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## DISPERSAL IN A MONOGAMOUS RODENT, *PEROMYSCUS CALIFORNICUS*<sup>1</sup>

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**Abstract.** In view of theoretical interest in the relationships between mating systems and dispersal patterns and the paucity of empirical data on dispersal in monogamous mammals, I studied natal dispersal in the monogamous rodent *Peromyscus californicus*. Genealogical relationships were determined using fluorescent pigment transfer and DNA fingerprinting, and dispersal distances were determined using dispersal fences and intensive trapping. Minimum dispersal distances were greater for females than for males. Philopatric males (those settling within one home-range diameter of their birth site) tended to be from smaller litters than non-philopatric males. Minimum dispersal distances of males were positively associated with natal litter size at weaning, whereas minimum dispersal distances of females were positively associated with number of sisters in the natal litter. These results suggest that intrasexual mate competition drives female dispersal, while resource competition drives male dispersal. Males remain closer to their natal range than females, most likely to acquire and defend resources to attract females. *Peromyscus californicus* is unusual among mammals in displaying both a monogamous mating system and female-biased dispersal.

**Key words:** dispersal; female-biased dispersal; male-biased philopatry; mate competition among females; mating system; monogamy; *Peromyscus*; philopatry; social influences on dispersal.

### INTRODUCTION

Dispersal is commonly recognized to be male biased in mammals and female biased in birds (Greenwood 1980, 1983, Dobson 1982, Anderson 1989, and references therein). Most of the hypotheses generated to account for sex-biased dispersal rely on either (1) resource competition, (2) intrasexual mate competition, or (3) inbreeding avoidance (see review by Johnson and Gaines 1990). One of the most widely adopted explanations for the difference in sex bias between mammals and birds is that proposed by Greenwood (1980, 1983), who argued that the bias towards male dispersal in mammals is due to the predominance of mate defense or polygynous mating systems. With polygynous mating systems, females invest more time and energy in their offspring than males, and would benefit from remaining philopatric to an area proven to have sufficient resources for successful reproduction. Males maximize reproductive success by mating with multiple females, and should disperse for both social (competition for mates from dominant older males) and genetic (inbreeding avoidance) reasons. In contrast, male-biased philopatry in birds is the result of monogamous or resource-defense mating systems. Males must acquire and defend resources to attract

females, which is probably best accomplished near the natal range.

Dobson (1982) expanded this theme by examining dispersal patterns among mammals with different mating systems. He predicted that in monogamous mammals natal dispersal should be similar between the sexes because competition for mates and/or resources would be similar for both males and females. He tested this hypothesis by examining dispersal patterns among mammals with different mating systems. For the 12 monogamous species for which dispersal information was available, Dobson's prediction was generally supported (11 of 12 species; but see Caley 1987).

More recently Anderson (1989) proposed the Resident Fitness Hypothesis (RFH) to account for dispersal patterns in rodents. He asserted that among monogamous rodents juvenile males should settle nearer the natal home range than with polygynous species because there would be less competition for mates between father and son. The lack of competition in this case is due to higher male investment in offspring and more certain paternity in monogamous males compared to polygynous males. Anderson also predicted that juvenile females could be more subject to paternal aggression in monogamous species than in polygynous species.

In practice, the study of dispersal in small rodents has been hindered by an inability to identify dispersing individuals reliably and by the vast amount of variation in the behavior and proximate motivation of dispersing individuals (Dobson 1982, Lidicker 1985, Jones

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1987). Ideally, a complete understanding of dispersal in any species requires knowledge of the genealogical relationships between individuals, correct identification of dispersing individuals, and knowledge of their ultimate fate. Comprehensive data from unmanipulated, natural populations are rare (Jones 1987, Lidicker and Patton 1987, Shields 1987).

The objective of this study was to examine natal dispersal patterns of a monogamous rodent, *Peromyscus californicus*, in natural populations. Data on biparental care (Dudley 1974, Gubernick and Alberts 1987, 1989), long-term association of mated pairs (Ribble and Salvioni 1990), and exclusivity of mating (Ribble 1991) indicate that *P. californicus* is monogamous (Dewsbury 1988). In this study I determined the parental relationships of all juveniles, using a combination of fluorescent pigment transfer and DNA fingerprinting (Ribble 1991). I then identified dispersing individuals with the use of dispersal fences and intensive mark-recapture trapping. I also compared persistence and reproductive history between mice of known origin (short-distance dispersers) and mice of unknown origin that immigrated into the study populations (long-distance dispersers).

#### METHODS

I conducted this study from June 1987 through April 1990 at the Hastings Natural History Reservation, Monterey County, California. In this area, *P. californicus* is found primarily along canyon bottoms and north-facing slopes dominated by *Quercus agrifolia*, *Umbellularia californica*, and *Aesculus californica*. The climate of Hastings is mediterranean (James 1966), with most of the rainfall (mean: 52 cm) occurring between November and April. The primary breeding season of *P. californicus* begins with the onset of winter rainfall and extends until early summer (Ribble 1990).

*Peromyscus californicus* was studied on two trap grids which were located 2 km from each other in different canyons. One grid (the Robertson Creek grid, Grid RC) was located along a permanent creek and remained relatively mesic throughout the year, while the other grid (the Madrone Canyon grid, Grid MC) was located along an intermittent stream that typically became xeric during the summer and fall months. Grid RC was a  $\approx 6 \times 11$  array of trap stations while Grid MC consisted of a  $6 \times 14$  array. Both grids had 10-m spacing between trap stations. From June 1987 through August 1989 I trapped each grid for five consecutive nights each month. During each trapping session, two large ( $8 \times 9 \times 23$  cm) Sherman traps were set and baited with rolled oats at each trapping station. Traps were set each day just prior to sunset, checked 2–3 h after sunset, and checked again at sunrise the following morning. All *P. californicus* were identified with numbered, metal ear tags, and classified as juveniles, subadults, or adults from pelage characteristics (McCabe and Blanchard 1950). Females were considered repro-

ductive once they became pregnant, and males were considered reproductive if they were mated to a reproductive female, judging from transfer of fluorescent pigment (Ribble and Salvioni 1990). After the conclusion of the primary portion of this study in August 1989, I trapped each grid for two to four nights at least three different times from September 1989 through April 1990.

The sizes of the two trapping grids were not the same due to the habitat configurations of the two trapping areas. In order to compare mouse abundance between grids, density (mice/ha) estimates were calculated using the mark-recapture estimation procedures in the CAPTURE computer program (Otis et al. 1978). Comparisons between CAPTURE and other density-estimation methods can be found in Montgomery (1987). Density estimates were generated only for trapping sessions in which  $>4$  *P. californicus* were captured. The CAPTURE program assumption of demographic closure (no births, deaths, immigration, or emigration) was usually satisfied during each 5-d trapping session (Ribble 1990). Although CAPTURE can incorporate variable capture probabilities into its estimates (the Heterogeneity, Behavioral response, and Time models; White et al. 1982), the "null" model, which assumes no variation in capture probabilities, was selected as the most appropriate model for most censuses (Ribble 1990), and I used the null model throughout this study for consistency. In those cases when the null model was not selected as the most appropriate, the null model estimate was within the 95% confidence interval of that of the selected model. For those trapping sessions on Grid MC with  $\leq 4$  mice, I recorded density as the number of marked *P. californicus* divided by the area of the grid with a 10-m boundary strip. Ten metres was the mean strip width calculated by CAPTURE on Grid MC during low density (5–7 mice tagged; Ribble 1990). The number of tagged mice on Grid RC was always  $>4$ .

Genealogical relationships of newly trapped juveniles were determined from October 1987 through December 1989 using a combination of fluorescent pigment transfer (Dickman 1988, Kaufman 1989) and DNA fingerprinting, as described in Ribble and Salvioni (1990) and Ribble (1991). All juveniles with known ancestry are considered "juveniles of known origin" throughout this study. I classified all other newly tagged subadult or adult mice captured at least three times on the trap grids as immigrants (i.e., mice of unknown origin and ancestry).

Date of birth for the juveniles of known origin was calculated from a regression of age against mass based on 11 juveniles with known birth dates. I included from one to three repeated mass measures on each juvenile in a linear regression analysis of age against mass ( $n = 23$ ; range of masses: 15.5–37.5 g). The calculated linear regression equation (age =  $-19.62 + 8.01$  (mass);  $r = 0.89$ ,  $P < .01$ ) was used to estimate birth dates because

it accounted for more of the variation in age ( $r^2 = 0.79$ ) than did an allometric predictive model ( $Y = aX^b$ ;  $r^2 = 0.76$ ).

In October 1987 I initiated studies of natal dispersal with the use of dispersal fences, which were erected 50–70 m down- or upstream from each trap grid. The other sides of the grids were bordered by grassland, oak savannah, or chaparral, which were not frequently used by *P. californicus* (Ribble 1990). The distances between the trap grids and the dispersal fences were designed to be  $>1$  home-range diameter of a typical *P. californicus*. The average home-range size of mature *P. californicus* is  $1161 \text{ m}^2$  (2 SE = 511,  $n = 16$ ; Ribble and Salvioni 1990). Home-range size does not differ between the sexes. Assuming a circular home range, 40 m represented one home-range diameter. The fences were constructed of 0.5 m high aluminum sheet metal and extended 50–70 m across all habitat utilized by *P. californicus*. Throughout this study I set and baited a sufficient number of Sherman traps along both sides of the fences to prevent capture success from exceeding 50% each night. Dispersal fences were trapped on average 57% of all nights each month from October 1987 through July 1989. Passageways every 10 m were left open when dispersal fences were not being trapped to allow mice to move freely through the fences. I also regularly trapped between the trap grids and dispersal fences to monitor any mice living in these areas.

Every individual captured was recorded and released on the opposite side of the fence. This procedure did not force dispersal. Mice could return to the side of capture by going around the end of the fence, entering a trap the next night, or going through passageways if the fences were not being trapped the next night. I assumed lactating females had a litter in a nest on the same side they were captured, so they were released on the side of capture.

I conducted a trapping survey extending as far as 1 km up- and downstream from each grid in May 1988 and 1989 in order to document long-distance dispersal by juveniles of known origin. Traps were baited and set at measured 20-m intervals for two consecutive nights. The location of each tagged *P. californicus* was recorded relative to the nearest trap grid.

I recorded dispersal distances only for those juveniles of known origin from trap grids that were (1) captured at or beyond a dispersal fence and did not subsequently appear on the trapping grid, or (2) captured as an adult. The only exceptions were four juveniles of known origin that were born next to the dispersal fences. Two of these juveniles matured and remained near the fence, and two dispersed across the trap grid and were eventually trapped beyond the opposite dispersal fence. Dispersal distances were calculated as the straight-line distance from the birth site (Ribble and Salvioni 1990) or the center of the natal range, to the center of the adult home range or the most distant trap location (dispersal fence or beyond). Mice

that were captured beyond the dispersal fences and classified as reproductive were judged to have successfully settled on a home range. The dispersal distances recorded for some juveniles captured at or beyond dispersal fences were probably underestimated since these mice could have dispersed further. Hence, the dispersal distances reported in this study should be considered minimum dispersal distances.

I compared dispersal distances with either Mann-Whitney  $U$  tests (for 2-group comparisons), or Kruskal-Wallis  $H$  tests (for  $>2$ -group comparisons; Sokal and Rohlf 1981). All percentages were tested with  $G$  tests adjusted with Williams' correction factor. Means throughout are reported  $\pm 2$  SE, and statistical significance was accepted at  $P \leq .05$ .

## RESULTS

Population densities of *Peromyscus californicus* generally increased each winter and spring during the rainy season and then subsequently decreased during the summer and fall (Fig. 1). Densities varied both within and among years on both grids, although the total variation tended to be greater on Grid RC (Grid RC cv = 81%; Grid MC cv = 64%). Densities on Grid MC ranged from a high of 24 mice/ha in April 1988 to a low of 1 mouse/ha in August 1987. Densities on Grid RC ranged from 26 mice/ha in April 1988 to 1 mouse/ha in October 1987.

From October 1987 to December 1989 I ascertained matrilineal relationships for 114 juvenile mice (64 from Grid RC and 50 from Grid MC) based on transfer of fluorescent pigments. I confirmed genetic relations for 98 of these juveniles using DNA fingerprinting (Ribble 1991). Sixteen juveniles were not confirmed with DNA fingerprinting due to lack of blood samples, but their maternal assignments were assumed correct for the purposes of dispersal analyses. Average litter size at weaning ( $\pm 2$  SE) was  $1.75 \pm 0.18$  (median and mode = 2, range: 1–3). The overall sex ratio (0.9 male: 1 female) at weaning was not significantly biased ( $\chi^2 = 0.32$ ,  $P < .45$ , 1 df). The observed frequencies of litters with various sex compositions did not significantly differ from that expected with a 1:1 sex ratio for either litters of two ( $n = 29$  litters;  $\chi^2 = 3.4$ ,  $P > .10$ , 2 df) or three ( $n = 10$  litters;  $\chi^2 = 2.8$ ,  $P > .40$ , 3 df). Average mass and calculated age upon first capture in the field were  $20.0 \pm 1.0$  g and  $42.0 \pm 2.9$  d, respectively, for the 114 juveniles of known origin.

I recorded minimum dispersal distances for 45% (51/114) of juveniles of known origin (Table 1, Fig. 2). The remaining 55% disappeared and were never captured as mature individuals. Of the mice that dispersed known distances, males and females differed in dispersal distributions (Fig. 2; Kolmogorov-Smirnov test,  $P < .02$ ), with males moving significantly shorter distances than females (Table 1). These intersexual differences indicated that dispersal was sex dependent, with females being more vagrant than males. The maximum re-

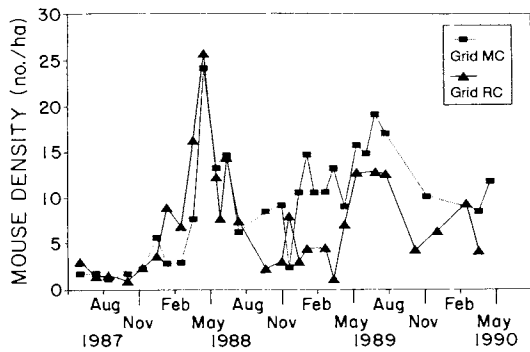


FIG. 1. Population density estimates of *Peromyscus californicus* on livetrapping Grid MC and Grid RC from 1987 to 1990 at the Hastings Natural History Reservation, California. Density estimates were calculated with the CAPTURE computer program using the null model (Otis et al. 1978). Monitoring of dispersal patterns began in October 1987.

recorded dispersal distances were 450 m and 791 m for males and females, respectively. All of the distances  $< 2$  home-range diameters were recorded for mice that had matured and established an adult home range. Sixty-seven percent (4/6) of males and 43% (6/14) of females that dispersed  $> 2$  home-range diameters from their birth site had matured and established an adult home range (Fig. 2).

Persistence on trap grids was calculated among juveniles of known origin as the number of days from birth to the last day the mouse was known to be alive on the trap grid. This measure excluded any days known alive beyond the dispersal fences. Male persistence tended to be greater than female persistence, but not significantly so ( $P = .10$ ; Table 1). The approximate age at dispersal, calculated as persistence on trap grids for 20 juveniles of known origin captured either at or beyond dispersal fences, was  $81.0 \pm 7.8$  d (range: 41–110). Age at dispersal did not differ between males ( $77.5 \pm 10.8$ ,  $n = 6$ ) and females ( $82.4 \pm 10.3$ ,  $n = 14$ ; Student's  $t = 0.57$ ,  $P = .58$ ).

Almost one half of males (48%; Fig. 2) remained within one home-range diameter of their birth site. Most of these males (11/13; 85%) were from litters with one or two offspring, whereas most males that dispersed  $> 1$  home-range diameter were from litters with three offspring (8/14; 57%). This effect of litter size on male dispersal tendency was significant ( $G = 5.0$ ,  $P < .05$ ). The proportion of males remaining within one home range was not significantly associated with either number of males ( $G = 0.9$ ,  $P > .5$ , 2 df) or the number of females in the natal litter ( $G = 1.6$ ,  $P > .3$ , 2 df). In contrast to males, relatively fewer females remained within one home-range diameter of their birth site (29%; Fig. 2). The proportion of females remaining within one home-range diameter of their birth site was not associated with litter size ( $G = 1.3$ ,  $P > .5$ , 2 df), number of males in the natal litter ( $G = 0.9$ ,  $P > .5$ ,

2 df), or number of females in the natal litter ( $G = 1.7$ ,  $P > .3$ , 1 df).

I compared dispersal distances of juveniles with known ancestry from litters with different litter sizes and numbers of same- or opposite-sexed siblings (Table 2). Males from larger litters tended to disperse farther than males from smaller litters ( $P = .06$ ; Table 2), because males from litters with three offspring at weaning dispersed significantly farther than males from litters with two offspring ( $U = 31$ ,  $P = .02$ ). Male dispersal distances did not significantly vary with the number of males or females in the natal litter. In contrast to males, female dispersal distances did not change with litter sizes (Table 2). Dispersal distances were significantly greater for females from litters with two females at weaning than those with only one female. The variance in dispersal distances was also greater for females from litters with two females (cv = 99%) than those from litters with one female (cv = 68%; Table 2). Furthermore, dispersal distances of females were also significantly greater for litters in which two females survived to dispersal age (mean  $\pm 2$  SE =  $245 \pm 126$  m, median = 188 m,  $n = 8$ ) compared to litters in which only one female survived to dispersal age (mean  $\pm 2$  SE =  $110 \pm 94$  m, median = 60.8 m,  $n = 16$ ;  $U = 25$ ,  $P = .02$ ).

Lastly, I examined the Spearman's rank-order correlations between dispersal distances and density (in mice per hectare; Fig. 1) at dispersal age, and between dispersal distances and the number of days from dispersers' own birth to the birth of their mother's subsequent litter. Male dispersal distances increased insignificantly with density ( $r_s = 0.33$ ,  $P < .10$ ). Female dispersal distances decreased insignificantly with the number of days to their mother's next litter ( $r_s = -0.40$ ,  $P < .10$ ).

Of all the juveniles of known origin with known dispersal distances, 46% (11/24) of females and 52%

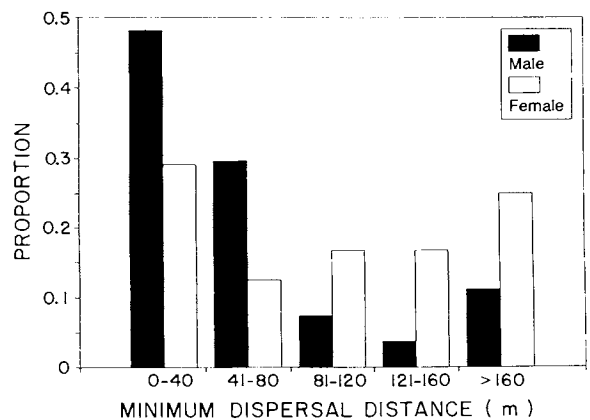


FIG. 2. Distributions of dispersal distances for *Peromyscus californicus* juveniles of known ancestry ( $n = 27$  males and 24 females). Dispersal distance is divided into 40-m intervals, which corresponds to the mean home-range diameter of adults.

TABLE 1. Summary statistics for persistence on trap grids and minimum dispersal distances of *Peromyscus californicus* juveniles of known origin and juveniles of unknown origin (immigrants). *U* is the resultant statistic of the Mann-Whitney test for differences between the sexes.

Statistic	Mice of known origin		Immigrants	
	Male	Female	Male	Female
<i>N</i>	27	24	17	23
	Persistence† (d)			
Mean ± 2 SE	345 ± 104	246 ± 95	236 ± 94	208 ± 97
Range	60–1030	42–868	40–770	4–694
Median	253	136	169	96
<i>U</i>	412		244	
	Minimum Dispersal Distance (m)			
Mean ± 2 SE	70 ± 37	155 ± 78	69 ± 37	50 ± 22
Range	0–450	12–791	3–317	0–190
Median	41	97	48	32
<i>U</i>	207*		233	

\* *P* ≤ .05.

† Persistence was calculated from date of birth to last known date alive on the trap grids for juveniles of known origin and from first capture date to last known date alive for immigrants.

(14/27) of males were classified as reproductive. Mice that were not classified as reproductive were either mice that established a home range but never mated (Ribble 1990) or mice that were never captured again. Four of the males that bred did so within their natal ranges. In all cases the males' fathers and in three cases the males' mothers were no longer known to be alive when the males' first litters were born. The male's mother had moved to an adjacent territory in one case. No females reproduced within their natal ranges.

A total of 17 male and 23 female immigrant mice (no known origin) were identified on both grids. Persistence for these immigrants was calculated as the number of days from first capture to last known day alive. Persistence and minimum movement distances

did not differ between the sexes (Table 1). Fifty-eight percent (10/17) of immigrant males and 52% (12/23) of immigrant females were classified as reproductive. Of the total number of reproductive mice identified in this study that I could positively identify as an immigrant or a mouse of known origin, 42% (10/24) of males and 52% (12/23) of females were immigrants.

DISCUSSION

In this study I established natal locations of 114 *Peromyscus californicus* juveniles and then ascertained minimum dispersal distances for almost half of these. Average litter size at weaning that I observed (1.75 ± 0.18; mode: 2) was very close to the average litter size at birth reported for this species (range: 1.8–2.5; Svihla

TABLE 2. Minimum dispersal distances (in metres; mean ± 2 SE; sample size in parentheses) of male and female juvenile *Peromyscus californicus* with known ancestry from litters of different size or numbers of same- or opposite-sexed siblings. *H* is the resultant statistic of the Kruskal-Wallis test for comparisons among categories.

Sex	Category of variable				<i>H</i> ( <i>P</i> )
	0	1	2	3	
	Litter size				
Male	...	34.0 ± 30.3 (3)	37.4 ± 19.1 (14)	126.6 ± 88.1 (10)	5.6 (.06)
Female	...	71.9 ± 119.3 (2)	196.0 ± 113.4 (15)	90.4 ± 95.6 (7)	2.9 (.24)
	Number of males in natal litter				
Male	...	36.5 ± 12.0 (14)	118.7 ± 83.6 (11)	37.4 ± 39.4 (2)	1.9 (.39)
Female	238.3 ± 147.6 (11)	100.3 ± 72.4 (9)	47.9 ± 18.2 (4)	...	4.3 (.12)
	Number of females in natal litter				
Male	38.7 ± 23.2 (11)	102.5 ± 71.8 (13)	44.7 ± 26.0 (3)	...	2.3 (.32)
Female	...	66.4 ± 26.1 (12)	243.2 ± 138.9 (12)	...	34* (.03)

\**P* < .05, Mann-Whitney *U* test.



1932, McCabe and Blanchard 1950, MacMillen 1964, Rood 1966, Drickamer and Vestal 1973). Thus, almost all juveniles that survived to emergence or weaning must have been captured. Furthermore, there was very little dispersal of juveniles of known origin prior to initial capture. All of the dispersal distances <2 home-range diameters involved mice that matured and presumably had settled on a home range. For the mice that dispersed distances >2 home-range diameters, 43% (6/14) of the females and 67% (4/6) of the males were mature and had also presumably settled on a home range. Thus, although not all dispersal distances in this study were recorded for animals that had completed dispersal and settled on a home range, the results indicate that females tend to be more vagrant than males (Table 1, Fig. 2).

All previous studies of natal dispersal patterns in other *Peromyscus* species have demonstrated that females tend to remain philopatric (Howard 1949, Fairbairn 1978, Krohne et al. 1984, Adler and Tamarin 1985, Wolff and Lundy 1985, Goundie and Vessey 1986, Wolff et al. 1988, Keane 1990). The mating systems of these *Peromyscus* range from facultative monogamy to polygyny and promiscuity (Wolff 1989). *Peromyscus californicus*, however, by being primarily monogamous, is therefore unique within the genus in both its mating system and in the existence of male-biased philopatry.

Dobson (1982) proposed that the predominance of male-biased dispersal among mammals is due to male mate competition. He further suggested that dispersal in monogamous mammals should not be sex biased since competition for mates and competition for resources should be similar in both sexes. Results from this study on *P. californicus* partially agree with Dobson's prediction in that virtually all juveniles leave their natal range. In *P. californicus*, reproductive mice (parents) almost never move (Ribble 1990), and the only opportunity for offspring to breed in the natal range occurs when the parents die. Reproductive competition with parents would discourage either sex from remaining in the natal area (Waser and Jones 1983). Once away from the natal range, however, dispersal distances did differ between males and females. This is not predicted by Dobson's model.

Anderson's Resident Fitness Hypothesis (RFH; 1989) suggests that in polygynous rodents fathers drive out juvenile males, but that in monogamous rodents juvenile males could successfully settle nearer the natal home range since there would be no competition for mates between father and son. Males in this study did tend to settle closer to home than other polygynous *Peromyscus* (Howard 1949, Fairbairn 1978, Krohne et al. 1984, Adler and Tamarin 1985, Wolff and Lundy 1985, Goundie and Vessey 1986, Wolff et al. 1988), as evidenced by 48% of males settling within one home-range diameter of their birth site (Fig. 2). Thus, Anderson's hypothesis appears to fit male *P. californicus*

relative to other polygynous rodents. The RFH hypothesis further predicts that females will always be subject to maternal aggression—regardless of the mating system—due to resource competition, but perhaps also to paternal aggression in monogamous species. As in Dobson's predictions, however, the RFH hypothesis does not predict a sexual bias in dispersal distances once away from the natal range.

Greenwood (1980) proposed that male-biased dispersal in mammals is due to the predominance of mate-defense mating systems, which results in male dispersal for social and genetic reasons. Among birds, Greenwood (1980) suggested that resource-defense mating systems result in male-biased philopatry because familiarity with local resources presumably provides an advantage in defending resources. Therefore, data from *P. californicus* might suggest that the dispersal patterns are due to a resource-defense mating system. This type of mating system occurs when one sex controls access to the other sex indirectly by monopolizing some critical resource (Emlen and Oring 1977). Ostfeld (1987) asserts that if breeding males have the same association with a resource in the presence of as well as in the absence of breeding females, then it is likely males are defending resources rather than females. *P. californicus* males usually settle first in the mated pair's home range (Ribble 1990), which is consistent with natal dispersal patterns. Males are also known to remain on a territory for up to 8 mo without a mate (Ribble 1990). Thus there is some evidence in *P. californicus* that males gain access to females indirectly by monopolizing critical resources. Critical resources for *P. californicus* probably include adequate cover (McCabe and Blanchard 1950), nest and shelter sites (Grinnell and Orr 1934, Merritt 1974, Cranford 1982), water (MacMillen 1964, Merritt 1974), and food (Merritt 1974).

Male-biased philopatry and female-biased dispersal have been noted in other mammal species. For example, *Saccopteryx bilineata* (white-lined bat) females tend to disperse farther from their natal roosts than males (Bradbury and Vehrencamp 1976); presumably this is due to males defending resources (foraging territories) rather than females (Greenwood 1980, but see Ostfeld 1987). Recent evidence from *Dipodomys spectabilis* indicates dispersal to be female biased at high density and to be due to differential effects of habitat saturation (Jones 1988). Other studies have found patrilineal inheritance of home ranges to be a critical factor in determining female-biased dispersal (Frame and Frame 1976, Pusey 1980, Howard 1986). All of these studies indicate that no single hypothesis will sufficiently explain all cases of female-biased dispersal in mammals (Greenwood 1980, Dobson 1982).

The differences in dispersal patterns between males and females in this study suggest that different factors affected each sex. Average age at first reproduction (250 d) and survival after home-range settlement do not differ between males and females (Ribble 1990). In the

case of males, the only significant association with philopatry and dispersal distances was litter size; males from larger litters tended to disperse longer distances than males from smaller litters. A possible explanation for this pattern is resource competition (Waser 1985, Keane 1990). In contrast, female dispersal distances were positively associated with number of females in the natal litter (Table 2). Female dispersal distances were significantly longer for litters in which two females survived to dispersal age compared to those litters in which only one female survived to dispersal age. The litters with two females could have been predisposed to disperse further distances due to litter-specific genetic or nest effects (Hilborn 1975, Beacham 1979, Dhondt 1979, Waser and Jones 1989). However, the data in this study indicate that the variance in dispersal distances for females with sisters is greater than that of single females. Males usually settle first on breeding home ranges, and are then followed by females (Ribble 1990). If sisters compete for available male home ranges, then on average females with sisters would have to go farther to find an unmated male. These data suggest that dispersal of females is due primarily to mate competition among females. Female *P. californicus* may also disperse farther when encounters with sisters are increased both in the nest and in their natal range (Waser and Jones 1989). The lack of association between number of males in the natal litter and dispersal distances further indicates that inbreeding avoidance is not likely an explanation for female dispersal patterns in *P. californicus*.

Despite the significant differences in dispersal tendencies, the percentage of juveniles of known origin that reproduced did not differ between the sexes. There was an overall tendency for male breeders to be juveniles of known origin (short-distance dispersers) rather than immigrants, and for female breeders to be immigrants. Given that dispersal probably incurs higher survival costs (Waser and Jones 1983, Jones 1986, Krohne and Burgin 1987), mice dispersing shorter distances probably survive better than long-distance dispersers for both sexes. In conclusion, the dispersal patterns observed in this study contrast markedly with dispersal patterns in other rodents and mammals in general, and are probably a consequence of the unusual mating system of this species.

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