

Comparative Ecology of Sympatric *Dipodomys agilis* and *Dipodomys merriami* Populations in Southern California

Leroy R. McCLENAGHAN

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Sympatric populations of *Dipodomys agilis* and *Dipodomys merriami* from San Diego County, California, were monitored by monthly live-trapping from September, 1978, through August, 1980. Demographic characteristics of the two species were closely correlated. Both populations displayed relatively stable numbers over the study. Kangaroo rats were most abundant in the winter and spring. Maximum densities for *D. agilis* of 45 per hectare and for *D. merriami* of 29 per hectare were observed. Numbers were lowest as the study concluded in the summer of 1980. Average monthly survival was 86.6% for *D. agilis* and 85.1% for *D. merriami*. There were no significant differences in survival between the sexes in either species. The average *D. agilis* remained on the study area for 10.4 months, while the average *D. merriami* remained for 8.3 months. Both species displayed seasonal heterogeneity in reproductive activity, with breeding being most intense in the spring. Periods of recruitment and reproduction were associated with reduced survival in both species.

[Department of Biology, San Diego State University, San Diego, California 92182, U.S.A.].

1. INTRODUCTION

Desert rodents in North America have been the focus of considerable investigation. The primary objective of recent studies has been to identify mechanisms facilitating the coexistence of syntopic species (Brown & Lieberman, 1973; Price, 1978; Reichman & Oberstein, 1977; Rosenzweig & Sterner, 1970; Thompson, 1982a, b). However, there exists a paucity of detailed studies on the dynamics of desert rodent populations (Conley *et al.*, 1977).

The desert-transition zone (Cooper *et al.*, 1976) in eastern San Diego County, California, is created by the intergradation of chaparral and Colorado Desert communities and contains floral and faunal elements of both these communities. The Pacific kangaroo rat, *Dipodomys agilis* Gambel, 1848 is a common habitant of chaparral habitats in southern California and northern Baja California, Mexico (Hall & Kelson, 1959). *Dipodomys agilis* is at the eastern limit of its distribution in the desert-transition zone. Merriam's kangaroo rat, *Dipodomys merriami* Mearns, 1890 is a kangaroo rat species whose distribution includes the hottest, driest deserts in North America (Lidicker, 1960). The desert-transition zone represents the western distributional limit for *D. merriami* (Hall

& Kelson, 1959), where it is found in sympatry with *D. agilis*. This paper reports the results of a two-year study of the dynamics of sympatric *D. agilis* and *D. merriami* populations in southern California.

2. STUDY AREA

This study was conducted 6.9 km NE of Jacumba California (R. 8E, T. 18S, SW 1/4 of Sec. 1). This site is situated 109 km E of San Diego, California, at an elevation of 988 m. Dominant plant species on the study area include juniper (*Juniperus californicus*), Spanish dagger (*Yucca schidigera*), Mormon tea (*Ephedra californica*), jojoba (*Simmondsia chinensis*), cholla (*Opuntia* sp.), desert agave (*Agave deserti*), creosote bush (*Larrea tridentata*), buckwheat (*Eriogonum* sp.) and desert apricot (*Prunus fremontii*).

The climate of this region is typical of Mediterranean-type environments. Winters are moist and cool, while summers are hot and dry. Annual precipitation in this region averages about 330 mm. Most of this precipitation comes in the months of December, January and February.

3. METHODS

A 7×7 trapping grid was established, with an interval of 10 m between stations (=0.49 ha). Two Sherman livetraps baited with crimped oats were set at each station such that one trap was under the canopy of the nearest shrub greater than 1 m in height, while the other was in the nearest open area having a diameter of at least 1 m. Trapping was conducted two nights each month from September, 1978 through September, 1980. The grid was run every three hours during the first night and once or twice during the second night of each trapping session. Traps were left open during the day except during the summer, when they were closed to avoid trap deaths of antelope squirrels (*Ammospermophilus leucurus*).

Upon their initial capture, individuals of both *D. agilis* and *D. merriami* were tagged in the right ear with a uniquely numbered monel fish fingerling tag. Information recorded for each individual captured included the following: location of capture on the grid; microhabitat of capture (open or shrub); weight to the nearest g; position of the testes (abdominal or scrotal) for males; and, for females, the condition of the vagina (perforate or not perforate), nipple size (small, medium or large) and whether or not the individual was obviously pregnant. All individuals were released at the site of their capture.

4. RESULTS

4.1. Trappability

Monthly population sizes for both *Dipodomys agilis* and *D. merriami* were estimated by the direct enumeration of individuals in the trappable population (Krebs, 1966). The accuracy of this technique is dependent upon the trappability of the species being censused (Hilborn *et al.*, 1976). Trappability for both *D. agilis* and *D. merriami* was quantified as the ratio of the number of each species captured in a trapping period to the number known to be alive during the interval. Differential trappability between males and females was tested for by treating the sexes separately. No significant differences in trappability between the sexes in

any month for either species were observed when these ratios were compared by chi-square tests of independence (Zar, 1974). Seasonal trappabilities were calculated by pooling monthly trappabilities (Table 1). In no season were males and females of either species found to display differential trappability. Seasonal heterogeneity in trappability was tested for by pooling males and females by season and then comparing trappabilities among seasons by chi-square. Both *D. agilis* and *D. merriami*

Table 1

Trappability of *Dipodomys agilis* and *D. merriami* measured as the percent of individuals known to be alive that were actually captured. Seasonal values were obtained by summing over months (Fall=Sept. — Nov.; Winter=Dec. — Feb.; Spring=March — May; Summer=June — Aug.). Numbers in parentheses indicate number known alive in each season. Italics represent values for seasons with statistically significant ($P < 0.05$) differences in trappability within each species.

Season	Trappability (%)	
	<i>D. agilis</i>	<i>D. merriami</i>
Fall 1978	81.8 (44)	73.9 (23)
Winter 1978—79	82.5 (57)	87.9 (33)
Spring 1979	61.8 (55)	41.7 (24)
Summer 1979	75.4 (65)	86.8 (38)
Fall 1979	80.4 (51)	79.3 (29)
Winter 1979—80	76.6 (47)	76.0 (25)
Spring 1980	91.1 (56)	85.3 (34)
Summer 1980	87.2 (39)	85.7 (14)
Total	79.0 (414)	78.2 (220)

displayed significant heterogeneity in trappability ($\chi^2=17.8$ and $\chi^2=24.1$, respectively). By subdividing these chi-square tests, it was found that trappabilities for spring 1979 were significantly lower in both *Dipodomys* species than in other seasons (Table 1). Trappabilities were homogeneous among the remaining seasons for *D. agilis* and *D. merriami*. Trappability over the entire study was high for both *D. agilis* (79%) and *D. merriami* (78%).

4.2. Changes in Numbers and Sex Ratios

Monthly values for the minimum numbers of *D. agilis* and *D. merriami* known to be alive are given in Figure 1. Numbers for both species were strikingly stable over most of the study. Slight peaks in numbers of both species occurred during winter 1978—79, summer 1979 and spring 1980. Lowest numbers for both *D. agilis* and *D. merriami* were observed as the study was concluded at the end of summer 1980. Patterns of change in the two species closely paralleled one another. In any given month, the number of *D. agilis* known to be alive on the study site

($\bar{x}=17.25$) was approximately twice that observed for *D. merriami* ($\bar{x}=9.17$). Monthly numbers of males and females known to be alive were compared for each species by chi-square tests. No significant departures from a 1:1 ratio were observed for either species in any month.

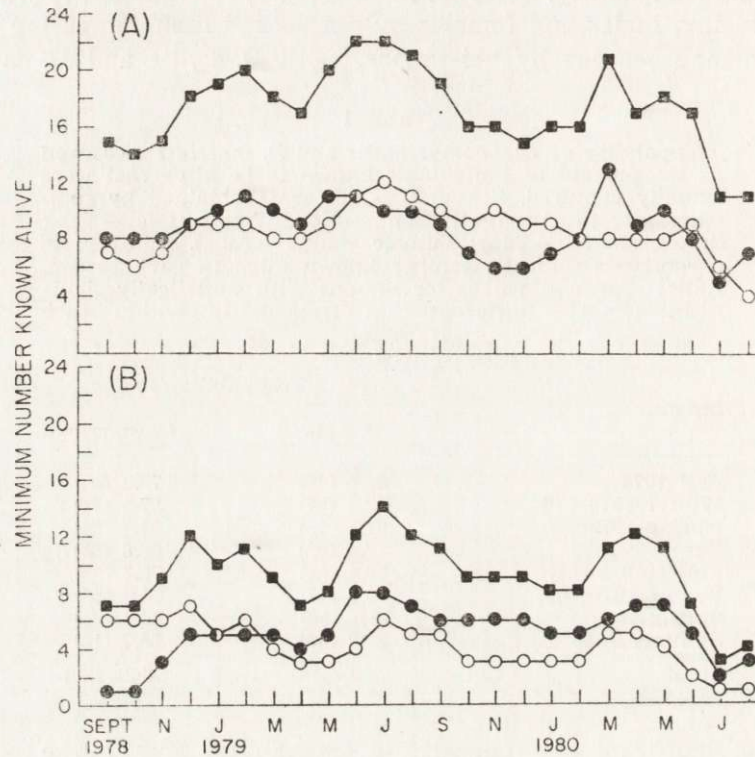


Fig. 1. Minimum numbers of *Dipodomys agilis* (A) and *D. merriami* (B) known to be alive from September, 1978, through August, 1980. Solid squares represent total numbers, while solid and open circles represent numbers of males and females, respectively.

4.3. Survival and Longevity

Survival was measured as the minimum survival rate for animals known to be alive in each month summed by season. The sexes were first considered separately. Chi-square tests indicated that survival was independent of sex in all seasons for both species. Minimum survival rates by season with sexes pooled are given in Table 2. For *D. agilis*, survival was high in the fall and winter and somewhat lower in the spring and summer. Spring and summer of 1980 were seasons of lowest survival. The average monthly survival rate for *D. agilis* over the course of the study was 86.6%. Patterns of survival were less clear in the *D. merriami* population, although lowest survival was again observed in the spring and summer of 1980. Survival in the *D. merriami* population

was generally high in the fall, but winter and spring displayed striking differences between years. Average monthly survival for *D. merriami* was 85.1%.

Estimates of average length of life on the study area for each species were calculated as the average number of months that individuals tagged during the first year of the study and recaptured at least once remained on the study area. The mean lengths of life ± 1 SE for *D. agilis* and *D. merriami* were 10.4 ± 1.2 and 8.3 ± 1.3 months, respectively. These means were not significantly different ($t=1.26$, $P>0.2$).

4.4. Recruitment

For both *D. agilis* and *D. merriami*, recruitment was assessed by summing for each season the monthly proportion of newly tagged individuals in the trappable population (Table 3). No significant hetero-

Table 2

Percent minimum monthly survival for *Dipodomys agilis* and *D. merriami*. Rates for males and females were homogeneous within seasons and have been pooled. Seasonal rates were obtained by summing monthly rates seasons. Sample sizes appear in parentheses.

Season	Minimum Monthly Survival (%)	
	<i>D. agilis</i>	<i>D. merriami</i>
Fall 1978	95.4 (44)	100.0 (23)
Winter 1978-79	96.5 (57)	75.8 (33)
Spring 1979	89.1 (55)	91.7 (24)
Summer 1979	82.1 (65)	89.5 (38)
Fall 1979	90.2 (51)	89.7 (29)
Winter 1979-80	97.9 (47)	96.0 (25)
Spring 1980	76.8 (56)	70.6 (34)
Summer 1980	64.1 (39)	57.1 (14)
Average ± 1 SE	86.6 ± 2.5 (414)	85.1 ± 3.6 (220)

geneity in recruitment within seasons between years was observed for either species. Average monthly recruitment over the entire study was 11.3% for *D. agilis* and 14.5% for *D. merriami*. Recruitment rates were heterogeneous among seasons in *D. agilis* ($\chi^2=14.8$, $P<0.001$), with recruitment in the summer being greater than that for other seasons (Table 3). While spring and summer appeared to be seasons of greatest recruitment in *D. merriami* no significant heterogeneity among seasons was observed ($\chi^2=5.1$, $P>0.1$).

4.5. Reproduction

Patterns of reproductive activity were explored by calculating the proportion of breeding adults in each population. Adults were identified on the basis of body weight (>57 g for *D. agilis* and >36 g for *D. merria-*

mi). Males with scrotal testes and females with perforate vaginas and/or medium or large nipples were judged to be reproductive. Seasonal reproductive parameters were obtained by summing over months (Table 3). Chi-square analysis was used to test for heterogeneity in breeding activity between sexes within seasons, within seasons between years for each sex and among seasons for each sex.

Differential breeding activity between the sexes in *D. agilis* was observed in winter 1978—79 ($\chi^2=14.2$, $P<0.001$), fall 1979 ($\chi^2=5.9$, $P<0.05$) and winter 1979—80 ($\chi^2=5.9$, $P<0.05$). A larger proportion of males than females were reproductive in these seasons (Table 3). For male *D. agilis*, no significant heterogeneity in breeding activity was observed for any season between years. However, there was considerable heterogeneity among seasons ($\chi^2=34.9$, $P<0.001$). By subdividing this chi-square, the seasons may be arranged with respect to breeding activity as follows: spring>winter, summer>fall. Female *D. agilis*

Table 3

Recruitment rates and percentages of adults in reproductive condition for *Dipodomys agilis* and *D. merriami*. Seasonal parameters were obtained by summing monthly values. Recruits were defined as any newly tagged individuals. Adults were identified on the basis of body weight (>57 g for *D. agilis* and >36 g for *D. merriami*) Males with scrotal testes and females with perforate vaginas and/or medium or large nipples were judged to be reproductive. Samples sizes appear in parentheses. F—fall, W—winter, Sp—spring, Su—summer.

Season	Recruitment Rate (%)		Reproductive Activity (%)			
	<i>D. agilis</i>	<i>D. merriami</i>	<i>D. agilis</i>		<i>D. merriami</i>	
			♂♂	♀♀	♂♂	♀♀
F. 1978	6.9 (29)	12.5 (16)	33.3 (18)	22.2 (9)	75.0 (4)	33.3 (12)
W. 1978—79	10.5 (57)	21.2 (33)	76.0 (25)	11.8 (7)	50.0 (14)	9.1 (11)
Sp. 1979	7.3 (55)	8.3 (24)	88.9 (18)	71.4 (14)	100.0 (7)	100.0 (3)
Su. 1979	20.0 (65)	21.1 (38)	56.2 (16)	58.8 (17)	66.7 (18)	36.4 (11)
F. 1979	3.9 (51)	3.4 (29)	47.1 (17)	5.6 (18)	6.0 (16)	9.1 (11)
W. 1979—80	4.3 (47)	0.0 (25)	93.8 (16)	46.2 (13)	70.0 (10)	44.4 (9)
Sp. 1980	16.1 (56)	26.5 (34)	100.0 (29)	90.5 (21)	100.0 (17)	100.0 (11)
Su. 1980	23.1 (39)	21.4 (14)	84.6 (13)	81.8 (11)	66.7 (9)	50.0 (2)
Av.±1SE	11.3±1.9 (399)	14.5±2.6 (213)	73.7±5.9 (135)	51.6±7.5 (120)	61.6±7.7 (95)	44.0±8.7 (70)

similarly showed no difference in the intensity of reproductive activity for any season between years, but significant heterogeneity among seasons was observed ($\chi^2=36.8$, $P<0.001$). Breeding activity for adult females was greatest in spring and summer and lowest in the fall and winter.

When proportions of breeding *D. merriami* males and females were compared within seasons, no significant differences were found (Table 3). Females displayed no differences in breeding activity for any season between years. Males also displayed no heterogeneity within seasons between years except for fall, where the proportion of breeding males in fall 1978 was significantly greater than that in fall 1979 ($\chi^2=8.8$,

$P < 0.001$). Significant heterogeneity in breeding activity among seasons was observed in both males ($\chi^2 = 41.5$, $P < 0.001$) and females ($\chi^2 = 25.7$, $P < 0.01$). Intensity of reproductive activity for males can be ordered as follows: spring > winter, summer, fall 1978 > fall 1979; for females: spring > winter, summer, fall.

4.6. Correlations of Demographic Parameters

Demographic parameters were averaged by season for each species. Correlation analysis was used to measure the correlation of demographic parameters within and between kangaroo rat populations (Table 4). Se-

Table 4

Correlations ($df = 6$) among seasonal demographic parameters for populations of *Dipodomys agilis* (above diagonal) and *D. merriami* (below diagonal). Interspecific comparisons are given on the diagonal. Comparisons are not statistically significant ($P > 0.05$) unless otherwise indicated.

	Min. no. alive	Survival rate	Recruitment	Male repro.	Female repro.
Min. no. alive	0.92**	0.20	0.21	0.02	0.01
Survival rate	0.22	0.81*	-0.85**	-0.31	-0.73*
Recruitment	0.27	-0.69	0.82*	0.22	0.65
Male repro.	-0.09	-0.08	0.35	0.53	0.67
Female repro.	-0.11	-0.17	0.21	0.83**	0.84**

* $P < 0.05$, ** $P < 0.01$

veral patterns emerge from the comparison of parameters within each species. First, changes in the numbers of each species were not significantly correlated with any of the other demographic variables in either *Dipodomys agilis* or *D. merriami* (Table 4). This probably reflects the relative stability in numbers displayed by both populations (Fig. 1). Second, there was a trend in both species for survival rates to be negatively associated with recruitment and reproductive activity. Correlations of survival rate with recruitment ($r = -0.85$) and with percent females breeding ($r = -0.73$) were significant in *D. agilis*. In *D. merriami*, the correlation between survival rate and recruitment ($r = -0.69$) was not quite significant. When seasonal demographic parameters were compared for the two kangaroo rat populations, correlations of the same parameter between populations (e.g. *D. agilis* survival vs. *D. merriami* survival) were significant and positive in four of the five possible comparisons; only male reproductive activity was not significantly correlated between the two populations.

5. DISCUSSION

Both *Dipodomys agilis* and *D. merriami* populations displayed similar patterns of change in numbers (Fig. 1). Kangaroo rats were most abun-

dant in late winter and spring and least abundant in the summer and fall. Previous studies have reported summer peaks in numbers for *D. merriami* (Reynolds, 1958; Chew & Chew, 1970) and winter peaks for *D. agilis* (MacMillen, 1964). In July, 1979, 36 kangaroo rats (22 *D. agilis* and 14 *D. merriami*) were known to be alive on the study site. Given that the trapping grid covered 3600 m² and allowing for a 10 m boundary strip, these numbers are equivalent to densities of 45 animals per hectare and 29 animals per hectare for *D. agilis* and *D. merriami*, respectively. While the area actually sampled by the grid may be somewhat greater than 0.49 hectares, these density estimates are noteworthy because they far exceed those reported for these species in other studies. Conley *et al.* (1977), in summarizing demographic characteristics for a variety of Chihuahuan Desert rodent species, cited a maximum density of 18.29 individuals per hectare for *D. merriami* from a study by Reynolds (1950). Christopher (1973) calculated a density of 18.5 animals per hectare for a population of *D. merriami* on the western edge of the Colorado Desert. Reported densities (individuals per hectare) for *D. agilis* include 10.8 (Christopher, 1973), 11.9 (MacMillen, 1964) and 13.0 (M'Closkey, 1972).

Both *D. agilis* and *D. merriami* displayed relatively high survival during the study. No differences in survival rates were observed between the sexes in either kangaroo rat population. M'Closkey (1972) also observed similar survival in *D. agilis* for males and females. Spring and summer were typically seasons of lower survival (Table 2). The association of reduced survival with high densities and reproductive activity is consistent with the results of studies on other desert rodents (Christian, 1980; Conley *et al.*, 1977; French *et al.*, 1966). Periods of good survival were typically those of low recruitment (fall, winter), while seasons with lower survival were characterized by higher recruitment rates (spring, summer). Average life spans for *D. agilis* and *D. merriami*, 10.4 and 8.3 months, respectively, were longer than those previously reported for these species. M'Closkey (1972) observed an average length of life of 4.4 months for *D. agilis*, while French *et al.* (1967) reported life spans of only 4.7 and 1.7 months for fenced and unfenced populations of *D. merriami* in Nevada.

In *D. agilis*, reproductive individuals of both sexes were present in all seasons, while reproductive males and females in the *D. merriami* population were present in all seasons except fall 1979 (no males). Generally, a greater proportion of males than females was reproductive in any given season. Bradley & Mauer (1971) reported the presence of reproductive males in all months of the year for *D. merriami* in Nevada, with spring peaks in breeding activity. MacMillen (1964) observed lactating *D. agilis* from January through July and reproductive males from December through July. In the present study, both *D. agilis* and

D. merriami displayed peaks in reproductive activity during the spring (Table 3). This result agrees with other studies in which an association between reproduction in desert rodents and the availability of green vegetation has been observed (Beatley, 1969, 1976; Bradley & Mauer, 1971; Christian, 1980; Reynolds, 1958). Demands for energy and water are increased by lactation in small mammals (Randolph *et al.*, 1977; Soholt, 1978) and green vegetation in the desert-transition zone is most abundant in the spring following the winter rains.

Nichols *et al.* (1976) have proposed a life history model for desert rodents in which species employ temporal shifts between a relative *r*-strategy and a relative *K*-strategy (MacArthur & Wilson, 1967) in response to environmental fluctuations. Periods of precipitation and increased plant productivity are exploited by desert rodents through increased reproduction. However, this exploitation confers a "cost" to the rodents in the form of reduced survival as individuals forage, search for mates and related activities. Exposure to mortality factors and reproductive rates are reduced during periods of environmental adversity as individuals spend more time inactive in their burrows. This model predicts high survivorship and low reproduction during adverse environmental conditions and negative associations of survivorship with reproduction and recruitment. Demographic patterns observed in this study of *D. agilis* and *D. merriami* conform to these predictions (Table 4).

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Leroy R. McCLENAGHAN

PORÓWNAWCZA EKOLOGIA SYMPATRYCZNYCH POPULACJI *DIPODOMYS AGILIS* I *DIPODOMYS MERRIAM*I W POŁUDNIOWEJ KALIFORNII

Streszczenie

Badania nad sympatrycznymi populacjami *Dipodomys agilis* i *D. merriami* prowadzono w okolicach San Diego od września 1978 do sierpnia 1980 r. włącznie, przy pomocy comiesięcznych odłowów w pułapki żywołowne (Tabela 1). Charakterystyka demograficzna tych dwóch gatunków była bardzo podobna (Tabela 4). W ciągu okresu badań obie populacje miały względnie stałą liczebność. *D. agilis* były liczniejsze w zimie i na wiosnę. Maksymalne zagęszczenie tego gatunku wynosiło 45 osobników/ha, a *D. merriami* — 29/ha. Najniższą liczebność zanotowano w lecie 1980 r. (Ryc. 1). Średnia miesięczna przeżywalność wynosiła 86,6% dla *D. agilis* i 85,1% dla *D. merriami* (Tabela 2). Nie wystąpiły istotne różnice w przeżywalności samców i samic obu gatunków. *D. agilis* pozostaje średnio przez 10,4 miesiąca na badanym areale, podczas gdy *D. merriami* tylko 8,3 miesiąca. Oba gatunki wykazują sezonową zmienność aktywności rozrodczej, przy czym najintensywniejszy rozród jest na wiosnę. Okres rozrodu i wychodzenia młodych z gniazd cechował się obniżoną przeżywalnością osobników obu gatunków (Tabela 3).