

Density effects on juvenile female dispersal in a population of golden-mantled ground squirrels

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Abstract

Dispersal, the movement of individual from their natal site to breeding sites or between breeding sites, is one of many mechanisms that species establish to increase the gene flow among population. Population density, which associates with competition, can have a great effect on the dispersal rate through increasing resource competition and agonistic interaction between individuals. Observation on an asocial species, the golden-mantled ground squirrel, shows that despite being a species with male-biased dispersal, many females exhibit natal dispersal. In this study, we looked at whether total and local density have any effect of female natal dispersal. We used 25 years of collected data on female juvenile location and activity at the Rocky Mountain Biological Laboratory to test our hypotheses: density has a positive effect on female juvenile golden-mantled ground squirrel dispersal. Our result shown that neither total nor local density have significant effect on dispersal. Thus, it is suggested that other social and environmental factors is the main contribution in the dispersal of this asocial species such as female kin density, food availability or predator presence.

Introduction

The knowledge about relationships between different population within a species is crucial to understand genetic diversity. Dispersal is one of the processes that establish these relationships. Two common types of dispersal in the animal world are natal dispersal, movement of individuals from birthplace to breeding site where they find mate, and breeding dispersal, movement of reproductive individuals from different breeding sites (Howard, 1960; Greenwood, 1980). This movement helps establishing connections between multiple population and increase gene flow as well as genetic diversity of the population. Yet, there is a cost that individuals must face when dispersing such as unfamiliar environment, both ecological and behavioral. The cost of dispersal depends on many factors including mating system, social structures, social behavior, and mate competition (Bryoms and Krebs, 1999). However, there is also a cost if the individual decides to remain philopatric, such as the stress from competition for mates and resources or inbreeding (Wolff, 1994).

In most mammal species, males are the sex that disperse to find mates while females remain philopatric (Wolff, 1993a; Wolff, 1994; Greenwood, 1980). An important component of sociality is the nonsexual social interaction of individuals that living in a group (Lacey and Sherman, 2007). Thus, philopatric females are those that set up the basis sociality of population since all the males disperse away. However, in some male-biased dispersal species, a small portion of females exhibits natal dispersal. Even if this is not a far travel, it could make a different between species with female natal dispersal and those without female natal dispersal. Recently, these dispersals are

classified as plastic behaviors, and many researchers are focusing on the environmental and social causes of this dispersal to understand the evolution of dispersal (Sakamoto et al., 2015; Stamps, 2001).

As a rough measurement for competition, density can affect the rate of dispersal due to resource competition (Wells and Vuren, 2017; Waser, 1985). Yet, the effects of density on dispersal may vary. There are two major hypotheses that attempt to describe the effect of density on dispersal. The first is positive dispersal which states that competition for mate and resources in high-density sites increase the chance of dispersal (Murray, 1967; Matthysen, 2005). This theory can also be interpreted as social intolerance between individual in a high-density population. Some example mammal species that exhibit positive dispersal are the red squirrel, red deer, Olympic marmot (Matthysen, 2005; Wauters et al., 2004; Barash, 1973; Albone et al, 1992). On the other hand, the negative dispersal, also known as “social fence” hypothesis, states that high density population reduces dispersal because the immigration of new individuals will increase negative encounters (Matthysen, 2005; Travis et al., 1999). Inversely, this hypothesis also predicts that low density population may increase dispersal as individuals emigrate from population that experiencing Allee effect (Kuussaari et al., 1998). Example of mammal species that exhibit negative dispersal include deer mouse, prairie vole. (Matthysen, 2005). However, this hypothesis is less likely to apply to asocial species.

The golden-mantled ground squirrel (*Callospermophilus lateralis*) is an asocial species that exhibits male-biased dispersal. Even though male is the main disperser in this species, females are also seen to exhibit natal dispersal with unknown cause. Being an asocial species, it is possible that social intolerance is the major cause of female natal dispersal of the golden-mantled ground squirrel (Armitage et al., 2011). Thus, in this study, I will test whether total and local density affect the natal dispersal of female juvenile golden-mantled ground squirrels. I hypothesize that density has a positive effect on female juvenile golden-mantled ground squirrel dispersal. I predict that in years with higher density, female pups would be more likely to disperse. I also predicted that in years with lower density, female pups would be less likely to disperse.

Method

Analysis was performed on long-term collected data about population size and location of individual golden-mantled ground squirrels at the Rocky Mountain Biological Laboratory (RMBL) from 1996-2020. For data collection, the population is censused each year from late May to the end of August. We observed, trapped the golden-mantled ground squirrels and noted their identity, activity range, and location in the Gothic town site. Each squirrel was identified by a unique combination of ear tags in both ears and unique dye mark that we put on when we first caught them.

The town site is divided into 6 localities, based on adult female home ranges (Wells & Van Vuren 2017): 1. Town: RMBL administration buildings up to the visitor center; 2. East Gothic: The hills behind Gothic Research Center up to Red Rock cabin; 3. Copper Creek Trail: From the town main road to almost Sage Meadow; 4. Dining Hall: Community Center up to Ore House; 5. Happy Valley: Lead King, Forest Queen, and area west of main road; and 6. Southwest Gothic:

From Barclay to Willey. The locality density of the adult females each year was calculated by using their locality starting from July. We only use the adult females that were seen at least twice, on two different days, in July-August to count only resident and not transient squirrels. For every adult that stay within one locality from July to August, (1) was added to the locality density. If the adult female activity range alternated between two localities, (0.5) was added to each locality density. Total density of each year was calculated by a sum of all female densities in the 6 localities.

Locality of yearling juvenile female after her first hibernation was collected and compared with natal locality to determine whether individual female juveniles dispersed from or remained philopatric in their natal locality. We used logistic regression model in R with dispersal is a binary variable and year as a random effects to account for unobserved variation of the environment among years. If the pup moved out of its natal locality, it was counted as dispersal (1). If the pup did not move out of its natal locality, it was counted as philopatry (0). We looked at the effect of both total and local density on the dispersal of yearling juvenile female. We only looked at female yearlings whose dispersal status could be confirmed. Hence, this is an underestimate of dispersal, as we were not able to count females who survived to their yearling spring but left the study area, but a good estimate of philopatry.

Results

There were total of 408 female juvenile squirrels recorded from 1995-2020 within the study area. By their yearling spring, 80 (20%) of these squirrels were philopatric, 18 had dispersed within the townsite, and 310 disappeared from the town site with unknown reason (predation, overwinter mortality, or dispersal). Out of 98 of juvenile female squirrels recorded with known philopatric status, 18.4% of the females dispersed and 81.6% of them were philopatric.

Total density effect on dispersal

Total adult female density from 1996 to 2020 ranged from 3 to 23 squirrels. There was no clear relationship between total density and percent juvenile female disperse (Figure 1). Linear regression showed a slightly negative relationship between the total female density and percentage of juvenile female dispersers, but total female density explained very little of the variation in juvenile dispersal ($\beta = -0.535$; $R^2 = 0.014$; Figure 2).

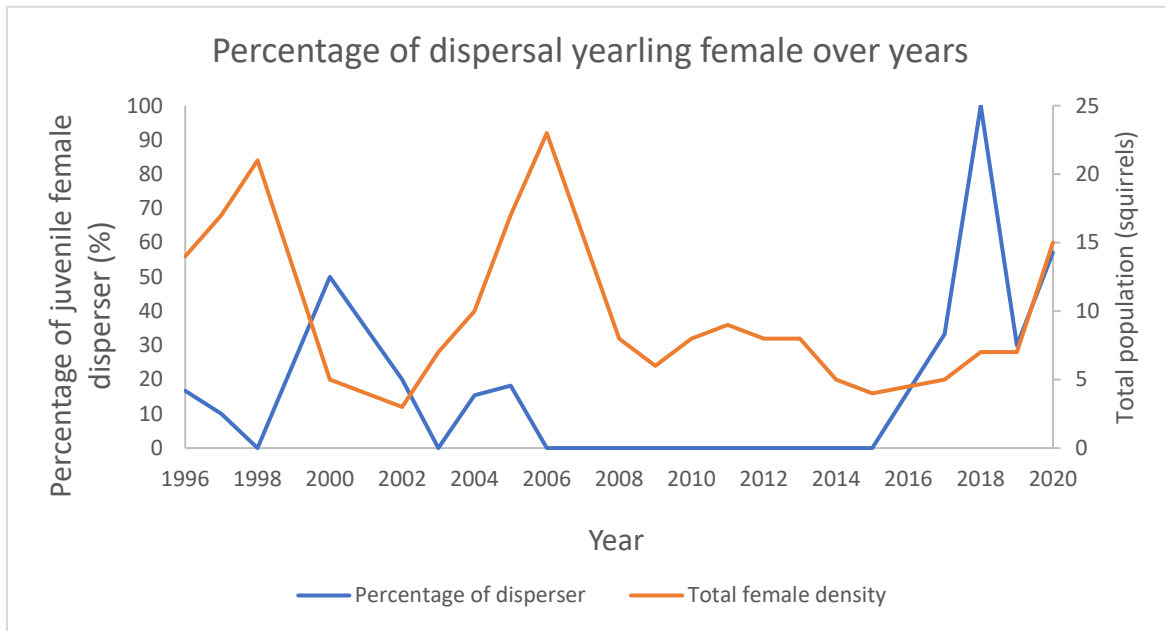


Figure 1: Percent yearling dispersal (blue line) and total female density (orange line) from 1996 to 2020

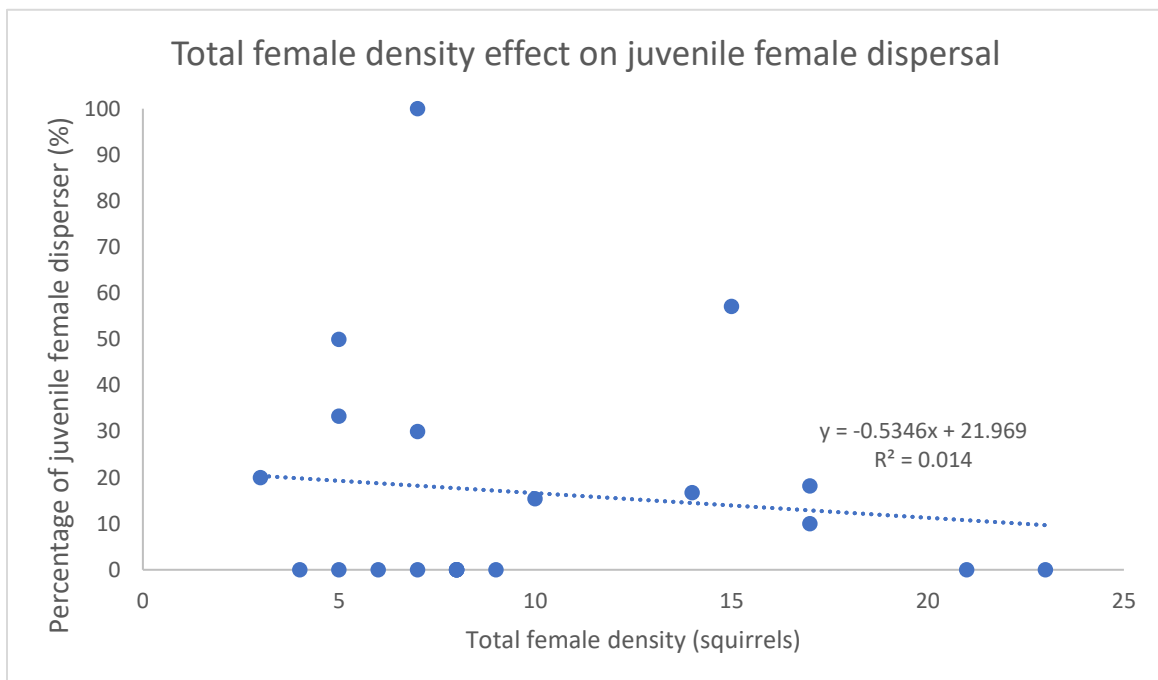


Figure 2: Effect of total female density on female juvenile dispersal

Local density effect on dispersal

Local female density ranged from 0-8 adult females. Linear regression showed that there was no relationship between local female density and the dispersal of yearling juvenile female ($\beta = -0.005 \pm 0.021$, $p = 0.83$). Generalized linear regression with year as random effect also confirmed that there was no relationship between local female density and dispersal of yearling juvenile female ($\beta = 0.009 \pm 0.1552$, $p = 0.95$) (Figure 3).

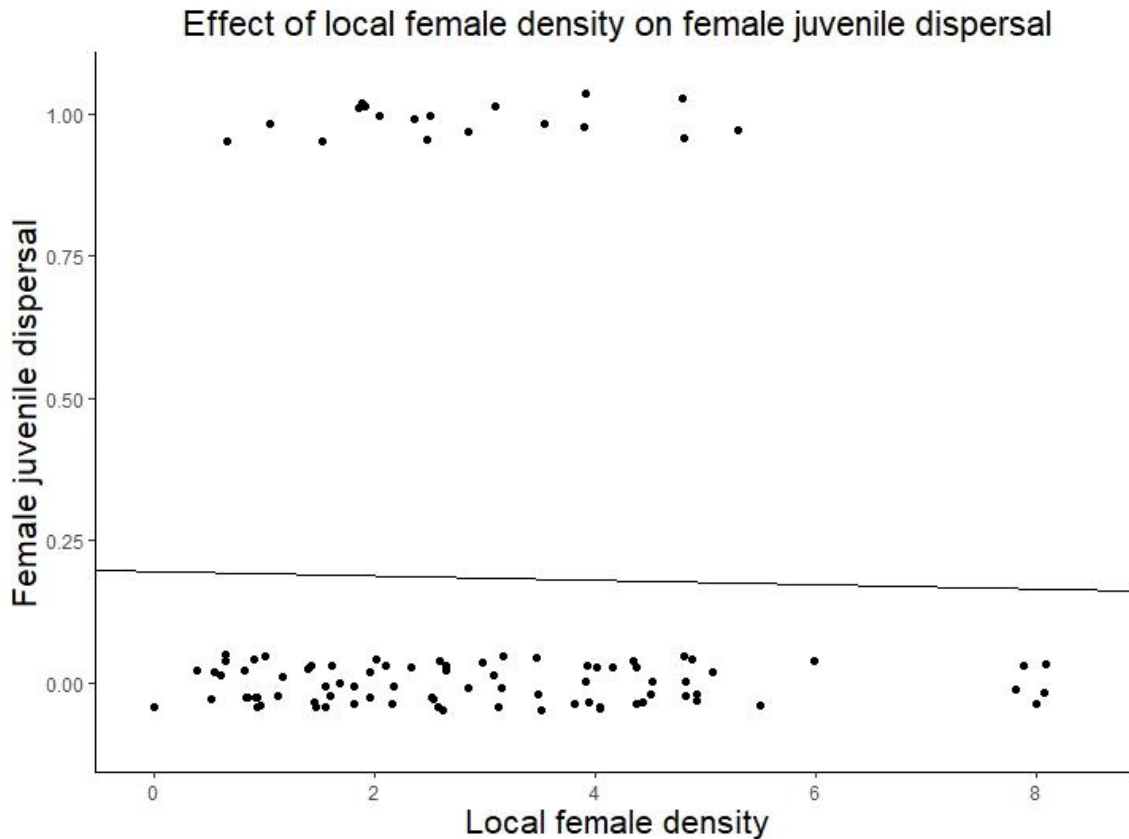


Figure 3: Effect of local female density on female juvenile dispersal from 1996 to 2020

Discussion

Although density-dependent dispersal is common in the mammal world, not all mammal dispersal is affected by density. In this study, 20% of female who had philopatric status at yearling is known dispersed from their born site. However, there was no effect of either total and local density on the dispersal of the female juvenile. Similar observation was also found in the yellow-bellied marmot (Armitage et al., 2011), common shrew (Hanski et al., 1991), and gray wolf (Gese and Mech, 1991). Thus, the effect of density on dispersal of different species is dissimilar. However, there was a limitation in our study since the dispersal of female juvenile squirrel in that we only looked at those who had known dispersal or philopatry status after their first hibernation. About 76% (310

out of 408) of the total female juvenile disappear with unknown cause. These disappearances could be a result of dispersal, accident, overwinter mortality, or predation.

Beside social intolerance, social cohesiveness could be a social factor that affects yearling decision to disperse (Armitage et al., 2011). Positive interaction between young and other individuals that living in the same area could increase their attractiveness to the population, leading to their philopatry (Blumstein et al., 2009). The golden-mantled ground squirrel is a relatively asocial species characterized by agonistic interactions between individuals. Ferron (1985) found that 71% of the interactions in this species were agonistic and most adult interactions with young were agonistic with some exception of neutral behavior between a mother and her young. Thus, these agonistic behavior between the pups and the adults within the locality could be a reason why pups choose to disperse.

Besides agonistic behavior between juvenile and adult females, interaction between the pups and their mother and among the pups could also be a factor that influences yearling dispersal (Ferron, 1985; Armitage, 1981; Jesmer et al., 2011). Even in asocial species, kin relationships can play an important role in female behavior and interaction (Wells and Vuren, 2017). This could be because competition between kin are less intense than between non-kin and there is cooperative interaction between female-kin. Thus, the presence of female kin can induce philopatry (Le Galliard et al., 2006; Schoepf and Schradin, 2012). However, if the juvenile female is living in an area with high kin-density, intense interaction between kin can also increase and lead to the female dispersal. Studies of other asocial species have shown that the maternal presence can affect the dispersal of daughter during breeding season, especially in spring, to avoid breeding competition with its own mother (Sakamoto et al., 2015).

Even though female natal dispersal is suggested to be a common phenomenon in asocial species, little research has been done to understand the cause and of consequences this kind of dispersal to the sociality of the species (Clutton-Brock and Lukas, 2012). By understanding the causes of female natal dispersal, our knowledge about the evolution of dispersal can be further enhanced. One possible cause of dispersal is the increasing of density of the population, which can be understand as increasing resource competition. However, our study suggests that female natal dispersal is not affected by either total and local density in the golden-mantled ground squirrel. Thus, other social and environmental factors - such as female kin density, food availability, presence of predator, or habitat disturbance from another species - could be larger contributors to dispersal. Future work can look at the effect of kin-density on female natal dispersal. Another suggestion is to look at how vegetation change per year affects the dispersal rate.

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