Assessing Cryptic Dispersal and Movement in the Lompoc Kangaroo Rat

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By

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Abstract

Lompoc kangaroo rats (LKR, *Dipodomys heermanni arenae)* are small rodents that reside in sand dunes from Pismo to Orcutt, including the Oceano Dunes State Vehicular Recreation Area (SVRA), in Oceano, CA. In the SVRA, some of these individuals live in habitat islands, which are habitat fragments of dense vegetation disrupted by empty, bare sand in between them. Recreational vehicle activity is permitted in the Oceano Dunes, which has caused persistence habitat fragmentation. Kangaroo rats are known to disperse between habitat islands and are suspected to do so via a special type of dispersal: cryptic dispersal. This dispersal mode, if it occurs in LKR, should be recognizable because first captures of new individuals should not be juveniles, but should be older.

I wanted to see if these LKR do indeed display cryptic dispersal and establish home ranges, despite the anthropogenic habitat fragmentation. Data was collected through quarterly, live trapping sessions, which occurred over a three-day period every three months, and covers multiple years. Individuals were ear-tagged and cataloged into a database. The information gathered from these trappings were used to test my hypotheses. I ran a variety of statistical analyses (t-tests, chi-squares, contingency table) and discovered interesting outcomes.

Heavier, more mature (non-juvenile) male kangaroo rats were commonly trapped as new individuals (i.e., first captures). There was a lack of evidence supporting or refuting a pattern of cryptic dispersal for females. When conducting chi-squares, significance was detected via a disproportionately high subadult new capture (non-juvenile) and recaptures disproportionately attributed to adults. Both of these results reinforce an inference of cryptic dispersal.

I also utilized the dataset to construct visuals to see if movement patterns were present. These visuals enlightened me on age-related time and pattern of movement. For example, new juvenile captures were highest in June, which could reflect seasonal reproduction. Adults were caught most frequently in December which might be the time that they would be fully mature. The lack of new juveniles trapped also backs up cryptic dispersal. The other visuals displayed how kangaroo rats typically stay on one habitat island and do not move to others. The few that did disperse provided interesting contrasts. Subadults did not disperse far distances and went back and forth between islands. Adults dispersed further and more directly; they did not “hop” to and from islands. Collectively, this information helps inform kangaroo rat movement and seemed to support my hypotheses.

Introduction

A common phenomenon in sexually reproducing species is dispersal (Greenwood, 1980). Dispersal can occur either via gametes, as in pollen, or via movement of individuals, as when a bird leaves its natal range. Regardless of the type of movement, this movement is critical for locating new mates, finding necessary resources, and expanding a population's ranges. According to Hargreaves and Eckert, 2013, dispersal is deemed successful if the individuals reproduce after they have moved. This assorts genetic diversity and ultimately influences the population's ability to potentially adapt to changing environmental conditions. There can be many selective pressures that affect why species disperse, but ultimately, dispersal is thought to enhance individual, population, and species level fitness.

Mammals tend to exhibit male-biased dispersal (Greenwood, 1980). There is a debate regarding the explanation for the existence of this bias. Researchers propose that it is an evolutionary mechanism to avoid inbreeding or a factor in avoiding intrasexual competition (Pusey, 1987). It is critical for these organisms to continually diversify so homozygosity does not increase and result in an inbreeding depression. Depending on the breeding strategy of the mammalian species (monogamous, polygynous, promiscuous) different forms of competition between males can drive the less fit individuals to search for mates elsewhere. The social structure of the species is also an important element in determining the varying patterns of dispersal.

One mammalian group of species who exhibits male-biased dispersal are kangaroo rats (*Dipodomys)*. They are known to disperse to neighboring territories during different life stages. These small rodents are fascinating dispersers since they do a specific type of dispersal: cryptic dispersal (Waser et al., 2006). Under cryptic dispersal, subadults or adults are caught during first captures, not juveniles. This age-related dispersal is somewhat novel, and somewhat elusive to detect.

I explored whether a particular species of *Dipodomys, D. heermanni arenae,* the Lompoc kangaroo rat, shows cryptic dispersal. The location of this research was the Ocean Dunes in Oceano, California. These dunes house a variety of species, ranging from migratory birds, lurking predators, and our focal species, the kangaroo rat. This study site also permits recreational vehicle activity, as people can drive and camp throughout the dunes. The introduction of this anthropogenic influence has disrupted the landscape. Habitat fragmentation from vehicular movement has increased chances of animal death, and disruption to dispersal routes. Continuous patches of vegetation have been severed by the riders, which creates gaps in the habitat. Even at the very beginning of the park being open and allowing vehicular recreation, remaining vegetation patches had been fenced off for protection. These fenced off areas are titled habitat islands, as the preservation of these areas is crucial for the wildlife living amongst them.

Habitat islands vary in size and interisland distance, as they are scattered all around the dunes. Immigration and emigration to and from the islands are necessary for maintenance of genetic diversity, gene flow, and resource acquisition increases. These metapopulation dynamics occur in this disjunct landscape, as dispersal is likely required for persistence of the population.

If dispersal could not happen, then the populations on these islands would likely go extinct. A paper written by Waser et al., 2006, states how, "[…] parentage analysis reveals that some offspring evade early detection and move substantial distances before their first capture. In a few cases, the approach even detects dispersal out of the natal 'deme' prior to first capture." Also, when the offspring do return to their home territory, they tend to settle near their natal burrows. This cryptic dispersal phase may be an imperative step for future colonization and survival. With these factors in mind, we hypothesize that Lompoc kangaroo rats display cryptic dispersal and that the first time a kangaroo rat is captured, it will likely not be a juvenile. Regarding their movement in general, we hypothesize that kangaroo rats establish a home range. If that is the case, then adult kangaroo rats will not move far from their familiar islands and, in contrast, subadults will move and explore various islands. In order to test these hypotheses, live trappings over three nights were conducted. The traps were set on multiple habitat islands, as the islands were varying distances from each other. Every individual caught was ear tagged and cataloged.

Methods

The dataset utilized in this research came from live trapping sessions in March, June, September, and December. Capture, mark, release, recapture methodology was performed, as each trapping session was three days in total and occurred at various habitat islands (see figure 2) around the Oceano Dunes, Oceano, CA (see figure 1). There were multiple participants who aided in collecting data, and plots were used to denote a sample section of each habitat island. Each plot was square, with 16 stations in a 4 x 4 array. There were two traps per station. Data collected from the field were then transferred over to an ongoing Excel spreadsheet. The parameters for data collection included identifying survey data, plot/island, observer(s), station number, species type, ID tag number, capture status, gender, age, breeding condition, weight, comments, error notes, and which ear the tag was placed on. I sorted through and isolated the kangaroo rat information. To test if kangaroo rats display cryptic dispersal, I narrowed down my necessary variables of interest to age, weight, gender, capture status, individual ID tag number, plot/island, and station. Age categories were juveniles, subadult pelage, subadult molt, and adults. Juveniles were distinguished by grey pelage and small size. Subadult pelage was distinguished by black hair and lack of grey hair growth on the tip of the tail. Subadult molt was distinguished by distinct molt lines among the body or face of the individual. Adults were distinguished by no molt lines, tufted tail, and coarser, orange, and brown pelage. I ran three statistical analyses on the software R and R studio to confirm or deny the present hypothesis.

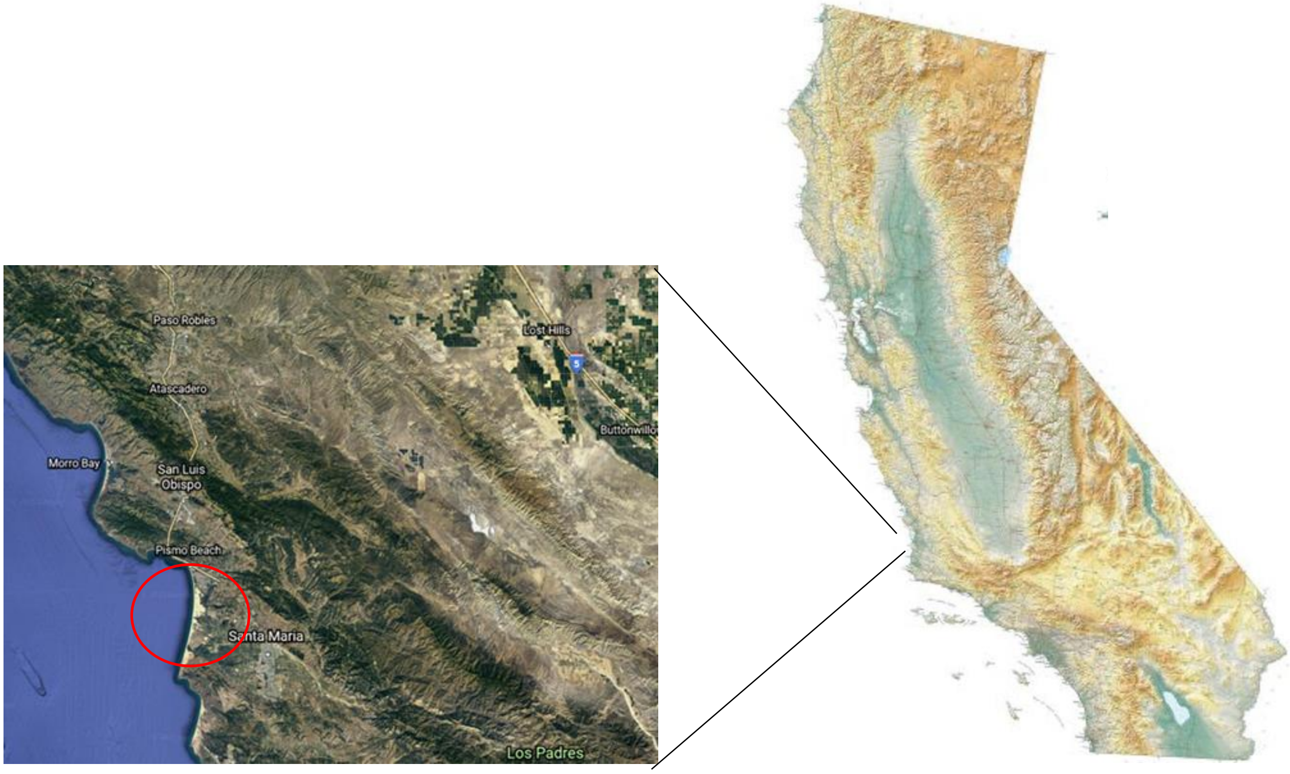

Figure 1: Location of study site. Area circled in red is the location of data collection, the Oceano Dunes State Vehicular Recreation Area in Oceano, CA. Location of Oceano in California is shown on the right.

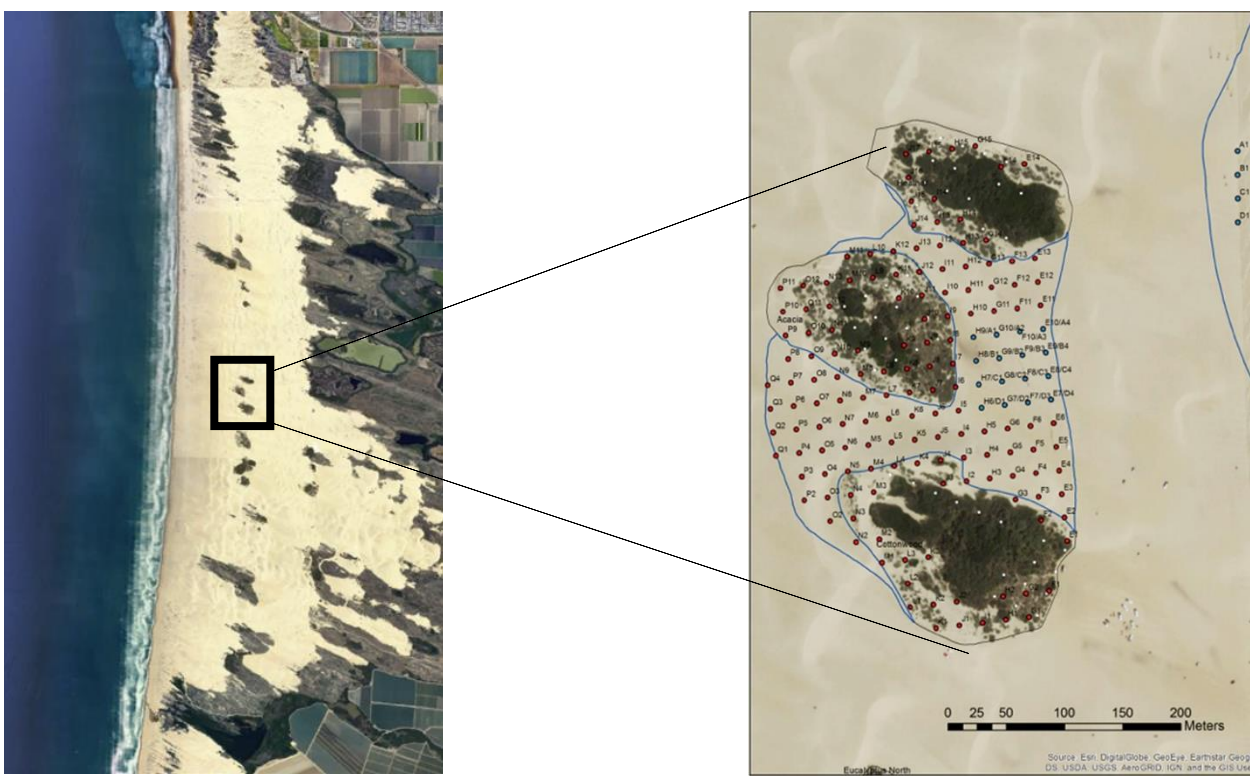

Figure 2: Habitat islands containing sample plots. Left panel, study area showing shoreline, and habitat islands that are inland from the shoreline. Vehicular riding is permitted on both sides of the habitat islands and east of the habitat islands is contiguous habitat. Right panel, enlarged image to distinguish habitat islands more clearly. Trapping stations on islands shown in white and all other points were for trapping between the islands.

The first analysis done was an unpaired t-test. It tested if there was significance between newly captured weights versus all captured weights. Males and females were analyzed separately once again due to sexual dimorphism, as pregnant females were excluded too. Their extra weight from carrying offspring would skew results. Weight was applied under the assumption that young individuals have less mass; this helped reinforce or reject age-specific cryptic dispersal.

To test cryptic dispersal in kangaroo rats one last time, a chi-square calculation was completed. I ran code to find out if the new captures were mostly all adults or if there were other ages overrepresented in the data sample. In order to do so, I counted all of the observed, new captures for juveniles, subadult pelage, subadult molt, and adults and then proceeded to calculate an expected value for all the new captures for the expected variable. R and R studio was utilized for running the calculation and identifying if significance was present.

In order to identify if kangaroo rats establish a home range, a contingency table was required. This table tested if there was significant difference between newly captured individuals versus recaptured individuals for each of the four age groups. In Excel, I utilized the same observed values of new captures for each age group of kangaroo rat and then counted the remaining recaptures. I totaled up the new and recaptured individuals for each age group, and then added each of those totals together to create a grand total. I then transferred it over to an online contingency table calculator to get my results. Upon having results from the contingency table, I continued further by doing four chi-squares comparing new captures versus recaptures on each of the age group categories from the table. I used the same data as provided in the contingency table for the observed and calculated the expected by averaging the total of new and recaptures for each age group. This enlightened me on which specific age(s) had significance and indication of dispersal.

Following the chi-squares, I constructed histograms to provide visualizations of my results. The first figure was a collection of four histograms that displayed trapping months versus number of new catches for each age group. I used the Excel data base to count new juveniles, subadult pelage, subadult molt, and adults were caught in the months of March, June, September, and December. This was done graphically to see if there were patterns of cryptic dispersal or if there were sessions where specific ages happened to be caught more plentifully.

The last visualization was done to evaluate movement in the kangaroo rats. I wanted to see how many rats occurred on more than one island, and if they occurred on more than one island. I also sought out to discover how many islands they potentially travelled to and what pattern(s) were present. In order to do this, I used the Excel data base and sorted everything by ID tag number and then by survey plot. I counted how many rats were on one, two, or more islands and plugged that information into another Excel sheet. I formulated another histogram to see the distribution of these numbers. After the results of that figure, I created maps by age category (adult, subadult) that followed each kangaroo rat's movement from different islands. This gave way to recognizing any dispersal patterns or any "unusual" activity.

Results

The utilization of R and R studio to run the two t-tests comparing weights of newly captured adults and all captured adults were informative. Males and females were tested separately since kangaroo rats display sexual dimorphism. Pregnant females, if any, were also excluded from these analyses since their extra weight would skew the results. There was a significant relationship found between the weights of newly, captured male adults and weights of all male adults (t-test; df=128, n=91, t=4.5771, p=1.101e-05). The weights of all adult males were typically higher, but since there were more newly, captured male weights, the mean of that group ended up being above the others (95% CI= 5.276249, 13.311883). There was not a significant relationship found between newly, captured female adults and all female adults (t-test; df=62, n=49, t=1.2861, p=0.2032).

To further test the potential presence of cryptic dispersal, a chi-square analysis was run to see all ages are captured at the same rate, by comparing capture rates across all of the age categories: juvenile, subadult pelage, subadult molt, adult (see figure 3). Upon constructing a Chi-squared table and running it through R and R studio, significance was detected (Chi-Square= 181.92, n= 208, p= 3.39e-39). This is a good indication that individuals of one or more categorie(s) are captured much more than expected. Further analysis is required to see which age categories are the ones yielding significance. To do so, I constructed a contingency table in Excel (see figure 4) comparing if captures in any age category were disproportionately new (versus recaptures). There was a significant relationship found between newly captured kangaroo rats and recaptured kangaroo rats (Chi-Square= 81.42, n= 731, p= 0.00001) with more recaptures overall. To specifically narrow down the age categories of interest, I performed four chi-squares, one for each age group. There was a significance found in the subadult pelage category (Chi-Square= 6.339, n=115, p= 0.0118), more of which were new than expected, and in the adult category (Chi-Square= 193.979, n= 582, p= 4.3e-44), more of which were recaptured than expected.

	A	B	C
1	Age	Observed	Expected
2	Juvenile	9	52
3	SaPL	71	52
4	SaMo	5	52
5	Adult	123	52

Figure 3: Chi-square input values. Data for first capture of each individual used to identify if first captures were mostly adults or if the other age categories were overrepresented. Juvenile defined by small size and grey pelage. Subadult pelage (SaPl) is older than juvenile and defined by black hair and lack of grey hair growth on the tip of the tail. Subadult molt (SaMo) is older than subadult pelage and defined by distinct molt lines on the pelage. Adult is the oldest age category and defined by a tufted tail. The lack of any molt lines and coarse, orange/brown pelage indicate adult hair has grown in.

	Age Category					
Capture Category	Juvenile	Subadult Pelage	Subadult Molt	Adult		Total
New	9	71	5	123		
Recapture	10	44	10	459		
Total	19	115	15	582		731

Figure 4: Contingency table comparing capture rate by age category and recapture category. Data for new captures and recaptures used to identify if any age groups displayed dispersal.

The construction of histograms regarding age of first capture across trapping sessions in different seasons revealed some particularly important information about the dispersal of the kangaroo rats. There are clear seasonal patterns present during the quarterly/seasonal trapping sessions (see figure 5). Newly captured juveniles are trapped most frequently in June, newly captured subadult pelages are trapped most frequently in June and September, newly captured subadult molts are trapped most frequently in September, and newly captured adults are present in all months, but highest in September and December. This gradual increase in numbers of new individuals caught in the progressing months displays that many individuals are not captured until they have been in the population for 3 to 6 months. For example, subadult pelage and subadult molt would have been in the population three months before they were captured. New adults would have been in the population around six months before they were first captured. This suggests there is a period in which new kangaroo rats are in the population, but are not being captured, which would support a cryptic dispersal hypothesis.

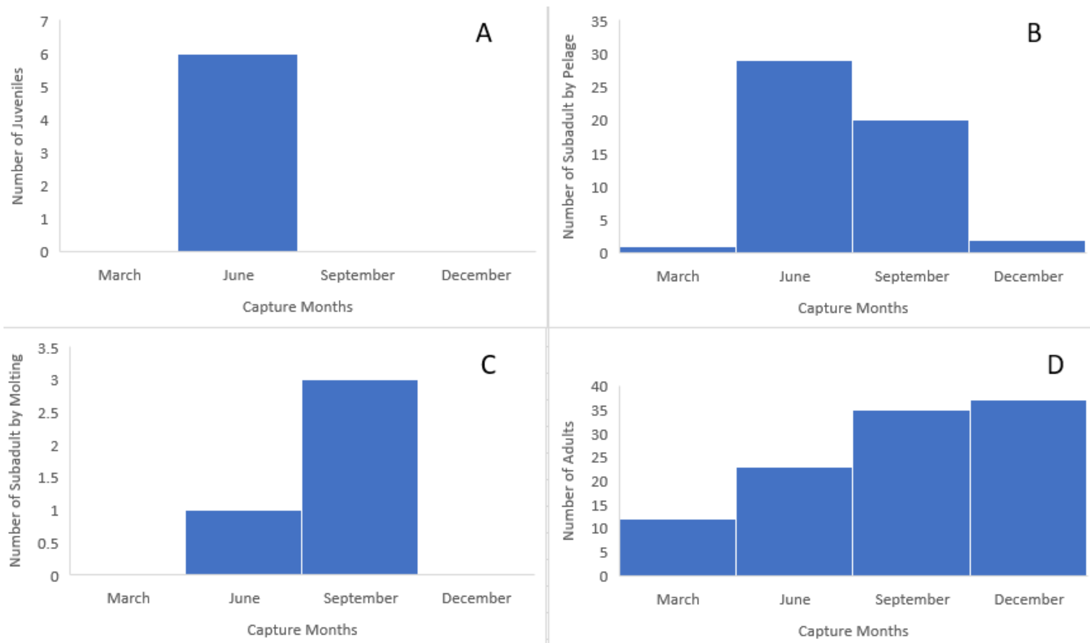

Figure 5: Month of first capture by age category. There are four age categories: juvenile, subadult pelage, subadult molt, adult. Juveniles are the youngest age category and are identified by their grey pelage and small size. Subadult pelage is the next age above juveniles and are identified by the black hair and the lack of grey hair growth on the tip of the tail. Subadult molt is even older than subadult pelage and identified by distinct molt lines on the body. Adult is the oldest age category, and identified by correct pelage color, texture, tufted tail, and hair growth throughout the body. Panel A represents the number of new juveniles caught throughout the quarterly trapping. Panel B represents the number of new subadult pelage caught throughout the quarterly trapping, this was an age category that was captured as “new” more often than expected. Panel C represents the number of new subadult molt caught throughout the quarterly trapping. Panel D represents the number of new adults caught throughout the quarterly trapping, this was an age category that was captured as “recapture” more often than expected. Juveniles show clear seasonality (June). Subadult pelage show clear seasonality (June, September). Transition from subadult pelage to subadult molt shows clear seasonality (September). Adults show increasing frequency of new captures from March to December.

The histogram displaying individual kangaroo rat occupancy at various habitat islands was interesting and helpful to understand if kangaroo rats establish home ranges (see figure 6) or move between habitat patches (as if dispersing). The majority of kangaroo rats stayed on one habitat island and did not disperse to neighboring islands (211 out of 231). The remaining 19 kangaroo rats dispersed to two or three different habitat islands. Some dispersed back and forth to the same ones, but that is dependent on the individual in focus. From the dataset, the majority of kangaroo rats that did disperse to multiple habitat islands were male and in the age categories of subadult and adult.

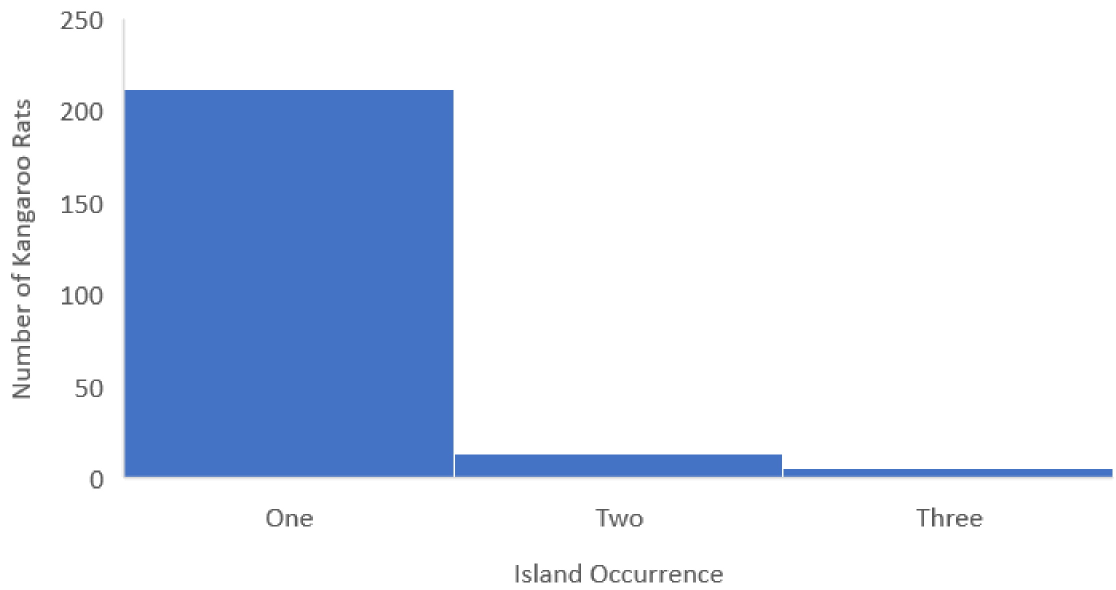

Figure 6: Habitat island use by kangaroo rats. Histogram displaying how many kangaroo rats disperse to two or three islands, or if they stay on one. All age categories pooled. Note, one island does not mean all kangaroo rats were on the same island (could be different). Same applies for multiple islands. 13 out of 231 kangaroo rats moved to two islands and 6 out of 231 kangaroo rats moved to three islands.

The dispersal maps created for adults versus subadults provided fascinating information (see figure 7). These maps show the specific locations occupied by individuals that moved between islands. Adults seemingly are more direct dispersers; they move from their original island to one new island (usually). The distance of their dispersal is much longer than subadults. Subadults disperse to many habitat islands and tend to go back and forth between them. From the visualizations, the patterns of travel are more chaotic. The distance between islands that they visit are much shorter.

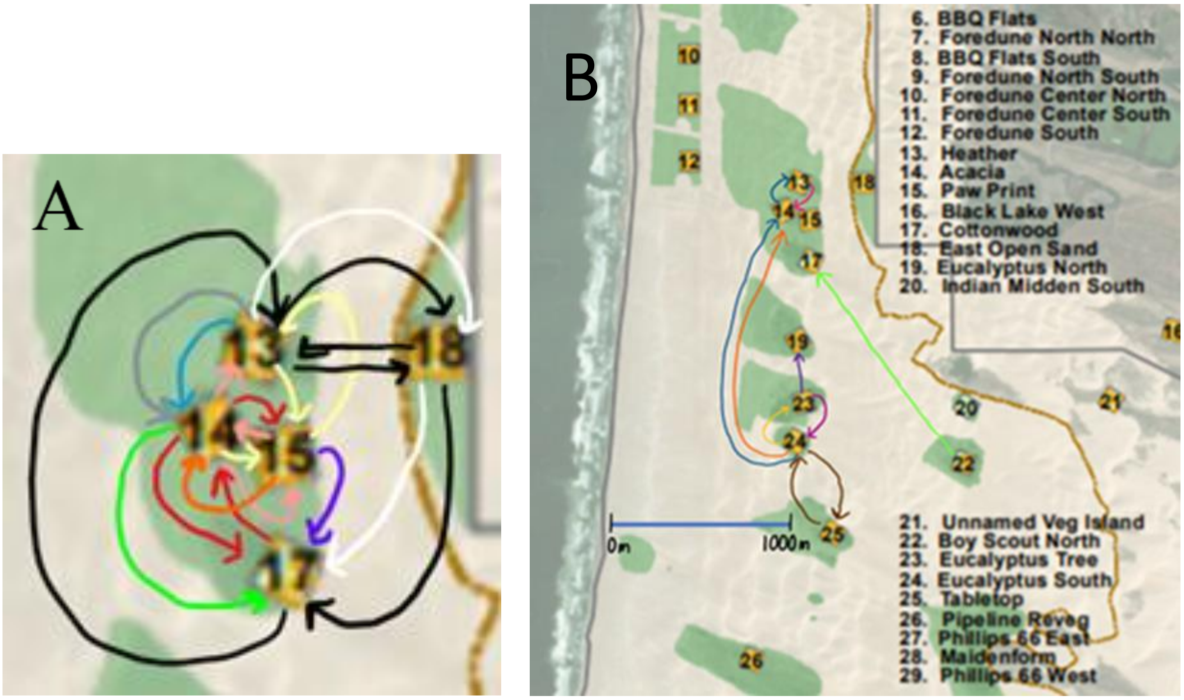

Figure 7: Kangaroo rat movement. Panel A is an enlarged representation of all non-adult kangaroo rat movement. Each colored arrow represents the movement of a different individual between study plots. Island numbers are shown in the figure, and island names are provided for reference. Out of ten individuals, only five visited three islands. The other five only visited one. None visited only two. Four individuals, arrows colored black, yellow, magenta, and pink show repeated movement back and forth between islands. Panel B is adult kangaroo rat movement. Each colored arrow represents the movement of a different individual between study plots. Out of eight individuals, only two visited two islands. The other six only visited one.

Discussion

The results from the first t-test analyses provide great foundation for our hypothesis. Since there was significance found between the weights of newly, captured males and all other males, this gives evidence that heavier, more mature males are commonly caught during the first capture. Cryptic dispersal is built on the notion that juvenile kangaroo rats should not typically be trapped during this age period. Juveniles may not be fit enough to explore their surrounding territories and still might be dependent on their mothers for necessary resources. By having this weight-related first capture statistic, it gives good starting support for this cryptic behavior. The lack of statistical support regarding the weights of newly, captured females and all other females is another good sign for cryptic and male-biased dispersal. Their lack of movement and trapping occurrence reinforces how the females are most likely persisting and residing in their burrows, and how the males are usually the ones dispersing to other habitat islands.

The chi-square analysis comparing capture rates across all age categories was another important element in determining the presence of cryptic dispersal. Significance was detected in this statistical analysis, which is a good indication that a particular age group was captured more frequently than others. This could be due to curiosity of the landscape, searching for mates, avoiding inbreeding, foraging, or any other movement-oriented goals such as dispersal. To provide more clarity on which age groups were specifically causing the significance, a contingency table was created between recaptures and new captures. This helped identify which group(s) were disproportionately caught during the trapping sessions. The results of this analysis were promising, as a significant relationship was found between newly captured kangaroo rats and recaptured kangaroo rats. Four additional chi-square analyses were done for each age group, and significance was found once again in the age categories of subadult pelage and adults. There were more new captures in the subadult category and more recaptures in the adult category, all of which reinforce cryptic dispersal. If dispersal is not cryptic, the new captures should have been disproportionately juveniles. The higher number of new captures of the subadult pelage category provides a potential indication of cryptic dispersal. This could mean that at this stage, the kangaroo rats are already developed enough to disperse on their own. This age category is also "one step" older than juvenile, which makes sense for the increased new captures. Once the juveniles are mature enough, they finally go off on their own, and are therefore trapped during sessions. Traps would be a completely new element in their environment and could cause curiosity. Since the traps are baited, these subadults could be intrigued by the presence of accessible food. The significance from recaptured adults also provides more support for cryptic dispersal. These individuals are clearly old enough to be moving amongst the habitat islands and might have enough knowledge to know that the traps provide food, temporary shelter, and impending freedom. Either way, the fact that the slightly older age category is providing such a spike in new captures and that adult recaptures are high is another solidification for cryptic dispersal in kangaroo rats.

Information from the first histogram (see figure 5) was enlightening on potential age-related behaviors due to the apparent aging across groups. Since juveniles are highest in June, that potentially signifies the reproductive season of the kangaroo rats. It also reflects cryptic dispersal since some adults are caught at a higher number than juveniles; this implies that the juveniles are somewhat cryptic and not discovered until later. The seasonal reproduction could be a huge determining factor for the increase in population size in the future months. The large amount of subadult by pelage kangaroo rats in June could be a signal that there is a short aging phase from juveniles and how they are more exploratory. Subadult by molt was the least frequently caught age group of kangaroo rats, but the transition into adults was fairly quick in terms of time. Perhaps these molting individuals are hard to capture since they grow into their adult forms faster than we trap. The adult age category has a wide distribution across the months with the highest individual count, and there is speculation of why. It could be possible that the newly captured adults in the months of September and December come from the reproduction season, whereas in March, those individuals could be from dispersal, or could represent survivorship from the year before.

The histogram (see figure 6) exhibiting kangaroo rat occupancy at the various habitat islands was informative regarding their movement. Since the majority of kangaroo rats stayed on one habitat island, this could indicate that home ranges are potentially built around natal burrows. The neighboring islands could also be too far, which would only allow the most fit and capable individuals to make the voyage. This might deter certain individuals since the risk of death or injury from dispersing is high. From the dataset, it was found that subadults and adults were the age groups that dispersed to multiple islands. This reinforces the idea of cryptic dispersal because juveniles showed no movement. Also, these age groups that are dispersing could be further indications of male-biased dispersal in the population. Due to the lack of juveniles moving amongst islands, it could be inferred that the mothers are tending to their young. If this is the case, then the individual dispersing should be predominantly male.

Dispersal maps (see figure 7) of subadult kangaroo rats and adult kangaroo rats provide stark differences in their movement. Visually, the adults seem to disperse in more direct pathways that are longer in distance. Adults may be strong enough to go further than subadults. Also, these adults could be dispersing further away to avoid inbreeding. Since they are in the most mature form, it is crucial that they do not interbreed with their relatives. Population fitness would decrease because of inbreeding and could cause future genetic abnormalities if inbreeding persisted. Subadults tend to disperse shorter distances and move back and forth between habitat islands more frequently. This could be building experience for the subadults while also familiarizing them with surrounding territories. Perhaps they are still somewhat reliant on their natal burrows or mothers for resource accessibility.

Each result from the statistical analysis has been critical in supporting our hypotheses. Kangaroo rats seemingly display cryptic dispersal phases, with the juveniles being “hidden” from our trapping sessions. The increase in frequency of new captures being subadults and recaptures being adults further reinforces this type of dispersal. The lack of female capture supports male-biased dispersal and cryptic dispersal. Despite the success from the statistics, there are some possible errors. The dataset from this project was not for an abundant sample size. Our sample size was fairly small, so more data would be helpful in providing stronger evidence for these hypotheses. Some kangaroo rats were excluded from the analyses (misinformation, missing tags, etc.) which could have skewed the results. Since the sample size is so limited, every kangaroo rat plays a role in the statistics.

Kangaroo rats are fascinating rodents that display metapopulation dynamics. Species as such fluctuate in population size due to immigration and emigration. They occupy a certain habitat island, may experience extinction depending on success of occupancy, and will recolonize over time if they find better resources. With this in mind, movement is large part of this species’ biology. Our data collection was done in the Oceano Dunes State Recreation Area, which pose many threats to the kangaroo rats and their movement patterns. Since vehicles are allowed throughout the dunes, this can disrupt dispersal routes or even kill some species if they are in transit. This can cut off vital resources or access to mates. Since there is male-biased dispersal, the loss of males could reduce reproduction in the upcoming seasons if death is high from the recreational vehicles. Dispersal phases could be shifted due to the timing of when vehicles are allowed in the state park. Eventually, it could isolate some habitat patches to the point that gene flow is discontinued. Either way, this is extremely detrimental for this species and could cause further population decline. Dispersal phases are vital for not only kangaroo rats, but many sexually reproducing species. It is the way to discover new territories, find new mates, acquire needed resources, and establish home ranges. These organisms rely on the capability of movement to survive.

It is possible that our data could support additional hypotheses. Kangaroo rats partake in a behavior called the dear enemy effect. This is when territorial animals become friendlier with their immediate neighbors. Boundary disputes eventually calm down as rivals become "dear enemies". Newly arriving individuals that are going to challenge the territory are met with far more aggression than known rivals in nearby territories. Kangaroo rats are territorial creatures, and their dispersal patterns could be altered because of this effect. This might influence which islands kangaroo rats move to, and perhaps why the subadults go back and forth between islands so much. Due to their younger age, they do not have enough experience to have long standing relationships with other competing males. The mature adults could be exhibiting more aggression to these younger individuals and could have become acquainted with other adults through time.

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