

Investigating Patterns of Juvenile Dispersal in Golden-Mantled Ground Squirrels,  
*Callospermophilus lateralis*

*Student:* Jessica (Yu-Tung) Huang  
and  
*Mentors:* Dirk Van Vuren and Caitlin Wells

Advanced Independent Research  
Summer 2011

## **Abstract**

Dispersal is the permanent relocation of an individual away from its natal burrow. This phenomenon is male biased in many mammal species and potential causes include inbreeding avoidance or resource competition. In this study, the dispersal behavior and exploratory excursion distances were recorded and analyzed for the golden-mantled ground squirrel pups (*Callospermophilus lateralis*) at the Rocky Mountain Biological Laboratory (RMBL). Daily observations of pup distances from natal burrows were recorded and compared between male and females pups and males with their sisters and their non-sisters. There was no difference in mean exploratory travel distances for males and females or the distances between males and their sisters vs. non-sisters. This could be because of high space availability, which may discourage pups from traveling farther than is necessary. An alternative hypothesis is that it is still too early in the active season to know whether or not dispersal will occur. Further studies should be made to know the dispersal behavior more confidently.

## **Introduction**

Dispersal, the permanent relocation away from an individual's natal site, is a central topic in ecology. This phenomenon drives immigration and emigration of individuals and helps small populations avoid deleterious genetic effects (Nunes 2007). Information on dispersal patterns can also be useful for conservation strategies and can serve as a model for other related organisms (Van Vuren 1998). Typical taxonomic patterns of dispersal have been characterized, but there is significant variation in dispersal behavior by species and sex (Greenwood 1980). The drivers of this variation are still unclear. Waser (1985) proposed a null model of dispersal, where juveniles settle in the first vacant home range they encounter; the frequency of vacant home ranges will depend on sex- and species-specific mortality rates. Research in a variety of rodent systems supports the hypothesis that inbreeding avoidance mainly drives dispersal, but other factors like conspecific aggression and resource competition can be important as well (Nunes 2007).

The timing of dispersal may depend on body size energetics. Small mammals such as golden-mantled ground squirrels have relatively small body sizes compared to other mammals (e.g. bears), and so can reach adult size faster; juvenile dispersal in these small-

bodied mammals can occur before the animals' first hibernation (Armitage 1981). Using this model, I expect that the golden-mantled ground squirrels will disperse before their first hibernation. .

Dispersal is usually preceded by exploratory excursions that increase in distance through time until the animal finds an appropriate environment (Neuhaus 2006). More specifically, male mammals tend to travel farther than females in these excursions and males disperse more than females as well (Greenwood 1980). This is called male-biased dispersal and it is the most common pattern of dispersal among mammals. Male mammals are mainly polygynous so they are thought to disperse in order to maximize their reproductive efforts, i.e. finding more unrelated female mates (Greenwood 1980). It is also stated in the Greenwood model that male-biased natal dispersal is a feature of male mammals that defend females as a resource to maximize reproductive success. When a male impregnates one female, he can continue to find another female and impregnate her and so on. By contrast, female reproductive success is maximized by the successful production of healthy offspring. This requires substantial maternal investment in gestation, lactation, and sometimes, additional maternal care after weaning; male mammals generally do not invest as much in their offspring as females do (Greenwood 1980) since they do not physically produce the young and rarely provide paternal care. This maternal investment also contributes to female philopatry, since it is more costly for females to risk dispersal (Guinness *et al.*, 1981). By following this theory, the dispersal trend for golden-mantled ground squirrels should be male-biased.

A well-studied social mammal at the RMBL, the yellow-bellied marmot (*Marmota flaviventris*), displays this pattern of male-biased dispersal and female philopatry (Armitage 1981). It would be interesting to see if this behavior is also present in the golden-mantled ground squirrels, an asocial species. Though the golden-mantled ground squirrels do not live in groups, the local population is still the source of potential mates. In both species, females tend to have a longer reproductive tenure than males (Nunes 2007). In other words, a son's reproductive lifespan may be more likely to overlap with his mother's than a daughter's reproductive lifespan overlapping with her father's. There is less of a chance for female pups to mate with their fathers (since fathers will likely not be present) than for male pups to mate with their mothers; this is the basis of Wolff's hypothesis for male-biased dispersal in

mammals as a mechanism of inbreeding avoidance (Nunes 2007). Thus, I expect that the males will disperse after their exploratory excursions.

Oppositely, it is thought that mammalian females tend to display philopatry because the benefits of staying near their natal area exceed the costs of dispersing. Mothers may want their own daughters in neighboring burrow to minimize conspecific infanticide by other unrelated females (Nunes 2007). By having more relatives around, it also increases safety for each female. A female who disperses runs the risk of not finding a suitable environment to raise her young, let alone sufficient resources to support herself (Greenwood 1980). Having all of these favored conditions (protection, familiarity of individuals and resources), a female can maximize her reproductive success by ensuring that her young will also reach reproductive success (Nunes 2007). A female golden-mantled ground squirrel would generally benefit more by staying near her natal site where she is familiar with her surroundings and the individuals around her.

My research focused on the distances that both female and male juvenile golden-mantled ground squirrels travelled on their exploratory excursions. These exploratory excursions can be used as a proxy to predict likelihood of dispersal. As individual move around, the excursions may result in the permanent relocation, or dispersal, of the individual. So I predict that, on average, males will travel farther than females during these excursions and males will eventually disperse more than females.

## **Methods**

The study was conducted in the Rocky Mountain Biological Laboratory town site in Gothic, Colorado near the East River Valley. My study used individuals born within the town site. Individuals were trapped using a Tomahawk live trap (Model 201, 40.6 x 12.7 x 12.7 cm, Tomahawk Live Trap, Tomahawk, Wisconsin, USA), with sunflower seeds mixed with peanut butter as bait, and given distinct markings that were then used to identify them during observations. Pups were caught immediately after emergence from the natal burrow. Individuals were also given unique ear tags upon first capture-each animal was weighed, and anogenital distance was also measured to determine sex.

Pup behavior was observed during periods of peak activity: from 8:00 to 11:00 and then from 15:00 to 17:00. If more than one litter was out at the same time, I allocated my

time between them by splitting my observation times evenly. Observations were kept at an unnoticeable distance so as to not alter the behavior of any of the individuals. During these observations, I recorded how far the each pup was from their natal burrow using a grid map of the study area. Each grid square is 7 x 7 square meters and each square corresponds to a letter-number code. For each pup, I used the map and a ruler to measure the farthest distance moved. I compared the distances traveled between males and females within each litter and then males and females collectively by standardizing (dividing the distance traveled by the number of days since the pup's emergence) for the different ages of the pups from different litters. After recording the female and male pup travel distances throughout the summer, I found the distance mean for both sexes. I used a student's T-Test to see if there was a significant difference between the two means of the male and female distances. I also calculated the distance between the each male in relation to his sisters and non-sisters to see if the male was traveling farther to avoid inbreeding. For each male and female, I took the most recent recorded location and measured the distance between him and her. I used a student's T-Test to test for significance between the mean proximity of male pups with their sisters and non-sisters.

## **Results:**

For this active season, only four litters emerged out of the expected 10. In the oldest litter, the average female distance was 65.54 meters the average male distance is 73.94. In the second oldest litter, the female pups traveled an average of 57.18 meters and the male pups traveled an average distance of 63.39 meters. The average distances of the female and male pups from the second youngest litter are 64.32 meters and 62.61 meters, respectively. Finally, for the youngest litter the average female distance was 8.75 meters and the average male distance was 14 meters. After standardizing the distances (Table 1), I found that the distances for all the female pups combined was 4.52 meters per day and all the distanced for males combined was 4.47 meters a day.

There was no significant difference in travel rate between males and females (Figure 1). Males did not travel at a faster rate (average distance per day) than females ( $t=0.04387$ ,  $df=17$ ,  $p=0.96552$ ).

In individual 91/65's litter, the largest and oldest litter, the difference between male and female pup distance averages was still not significant ( $t=1.17866$ ,  $df=5$ ,  $p=0.29156$ ).

If inbreeding avoidance drives male exploratory behavior, then male pups should be closer to their non-sisters than to their sisters. I compared the distances traveled between each male pup from each litter with their sisters and then their non-sisters (Table 2, Figure 2 and 3) to see if there was a noticeable distance in their most recent locations. I included all the litters but 91/65's litter because her litter was on the other side of the town site, whereas the rest of the litters were near each other. This would have created a bias in distances to most non-sisters, making the data harder to analyze and interpret. All the males were closer to their sisters than their non-sisters (though not statistically significant), suggesting that they may be dispersing for other reasons than inbreeding avoidance.

## Discussion

The purpose of this study was to determine whether or not males travel farther than females in their exploratory excursions, which can affect the likelihood of dispersal (Greenwood 1980). I found that within three of four litters, the average distance traveled by males was greater than the females. These differences were non-significant, likely due to such a small sample size (e.g.  $n=3$ ,  $n=5$ ), but are consistent with my hypothesis that males will explore farther than females. However, after standardizing distance traveled by the age of the pups, there was no significant difference in the rate of travel by males or females.

Male-biased dispersal has been seen in many mammal populations (Greenwood 1980), but it was not seen in this study. In a study by Jesmer (2011), it is suggested that male-biased dispersal may not be prominent in golden-mantled ground squirrels. The study found that though some individuals may disperse within their first year, there is no clear sex-biased trend of dispersal and that which individuals can be variable due to resource availability or kin relationships (Jesmer 2011)

The observed lack of difference between male and female dispersal rates is consistent with Waser's (1985) null model of dispersal. According to the model, ideally the pups would not disperse at all because the risk – from higher possibility of predation and starvation in unfamiliar environments - is too high. There are fewer risks with staying near the natal burrow where surroundings are familiar and the individuals around are familiar too.

However, this is not possible for asocial, territorial species. Thus, Waser's model also suggests that the pups will settle in the first vacant home range they encounter: they will disperse as far as they have to, but no farther. Since there is a low density of both female and male adults in our population, space should be available nearby the natal burrow. Therefore male and female pups may not have to travel very far before settling in a new area.

Lack of significant patterns between males and female exploratory behavior can be due to many factors like the small sample size that was used. Out of 10 expected litters this summer, only 4 emerged and were able to be included in this study. The absolute distance that was measured may minimize differences between the sexes because of the large variation in litter emergence times: older litters, which had a several week head-start on travel from their natal burrow, contained high numbers of females. Correcting for number of days between emergence and last sighting standardized travel rates (instead of absolute distance) for comparison, but minimized variation.

An alternative explanation is that it may also be too early in the season to see an obvious trend between the male and female pups. Pups may not hibernate until September leaving ample opportunity for dispersal later in the season. Although it may be too early to see a pattern with all the pups, the trend that males move farther at a faster rate than females is apparent in individual 91/65's litter. Even though it is not significant, the trend is there in this older litter and may be heading towards male-biased dispersal.

Another reason could be that dispersal in this population may not be driven by inbreeding avoidance, but by resource and space competition. If the males were traveling farther to avoid breeding with their sisters, there would be a clearer pattern of closer distances between males and their non-sisters than with their sisters. But if there are available resources and space near the natal burrow, then the males might prefer to have those assets for a new location to live. Distance traveled from the natal burrow, however, does not tell us the direction of travel: the distances traveled between female and male pups may be the same, but they could be traveling in opposite directions. If the males were avoiding inbreeding with siblings, then the open space or available resources would not affect their decision to disperse.

Even though we found no significant data that would support that males do explore farther than females, the trend that may lead to male-biased dispersal is still apparent. These

results are preliminary, and we will be able to draw stronger conclusions from data collected closer to hibernation. Dispersal is an important topic in animal behavior; therefore longer studies may be necessary to fully understand the exploratory and dispersal behavior of this species.

## Literature Cited

Armitage, K.B. 1981. Sociality as a Life-History Tactic of Ground Squirrels. *Oecologia* 48:1, 36-49.

Blumstein, D.T., Wey, T, Tang, K. 2009. A test of the social cohesion hypothesis: interactive female marmots remain at home. *Proceedings of the Royal Society B* 276, 3007 – 3012.

Greenwood, P.J. 1980. Mating Systems, Philopatry, and Dispersal in Birds and Mammals. *Animal Behavior* 28:4, 1140 – 1162.

Guinness, F.E., Albon, S.D., Clutton-Brock, T.H. 1981. Parental Investment in Male and Female Offspring in Polygynous Mammals. *Nature* 289. 487-489.

Jesmer, B.R., Van Vuren, D.H., Wilson, J.A., Kelt, D.A., Johnson, M.L. 2011. Spatial organization in female golden-mantled ground squirrels. *The American Midland Naturalist*, 165(1): 162-168.

Neuhaus, P. 2006. Causes and Consequences of Sex-Biased Dispersal in Columbian Ground Squirrel. *Behaviour* 143, 1012-1031.

Nunes, S. 2007. Dispersal and Philopatry *Rodent Societies: An Ecological & Evolutionary Perspective*. Ed. Jerry Wolff and Paul W. Sherman. Chicago: University of Chicago, 2007. 150-62. Print.

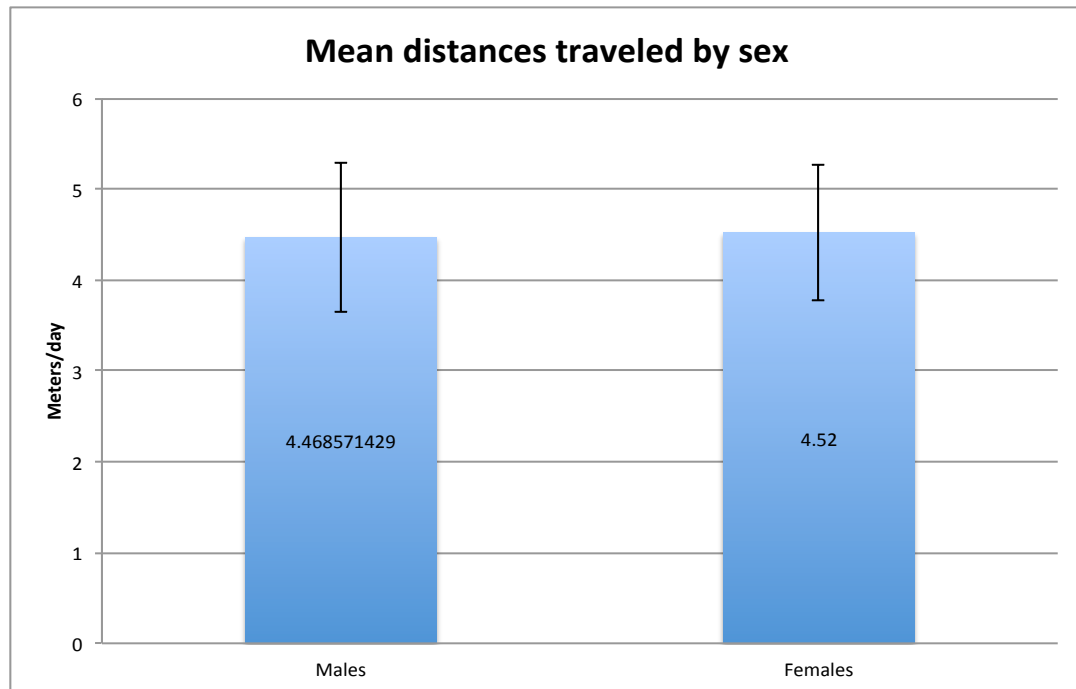
Van Vuren, D. 1998. Mammalian Dispersal and Reserve Design. Pages 369 – 393 in T. Caro, editor. *Behavioral Ecology and Conservation Biology*. Oxford University Press, New York, New York, USA.

Waser, P. 1985. Does Competition Drive Dispersal? *Ecology* 66:4, 1170-1175.

**Table 1: Analyzed data of each individual pup that shows the distances travelled. (In order of litter age, oldest to youngest)**

| Mother ID | Pup ID  | Sex of Pup | Days between emergence and last sighting | Farthest distance travelled (m) | Standardized distance (m/day) |
|-----------|---------|------------|------------------------------------------|---------------------------------|-------------------------------|
| 91/65     | 688/737 | Female     | 22                                       | 49.50                           | 2.25                          |
| 91/65     | 750/738 | Female     | 26                                       | 44.27                           | 1.70                          |
| 91/65     | 692/739 | Female     | 5                                        | 35.69                           | 7.14                          |
| 91/65     | 745/690 | Male       | 4                                        | 35                              | 8.75                          |
| 91/65     | 832/854 | Female     | 19                                       | 63.78                           | 3.36                          |
| 91/65     | 855/833 | Male       | 26                                       | 112.87                          | 4.34                          |
| 91/65     | 834/856 | Female     | 23                                       | 134.47                          | 5.85                          |
|           |         |            |                                          |                                 |                               |
| 812/599   | 835/858 | Male       | 18                                       | 63.39                           | 3.52                          |
| 812/599   | 836/859 | Female     | 20                                       | 63.39                           | 3.17                          |
| 812/599   | 838/860 | Female     | 19                                       | 50.96                           | 2.68                          |
|           |         |            |                                          |                                 |                               |
| 678/886   | 91/78   | Female     | 8                                        | 86.49                           | 10.81                         |
| 678/886   | 743/51  | Female     | 8                                        | 50.48                           | 6.31                          |
| 678/886   | 97/77   | Female     | 12                                       | 56                              | 4.67                          |
| 678/886   | 90/81   | Male       | 12                                       | 62.61                           | 5.22                          |
|           |         |            |                                          |                                 |                               |
| 587/879   | 839/862 | Male       | 4                                        | 7                               | 1.75                          |
| 587/879   | 840/863 | Female     | 5                                        | 14                              | 2.8                           |
| 587/879   | 841/864 | Female     | 1                                        | 3.5                             | 3.5                           |
| 587/879   | 842/865 | Male       | 5                                        | 21                              | 4.2                           |
| 587/879   | 746/52  | Male       | 4                                        | 14                              | 3.5                           |

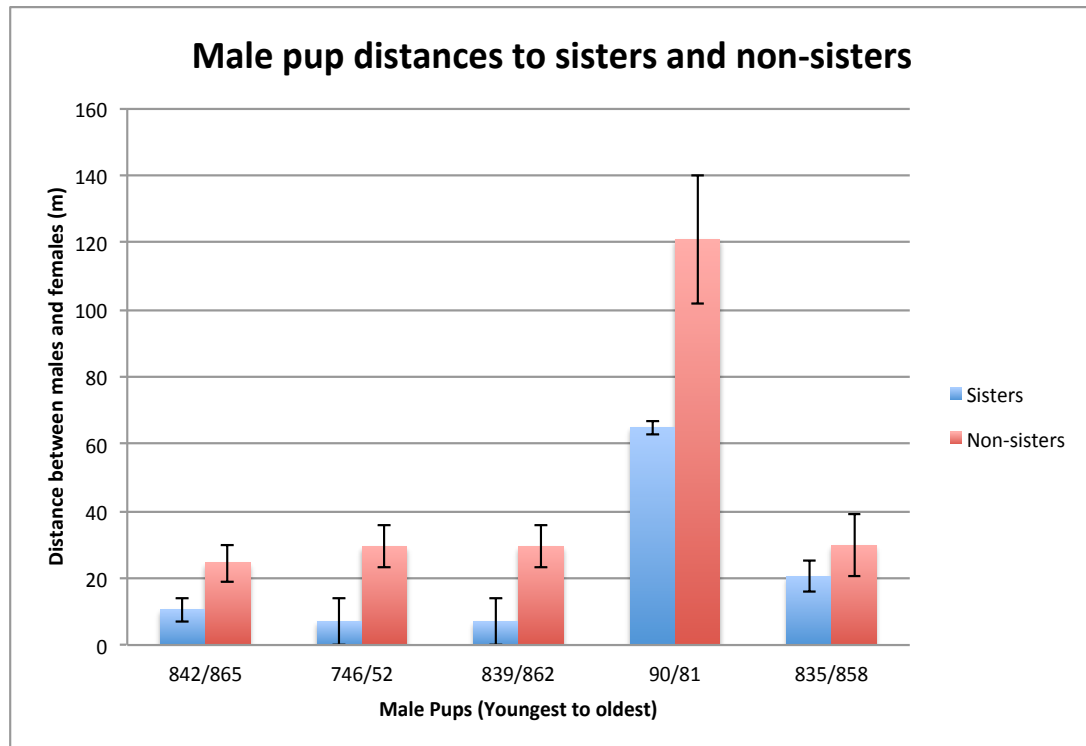
**Figure 1: Mean distance traveled by male and female pups as measured in meters per day from day of emergence to last known location. Male pups did not travel significantly farther from their natal burrow than female pups ( $t=0.04387$ ,  $p=0.9552$ )**



**Table 2: Male distance relative to sisters and non-sisters**

| Male Pup ID | Average distance to sisters (m) | Average distance to non-sisters (m) | T-Test value | Degrees of Freedom | p-value |
|-------------|---------------------------------|-------------------------------------|--------------|--------------------|---------|
| 90/81       | 64.72                           | 120.81                              | 2.48049      | 5                  | 0.05581 |
| 835/858     | 20.45                           | 29.75                               | 0.58668      | 5                  | 0.58290 |
| 842/865     | 10.5                            | 24.47                               | 1.45707      | 5                  | 0.20488 |
| 746/52      | 7                               | 29.27                               | 2.02644      | 5                  | 0.09856 |
| 839/862     | 7                               | 29.27                               | 2.02644      | 5                  | 0.09856 |

**Figure 2: Mean distances between male pups and their sisters and non-sisters measured in meters between their last known locations. Male pups were not significantly closer to non-sisters than to sisters ( $t=1.34$ ,  $p=0.1884$ ).**



**Figure 3: Mean distances of all sisters and non-sisters pooled together shows no significant results. Males were not significantly closer to their sisters than their non-sisters. (This figure goes along with Figure 2).**

