

Juvenile Dispersal in *Peromyscus Boylii*

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Abstract Using trapping data from two breeding seasons, I examined dispersal in juvenile *Peromyscus boylii* (*P. boylii*) at Hastings Natural History Reservation (HNHR) in Monterey, California. Female and male juveniles were analyzed separately to test for differences in dispersal between sexes. Dispersal distance was determined by the distance from where the animal was first trapped (presumed place of emergence from nest) to where the animal was first trapped in a reproductive state. These distances were compared to the diameter of an average adult home range calculated by 95% kernel estimates of home range size. Dispersers were juveniles that traveled greater than the diameter of an average adult home range. Of 50 juvenile females that were examined, six (12.0%) were found to be dispersers. Of 35 juvenile males, three (8.57%) were dispersers. There are three possible explanations for these results: 1. dispersal is not important to *P. boylii*, 2. dispersal is important, but not when resources are abundant, or 3. that dispersal is important, but it occurred outside the time period of the data collection.

Introduction

Dispersal is the permanent movement of an organism away from its birthplace (Lidicker 1975). There are three major components of dispersal: leaving the natal site (emigration), traveling across unfamiliar territory (transience), and settling into a new home range (immigration) (Wolff 1994). These components inflict costs and constraints on individual dispersers such as energy expenditure for traveling, increased predation risk, or the possibility of being forced to settle in a habitat of inferior quality. Since most mammals exhibit dispersal behavior there must be reasons and/or benefits that would cause an animal to abandon their natal territory, which is presumably suitable habitat. Possible reasons for dispersal could include being forced away by conspecifics or avoiding inbreeding. Possible benefits for dispersal could be higher status in a new group or living in a more productive habitat.

Dispersal has wide-ranging effects on many levels of organization – the individual, population, and species. For the individual, survival, growth, and reproductive success can all be influenced by dispersal or the lack thereof (Ran 2001). Results from a study on *Crocidura russula* show a direct dependence of dispersal on reproductive opportunities in first-litter juveniles (Favre *et al.* 1997). Furthermore, Getz *et al.* (1994) found that dispersers of *Microtus ochrogaster* survived longer than philopatric individuals (those that remain in their natal territory). At the population level, demography, structure, and dynamics can potentially be affected by dispersal. Krohne and Hoch (1999) completed a landscape-level study on *Peromyscus leucopus* and found that dispersal constantly homogenizes the separate demographics of metapopulations. For the species, dispersal can have an effect on persistence, evolution, and distribution. For example, a study of 27 holarctic species of rodents found that dispersal serve colonization and reparation purposes to maintain a stable existence (Lukyanov 1999). Additionally, dispersal maintains both genetic variability and gene flow between subpopulations (Boonstra *et al.* 1987). Dispersal can also play an important role in behavioral and social systems (Wolff 1993).

For several decades dispersal and philopatry have been studied within mammals. During this time several explanations for dispersal have been suggested for the diverse taxa studied. Researchers often find it difficult to distinguish between two or more of these explanations

because they are often not mutually exclusive. For example, related species could potentially have a different reason for dispersal such as social system as well as population density.

Sometimes dispersal is found to be caused by intraspecific competition, where juveniles are inferior competitors compared to experienced adults and are driven out of their natal home range. Competition can arise due to scarcity of resources, like food and nest sites, or even scarcity of potential mates (Ribble 1992, Byrom and Krebs 1999, Loew 1999). Inbreeding avoidance is also a major cause of dispersal (Wolff 1993, Getz and Carter 1998, Loew 1999, Perrin and Mazalov 1999). Associated with inbreeding are potentially negative genetic consequences such as heterosis and expression of recessive, deleterious alleles (Loew 1999). Dispersal can be influenced by characteristics of a species, for example, the range and level of intraspecific differentiation (Lukyanov 1999). Female dispersal behavior can simply be influenced by the distribution of food throughout the environment, while male dispersal behavior can simply be influenced by the distribution of females (Lurz *et al.* 1997).

Each of these explanations for dispersal may differ between sexes, giving rise to sex-biased dispersal. Sex bias is common in mammalian dispersal. Among mammals, male-biased dispersal is the most common due to the predominance of polygynous mating systems. In polygynous mating systems females remain philopatric where the quality of habitat is proven to ensure that there are enough resources to raise their young; while males put their effort into mating with multiple females and benefit by dispersing over large areas to maximize the number of mating encounters (Ribble 1992).

The genus *Peromyscus*, commonly known as deer mice, is distributed over much of North and Central America and is found in a variety of habitats (Hall 1981). *Peromyscus* are generalist omnivores with a longevity of less than two years. Within the genus *Peromyscus*, research on dispersal has been conducted for only four species (*P. californicus*, *P. leucopus*, *P. polionotus*, and *P. maniculatus*). Ribble (1992) found that dispersal in the monogamous *P. californicus* (Dewsbury 1988) was female-biased with females dispersing significantly greater distances than males. *P. polionotus* is another monogamous species (Foltz 1981) and it is represented by dispersal that shows no sex bias (Swilling and Wooten 2001). *P. leucopus* is characterized by male-biased dispersal (Krohne *et al.* 1984) and has a mating system that ranges from polygyny to promiscuity to facultative monogamy (Wolff 1989). The last species of *Peromyscus* for which studies on dispersal have been completed is *P. maniculatus*. *P. maniculatus* has a promiscuous

mating system (Birdsall and Nash 1973) and has been shown to exhibit male-biased dispersal (Fairbairn 1978).

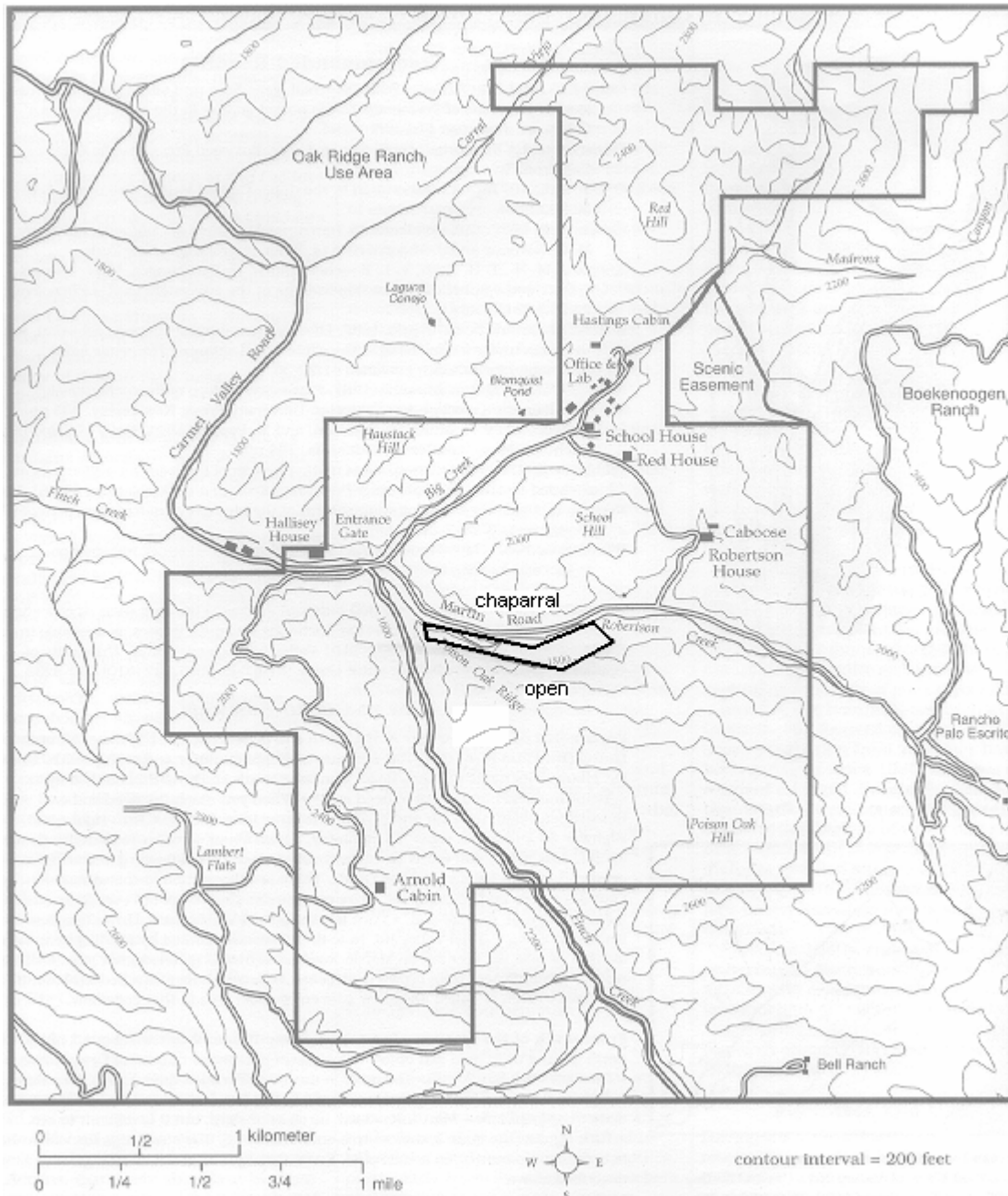
P. boylii, the brush mouse, is distributed over most of the southwestern United States and Mexico. The mean weight of a reproductive female is 25 grams. In Monterey County, CA this mouse is associated with poison oak/oak riparian woodland. The habitat selection and diet preferences of the brush mouse suggest that this mouse is a specialist on coast live oak (*Quercus agrifolia*; Kalcounis-Rueppell and Millar 2002). In coastal California this specialization is thought to be one of the factors limiting the species' distribution to oak woodland and oak brush. Although little is known about dispersal patterns in the brush mouse, its breeding system is characterized by promiscuous mating by both males and females (Kalcounis-Rueppell 2000). At relatively high population densities (>40 adults/ha) neither males nor females are territorial. Also, there is no paternal care or long-term pair bonds between parents. Furthermore, there is behavioral and genetic evidence for multiple mating by both males and females.

The purpose of this study is to determine the pattern of dispersal in juvenile *P. boylii*. Given the promiscuous breeding system of *P. boylii* I predict a male-biased dispersal pattern, similar to the other promiscuous species within the genus *Peromyscus*. To test this hypothesis I used existing live-trapping data from Kalcounis-Rueppell and Millar (2002) and Geographic Information Systems (Environmental Systems Research Institute 1996) to estimate dispersal and examine dispersal patterns for juvenile *P. boylii*.

Methods

The data used for my analysis consisted of trapping records that used mark and recapture techniques to monitor a population of *P. boylii* at HNHR during 1997 and 1998. The weight, sex, whether juvenile or adult, day of capture, and reproductive condition was determined for every trapped animal. Each newly captured mouse was pierced with a unique metal tag through the ear in order to identify recaptures. One live trapping grid was used, located along Robertson Creek within Madrone Canyon of HNHR in Monterey County, California (36° 12' N, 121° 33' W; Fig. 1). The grid was chosen based on the habitat present that is favorable to *P. boylii*. Live trapping occurred at least weekly from 25 December 1996 to 25 March 1997 and 24 December 1997 to 3 April 1998. The Robertson Creek grid had a trap configuration of 4 x 34 with an adjacent side grid of 6 x 13 (Fig. 2). The traps were spaced 10 meters apart from one another.

Each trap station had one Sherman trap and one Longworth, which are variations of box traps. All traps were baited with rolled oats. Grids were trapped at least weekly, which allowed for a



determination of pup emergence and place of first reproduction for the animals that stayed on the grid.

Figure 1. Map of Hastings Natural History Reservation. The trapping grid is outlined in the middle of the map. Types of habitat surrounding the grid are labeled. Map by Eric Rainbolt and Emily Prud'komme.



Figure 2. Robertson Creek Trap Grid. Each point represents a trapping station. (3 cm = 100 m)

In this study the trapping data was examined to determine if natal dispersal was present in either sex. For each individual that was captured as a juvenile and later as a reproductive adult, the distance was calculated from the site it was first captured to the site it was found to first be reproductive (50 juvenile females and 35 juvenile males met these standards).

Adult home ranges were calculated using 95% kernel home range estimates with the animal movement extension in ArcView 3.2 (Hooge and Eichenlaub 1997, ESRI). Kernel home ranges are a probability measurement and are considered the most robust of the probabilistic techniques (Hooge 1999). A 95% kernel represents an area where there is a 95% probability that the animal is inside that area; it is regarded as the area of active use. Individuals that were captured at least 10 times, all as an adult, were used to calculate home ranges (17 females and six males were used for these calculations). Home ranges were assumed to be circular and a diameter was calculated for each area and then averaged over females, males, and all adults. A juvenile was considered a disperser if the distance calculated above was greater than the diameter of an average adult home range. Using the average adult home range to determine the status of dispersers probably overestimates the level of dispersal in the population because it assumes that a juvenile only moves one home range distance away from where it was born to disperse.

Despite this, this method of assessing dispersal has been used in similar studies of dispersal patterns in small mammals including *Peromyscus* (Swilling and Wooten 2001).

Chi-square calculations were performed to test for the presence of sex bias in natal dispersal, assuming that there was no difference in movement between female and male juveniles (StatSoft 2000). I also used chi-square tests to determine if the sex ratio of emerged young (male:female) was the same as the sex ratio of juvenile young that were later captured as reproductively active individuals, in order to establish if there appeared to be any undocumented dispersal (by my method described above). Levels of alpha at .05 and below were considered significant.

Results

P. boylii was captured 940 times in the 1996-97 season and 1,651 times in the 1997-98 season.

Average movement (\pm 1 standard error) of juvenile females was 29.2 m \pm 9.3 and average movement of males was 20.5 m \pm 8.6 (SAS Institute Inc. 1999). The average movement of all juveniles was 25.6 m \pm 6.5.

Mean home range size calculated by 95% kernels for females was 1,789.3 m² \pm 843.2, for males was 6,661.3 m² \pm 4314.9, and the combined average was 3,060.3 m² \pm 1301.6. The corresponding diameters of these home ranges were 35.3 m \pm 8.0, 71.7 m \pm 25.9, and 44.8 m \pm 9.3 respectively.

Nine (18.0%) females dispersed and two (5.71%) males dispersed when comparing juvenile movement with adult home ranges of their own sex. If the overall average diameter of home ranges (44.78 m) is used for determination of dispersal then six (12.0%) females and three (8.57%) males dispersed. There was no statistically significant difference between female and male dispersal when comparing juvenile movement with adult home ranges that correspond to its own sex ($\chi^2 = 2.40$, $p = .879$) or when comparing juvenile movement to the overall average diameter ($\chi^2 = .231$, $p = .369$). When comparing average movement of all juveniles and overall average home range size, juveniles dispersed on average .57 home range diameters.

The sex ratio of emerged juveniles used for the analysis was 1:1.4 (males:females). A total of 163 (81 males and 82 females) individuals were captured as juveniles but never trapped in a reproductive state. The sex ratio of all trapped juveniles was 1:1.13. There was not a significant difference between these sex ratios ($\chi^2 = 1.08$, $p = .7$).

Discussion

I found that juveniles of *P. boylii* at HNHR did not disperse and the pattern of no dispersal was similar between males and females. Three explanations can be derived to interpret these results. The first is that *P. boylii* adopts a strategy of natal philopatry and dispersal is not important. Second is that dispersal is important but only when resources are limiting. And the final explanation is that juveniles do disperse but the data was faulty in the sense that it could not reveal dispersing individuals. It is unlikely that dispersal is not important to this species. It is rare for small mammals not to display some kind of natal dispersal, especially with a promiscuous mating system. I believe this to be the least probable explanation out of the three, because past studies on dispersal within the genus *Peromyscus* have all showed natal dispersal for species with promiscuous mating systems. If there was never any dispersal, eventually the species would suffer through extreme mate and resource competition.

A more likely explanation is that juveniles are not showing any dispersal because the habitat is not saturated with individuals because of abundant food and nest resources in the years of this study. In a study completed in the same area from which the data originated, Kalcounis-Rueppell and Millar (2002) found that *P. boylii* was a specialist on coast live oak, and the years of this study were above average mast years. Furthermore, during this study, both males and females were not territorial against any conspecifics (Kalcounis-Rueppell 2000). If there is no territoriality and the habitat is of high quality, juveniles are able to remain near their natal territory without reducing the availability of food and nest sites. Nothing is forcing the juveniles to disperse, such as competitive adults. If resources do become limiting then juveniles may start to disperse to other suitable habitat so that intraspecific competition does not become a problem. If *P. boylii* is temporarily philopatric then mate competition and/or inbreeding could arise at low densities. However, the high quality of the habitat should be able to sustain a large enough population so that mates are not limiting and unrelated individuals are always nearby. Since the mating system is promiscuous, the defense of mates (and their territories) may not be as important as the quality and quantity of mates. This social system may reduce local competition for resources and preclude dispersal. This question would be interesting to address in years of low acorn production and at varying population densities.

The data may not be complete enough to make any conclusions about natal dispersal. When using trapping data to monitor movement there is always the problem of not being able to trap animals outside of the grid. However, *P. boylii* is limited to riparian habitat and the trapping grid follows the riparian corridor with barriers of unsuitable habitat above and below the grid (Kalcounis-Rueppell 2002). Directly north of the grid is a dirt road and a steep chaparral covered hill. Directly south of the grid is open grassland habitat and a paved highway (Fig. 1). If juveniles are dispersing off the grid, then they are moving along the length of the grid. Since juveniles have to move along the length of the grid there is a good chance of trapping them as they move this considerable distance, unless they emerge as pups near the ends of the grid. There is still the possibility of long distance dispersers that were not accounted for by the trapping data.

Another issue is that data was only collected for approximately three months that encompassed the peak breeding season (late December to late March or early April) out of each year (1997 and 1998). The juveniles could very well be dispersing at the tail end of the breeding season or during the summer. Juveniles could be waiting for a period of time (as long as three months) after emergence to disperse. This would mean that dispersal might occur with individuals that can reproduce, which is possible, but rare among small mammals.

Of all juveniles trapped, 67% were trapped as a juvenile but never trapped in a reproductive state. These individuals could have dispersed outside of the grid, become trap-shy, died, or been captured at the very end of the season and not given enough opportunities to be trapped again. Interestingly, there is a difference in the sex ratio between individuals that were tracked from juvenile to adult and individuals trapped only as juveniles (1:1.4 and 1:1.13, male:female respectively). The difference is not significant but it suggests that newly emerged male juveniles are either dispersing more or dying more than newly emerged females. The difference, I believe, is due to dispersal since it is not likely that there would be sex specific differences in mortality rates for newly emerged juvenile *Peromyscus*. Also this would result in the species fitting among the other models of male-biased dispersal in promiscuous *Peromyscus* sp. Therefore, although I believe that it is probable that I missed some male dispersal in my analysis, my study highlights variation in juvenile dispersal among *Peromyscus*; and suggests the need for long term studies to address variation in dispersal within *P. boylii* at different resource and population densities, and using alternate methods such as radio-telemetry to assess dispersal behavior.

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