	5	129.1925	5.5719	-59.2870	0.0036
77	mass_10 + dens_fem_juv + num_sis + dens_nonrel	5	129.2522	5.6316	-59.3168	0.0035
78	emerge_day + fem_dens + dens_fem_juv	4	129.2675	5.6470	-60.4297	0.0035
79	emerge_day + dens_fem_juv + dens_rel	4	129.2882	5.6676	-60.4400	0.0035
80	emerge_day + num_sis + dens_rel + dens_nonrel	5	129.3202	5.6996	-59.3508	0.0034
81	emerge_day + mass_10 + num_sis + dens_nonrel	5	129.3727	5.7521	-59.3771	0.0033

82	mass_10 + dens_fem_juv + dens_bf	4	129.3881	5.7675	-60.4900	0.0033
83	mass_10 + num_sis + dens_rel + dens_nonrel	5	129.3894	5.7688	-59.3854	0.0033
84	mass_10 + fem_dens + dens_fem_juv	4	129.4256	5.8050	-60.5087	0.0032
85	mass_10 + dens_fem_juv + dens_rel	4	129.5425	5.9219	-60.5672	0.0030
86	emerge_day + dens_fem_juv + dens_bf + dens_nbf	5	129.7615	6.1409	-59.5715	0.0027
87	emerge_day + dens_fem_juv + num_sis + dens_bf	5	129.7647	6.1441	-59.5731	0.0027
88	emerge_day + dens_rel + dens_nonrel	4	129.8716	6.2510	-60.7317	0.0026
89	mass_10 + dens_fem_juv + num_sis + dens_bf	5	129.8810	6.2604	-59.6312	0.0026
90	emerge_day + mass_10 + num_sis + dens_bf	5	129.8824	6.2618	-59.6319	0.0026
91	emerge_day + fem_dens + dens_fem_juv + num_sis	5	129.9169	6.2963	-59.6492	0.0025
92	mass_10 + dens_fem_juv + dens_bf + dens_nbf	5	129.9354	6.3148	-59.6584	0.0025

93	emerge_day + mass_10 + dens_fem_juv	4	129.9575	6.3369	-60.7747	0.0025
94	emerge_day + mass_10 + dens_fem_juv + dens_nbf	5	129.9628	6.3422	-59.6721	0.0025
95	emerge_day + mass_10 + fem_dens + num_sis	5	129.9777	6.3571	-59.6796	0.0024
96	emerge_day + dens_fem_juv + num_sis + dens_rel	5	129.9842	6.3636	-59.6828	0.0024
97	emerge_day + mass_10 + num_sis + dens_rel	5	129.9878	6.3672	-59.6846	0.0024
98	mass_10 + fem_dens + dens_fem_juv + num_sis	5	129.9882	6.3676	-59.6848	0.0024
99	emerge_day + mass_10 + dens_fem_juv + num_sis	5	130.0469	6.4263	-59.7142	0.0024
100	mass_10 + dens_rel + dens_nonrel	4	130.0478	6.4272	-60.8198	0.0024
101	mass_10 + dens_fem_juv + num_sis + dens_rel	5	130.0696	6.4490	-59.7255	0.0023
102	emerge_day + mass_10 + dens_rel	4	130.1915	6.5709	-60.8917	0.0022
103	emerge_day + dens_fem_juv + dens_rel + dens_nonrel	5	130.3842	6.7636	-59.8828	0.0020

104	emerge_day + mass_10 + dens_nonrel	4	130.4749	6.8543	-61.0334	0.0019
105	emerge_day + mass_10 + dens_bf + dens_nbf	5	130.6017	6.9811	-59.9916	0.0018
106	mass_10 + dens_fem_juv + dens_rel + dens_nonrel	5	130.6464	7.0258	-60.0139	0.0018
107	emerge_day + mass_10 + dens_bf	4	130.6591	7.0385	-61.1255	0.0017
108	emerge_day + mass_10 + fem_dens	4	130.6754	7.0548	-61.1336	0.0017
109	emerge_day + dens_fem_juv + num_sis + dens_bf + dens_nbf	6	130.8274	7.2068	-58.9762	0.0016
110	emerge_day + mass_10 + dens_fem_juv + num_sis + dens_nbf	6	130.8573	7.2367	-58.9912	0.0016
111	emerge_day + mass_10 + num_sis + dens_bf + dens_nbf	6	130.8694	7.2488	-58.9972	0.0016
112	mass_10 + dens_fem_juv + num_sis + dens_bf + dens_nbf	6	130.9083	7.2877	-59.0167	0.0015
113	emerge_day + mass_10 + dens_fem_juv + dens_nonrel	5	131.1950	7.5744	-60.2882	0.0013

114	emerge_day + dens_fem_juv + num_sis + dens_rel + dens_nonrel	6	131.3158	7.6952	-59.2204	0.0013
115	emerge_day + mass_10 + dens_fem_juv + dens_bf	5	131.3422	7.7216	-60.3618	0.0012
116	mass_10 + dens_fem_juv + num_sis + dens_rel + dens_nonrel	6	131.4234	7.8028	-59.2742	0.0012
117	emerge_day + mass_10 + dens_fem_juv + num_sis + dens_nonrel	6	131.4484	7.8278	-59.2867	0.0012
118	emerge_day + mass_10 + dens_fem_juv + dens_rel	5	131.4594	7.8388	-60.4204	0.0012
119	emerge_day + mass_10 + fem_dens + dens_fem_juv	5	131.4643	7.8437	-60.4229	0.0012
120	emerge_day + mass_10 + num_sis + dens_rel + dens_nonrel	6	131.5730	7.9524	-59.3490	0.0011
121	emerge_day + mass_10 + dens_fem_juv + num_sis + dens_bf	6	132.0065	8.3859	-59.5658	0.0009

122	emerge_day + mass_10 + dens_fem_juv + dens_bf + dens_nbf	6	132.0066	8.3860	-59.5658	0.0009
123	emerge_day + mass_10 + dens_rel + dens_nonrel	5	132.0794	8.4588	-60.7304	0.0009
124	emerge_day + mass_10 + fem_dens + dens_fem_juv + num_sis	6	132.1590	8.5384	-59.6420	0.0008
125	emerge_day + mass_10 + dens_fem_juv + num_sis + dens_rel	6	132.2207	8.6001	-59.6729	0.0008
126	emerge_day + mass_10 + dens_fem_juv + dens_rel + dens_nonrel	6	132.6275	9.0069	-59.8763	0.0007
127	emerge_day + mass_10 + dens_fem_juv + num_sis + dens_bf + dens_nbf	7	133.1142	9.4936	-58.9676	0.0005
128	emerge_day + mass_10 + dens_fem_juv + num_sis + dens_rel + dens_nonrel	7	133.6127	9.9921	-59.2169	0.0004