

Population Fluctuations and Extinctions of Small Rodents in Coastal Southern California

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Summary. The population dynamics of three sympatric rodents, *Microtus californicus*, *Mus musculus*, and *Reithrodontomys megalotis* was studied at four sites in coastal southern California. The study was undertaken to determine the extent of local demographic diversity in rodent populations.

The populations of all rodent species became extinct on one site, while on another site the populations fluctuated widely and on two other sites the populations remained relatively stable. The most common species, *Reithrodontomys*, exhibited differences in reproduction, age class structure, recruitment, and survivorship on the two sites which were monitored for relatively long terms. Immigration was the main source of new individuals entering the sites where the *Reithrodontomys* population was most persistent.

On a local scale, some life history characteristics are affected in a density dependent fashion. When viewed on a global scale, the non-equilibrium nature of the rodent populations becomes clear.

Introduction

There is an increasing appreciation for understanding the importance of disturbances and non-equilibrium situations within ecological systems and how they influence processes such as extinction and population regulation. Models proposed by Hutchinson (1951) and Skellam (1951) on non-equilibrium coexistence explain how two ecologically similar species could coexist in a patchy environment. In Hutchinson's model, an inferior competitor can exist with a superior competitor if the superior competitor occasionally becomes extinct in certain habitat patches. The inferior competitor can invade such patches and colonize the area. This colonizing or "fugitive species" could occupy environments where the physical environment is harsh or variable or where populations fluctuate greatly (Horn and MacArthur 1972). Levin's (1976) recent analysis suggests that when disturbances are localized and asynchronized regionally, fugitive strategies may maintain species in a community through spatio-temporal heterogeneity. A fugitive species may be doomed locally but survives globally by a balance between dispersal, competitive, or escape ability.

Non-equilibrium states as influenced by local population extinctions is the essence of the population regulation model proposed by Andrewartha and Birch (1954). They reasoned that a species consists of many local populations that vary independently. Some local populations may go extinct and colonists from extant populations will repopulate these areas. The scheme

of Andrewartha and Birch (1954) does not require density dependent action within a local population. All that is required is a positive intrinsic rate of growth, r_m , some of the time in most populations and sufficient interchange between populations to recolonize places where random extinction has occurred. Random extinction can occur through biotic or abiotic disturbances (see Connell 1978; Sousa 1979). The importance of non-equilibrium population dynamics in the Andrewartha and Birch (1954) sense has been suggested by field studies of invertebrates (see Ehrlich 1965; Menge 1979; Spight 1974 for examples). Aside from "cycling" rodent populations (see Krebs and Myers 1974) local population extinctions of vertebrates are less well known but may be more common than is generally believed (see for examples: Errington 1963; Leck 1979; Lidicker 1966; Willis 1974). Furthermore, Lidicker (1978) predicts that demographic diversity among rodents is expected among different populations of the same species.

To test the Andrewartha and Birch (1954) model, I monitored rodent populations in Santa Barbara, Co., California. It was my hypothesis that these populations would show differences in demographic parameters which would influence both local and global population changes. To support the model, the existence of population size asynchrony must be established. Some populations should be at high density, while others should be at low density. As further support for the model, dispersal to areas of low density should be observed. It is important to document these differences for another reason. Many ecological studies of vertebrates are conducted on only one site for relatively short time spans. These short term studies may not give us an accurate ecological picture of the system (see Hayne 1978 and Wiens 1977 for discussions).

Materials and Methods

Study Areas

Four live-trap grids were established in the vicinity of the University of California, Santa Barbara, campus (Fig. 1). The climate in this area is Mediterranean-like with moderate temperatures throughout the year. There is a summer drought and winter rainy season. Frost is rare. Blaustein (1978) provides detailed climatological data. Grids were as large as possible, given the terrain. Natural barriers (i.e., inlets, hedge rows, and trees) bordered each grid. Areas were chosen to be as similar as possible in vegetation and terrain.

Goleta Slough grid 1 (9 × 9 configuration with 10 m spacing) was located about 1.6 km from the Pacific Ocean in a disturbed (=introduced plant species) grassland bordering a coastal salt marsh. The dominant plants were grasses (*Bromus*, *Lolium* and *Avena*) with inter-

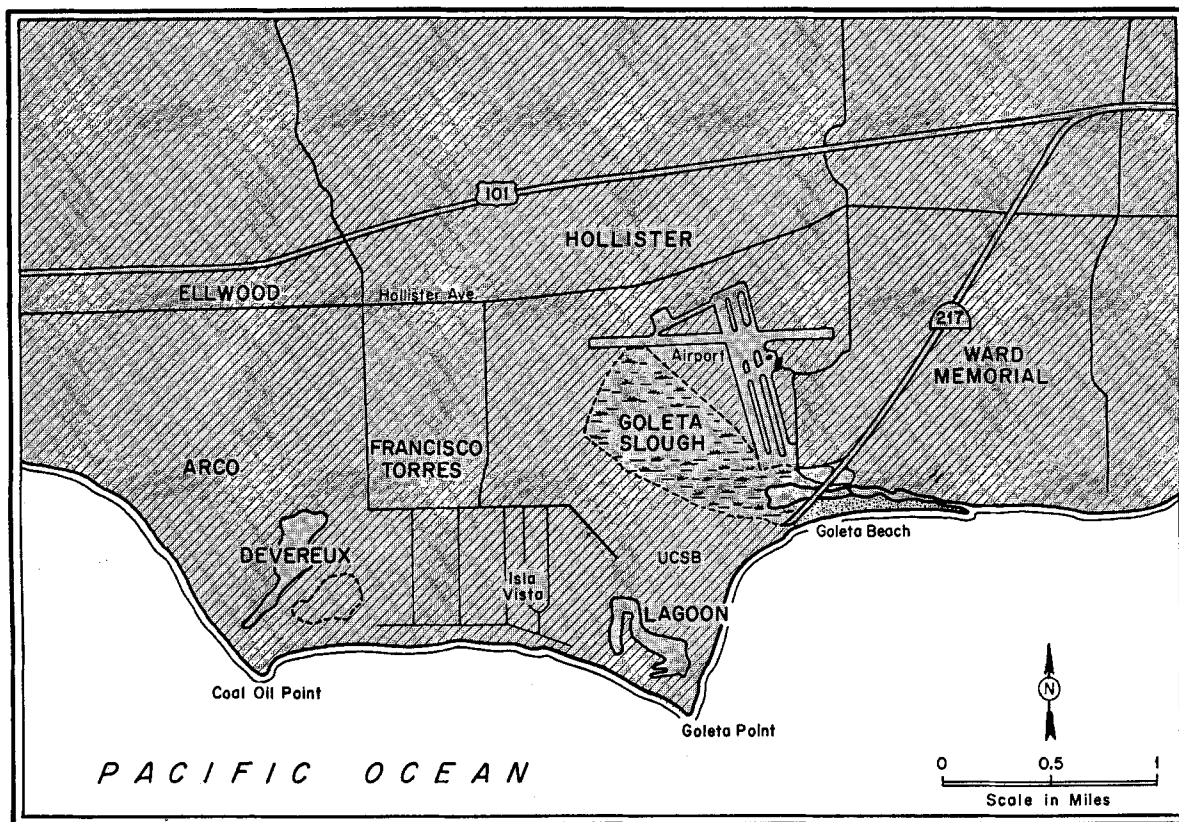


Fig. 1. Map showing study areas where grids were placed

spered coyote bush (*Baccharis pilularis*). Trapping was conducted from July 1974 through June 1976 for a total of 23,004 trap periods (one trap check = one trap period).

Goleta Slough grid 2 (8 × 8.5 m spacing) was located about 100 m from the southeast border of Goleta Slough 1. Dominant vegetation on this grid consisted of the grasses *Bromus*, *Lolium* and *Avena*. The southern portion of the grid had a stand of fennel (*Foeniculum*). Trapping was conducted from February through May, 1975 for a total of 1,792 trap periods.

The Devereux grid (9 × 9, 10 m spacing) was located on the University of California Coal Oil Point Reserve and was about 0.8 km from the ocean in a coastal strand community and adjacent disturbed grassland. Bush lupine (*Lupinus arboreus*) and beach primrose (*Camissonia cheiranthifolia*) dominated the strand. Wild mustard (*Raphanus sativa*) and the grasses *Bromus*, *Lolium*, and *Hordeum* dominated the grassland. *Baccharis pilularis* was found throughout the grid, except on the extreme northeast portion, which was sandy. Trapping was conducted in February 1974 and from July 1974 through March 1976 for a total of 13,527 trap periods.

The Lagoon Central grid (7 × 7, 8 m spacing) was located on a coastal bluff in a disturbed grassland community. Dominant vegetation was *Bromus*, *Raphanus* and *Lupinus arboreus*. Trapping was conducted in February and March, 1976 (total = 441 trap periods). Blaustein (1978, 1980) provides further details concerning grid structure and placement.

Trapping Procedures

Rodents were live-trapped on grids, with large Sherman aluminum live-traps baited with a mixture of rolled oats and sunflower seeds. Upon capture, I noted species, weight (to the nearest 0.5 g) sex, relative age (adult, subadult, juvenile) reproductive condition, and trap coordinates. All rodents were marked individually by toe-clipping and ear-notching. Animals were released at their points of capture.

Trapping was conducted for at least three consecutive days per month on Goleta Slough grid 1 and at Devereux. Traps were checked

at dawn, noon and dusk on these grids. Two trapping sessions were conducted on Goleta Slough grid 2. The first session lasted from 18 February to 3 March 1975 (12 days, 768 trap periods). The second session lasted from 9 April through 21 May 1975 (16 days, 1,024 trap periods). Traps were checked at dawn, as they were during the 9 day session on the Lagoon Central grid.

Density estimates on the Goleta Slough 1 and Devereux grids were based on the minimum number of individuals known to be alive during a three day monthly trapping session.

Analysis of Demographic Parameters

Since it was not possible to determine exact ages, rodents were placed into one of three age classes based on a combination of pelage and weight characteristics: adults, subadults and juveniles (DeLong 1967; Fisler 1965; Hooper 1952; Krebs 1966; McCabe and Blanchard 1950).

Dates of first and last capture of individuals provided a crude estimate of survival; however, it cannot be known for sure whether animals that are no longer captured have died, moved away or will no longer enter traps. Survivorship was computed for animals on the Goleta Slough grid 1 and at Devereux.

Females were placed into three reproductive classes: reproductively active – pregnant or lactating; potentially reproductive – show signs of estrous cycling as exemplified by having perforated vaginal orifices; non-reproductive – non-pregnant, non-lactating females which showed no signs of estrous cycling. Males were classified as having abdominal testes (reproductively inactive) or testes which have descended into the scrotal sac (reproductively active).

Recruitment refers to the rate at which individuals enter the populations due to natality or immigration. It is not certain which of these two sources is most important at any given on the study areas, but if reproduction is low, one can infer that immigration was an important source of new animals entering a particular area. If new animals were adults it is likely immigration occurred.

Variance-ratio tests (F-test, Bailey 1972; p. 50) were used to test the equality of variances before testing differences between sample means. If the variances were statistically different from one another

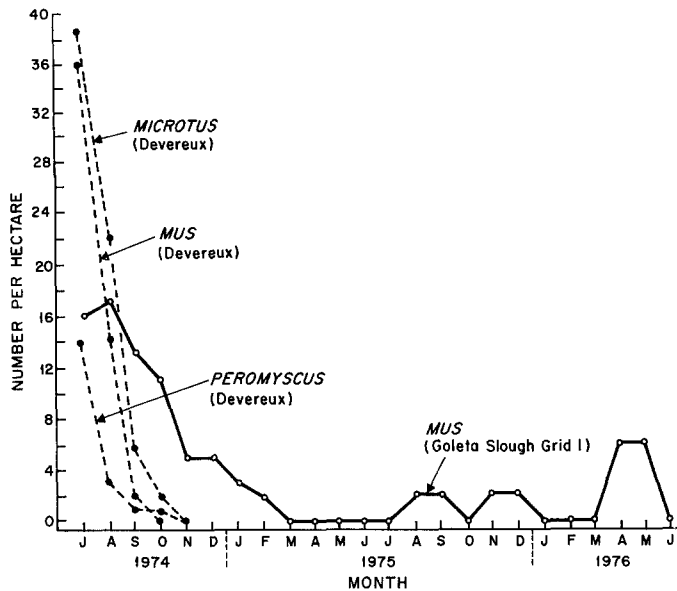


Fig. 2. Population densities of rodents at Devereux. Density estimates were based on interpolation from the number of individuals captured per three day trapping session

I used the Welch-Aspin test (Snedecor and Cochran 1967; p. 115-116) to analyze differences between means. If the variances were not statistically different, t tests were used to test differences between means. Non-significance in all statistical tests conducted indicates $P > 0.05$.

Results

The most common mammal species captured during the study were the western harvest mouse (*Reithrodontomys megalotis*), the California vole (*Microtus californicus*) and the house mouse (*Mus musculus*). The deer mouse (*Peromyscus maniculatus*) was rare during the study.

General Population Trends

The most striking result was the extinction of all four rodent species on the Devereux Grid (Figs. 2, 3). An abrupt decline in *Peromyscus*, *Microtus* and *Mus* occurred in July and August 1974 at Devereux (Fig. 2). During this time on the same grid the *Reithrodontomys* density increased from 65 to more than 90 per ha after which this species' density drastically fell (Fig. 3). Only *Reithrodontomys* was captured after November 1974 at Devereux. However, *Reithrodontomys* disappeared from Devereux after February 1975 until August 1976 when one subadult male and one juvenile female were captured. In September 1976, a pregnant female and subadult male *Reithrodontomys* were captured. The population of *Reithrodontomys* failed to recover from the 1974 crash. No other rodent species was captured at Devereux from November 1974 to August 1978 when monitoring of mammals on this area ceased.

The populations of *Reithrodontomys* on Goleta Slough grid 1 underwent an abrupt increase in numbers at the same time the population of *Reithrodontomys* was crashing at Devereux (Fig. 3). Two distinct population phases were apparent. The high density phase lasted from July 1974 through February 1975 when an average of 35.5 *Reithrodontomys* per ha/month was captured. The low density phase lasted for the remainder of the study with an average of 9.6 *Reithrodontomys* being captured per ha/month. Differences between the mean densities for these two periods were statistically significant (Welch-Aspin test, $t=4.26$, $df=7$ $P < 0.001$).

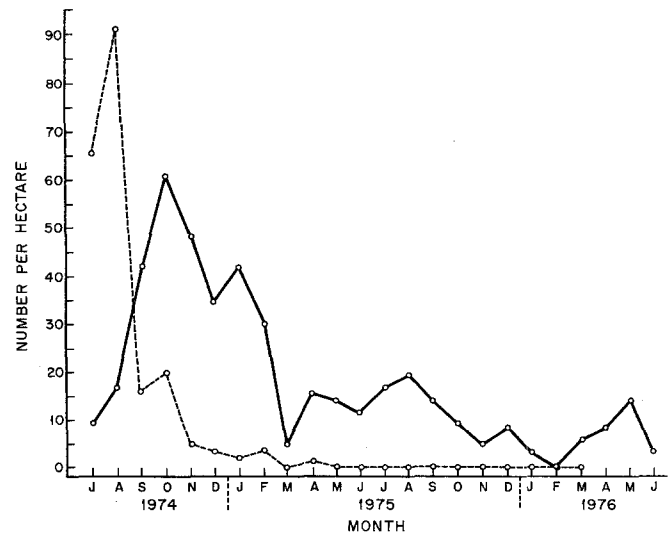


Fig. 3. Population densities of *Reithrodontomys* on the Devereux (dashed) and Goleta Slough 1 (solid) grids. Density estimates were based on interpolation from the number of individuals captured per three day trapping session

There was no consistent annual pattern concerning months showing typically high populations. For example, there were 31 *Reithrodontomys* per hectare in February, 1975, a relatively high density, and no *Reithrodontomys* were captured in February, 1976. Similarly, by comparing October, 1974 with October, 1975, gives 61 and 9 *Reithrodontomys* per hectare respectively. The *Mus* population in the Goleta Slough also fluctuated, peaking at 17 per ha in August 1974 (Fig. 2). After this time *Mus* were not abundant on this area.

Whereas the Devereux grid had virtually no rodent species present and Goleta Slough grid 1 populations were declining, just 100 m away, separated by an inlet, there were abundant populations of *Microtus* (27 individuals) and *Reithrodontomys* (25 individuals) during the short term trapping on Goleta Slough grid 2. In April and May the *Microtus* population declined and only 9 individuals were captured whereas the population of *Reithrodontomys* remained high (25 individuals) on this area throughout this period. Correcting for trap effort, the calculated densities of *Reithrodontomys*, *Microtus* and *Mus* on the Lagoon Central grid were 41, 43 and 12/ha respectively. These are high densities considering almost no animals were captured during this time span (February and March, 1976) at Devereux and on Goleta Slough grid 1 (Figs. 2, 3).

Reithrodontomys Demography

Population changes were asynchronous on the 4 grids and the most common species, *Reithrodontomys*, was divided into local populations (demes). These populations occupied discrete patches of habitat which were separated by areas unfavorable to their growth and persistence (see Blaustein 1980 and Fig. 1). These patches may change in space size or quality in time. If new empty patches arise, they are colonized by migrants from established populations. However, local extinctions may occur (Blaustein 1980; Figs. 2, 3). Reproductive failure of a local population is often the first evidence of imminent local extinction. In some species, many local populations may not be self-perpetuating due to low reproduction. These populations receive emigrants from demes with reproductively active adults (Gill 1978).

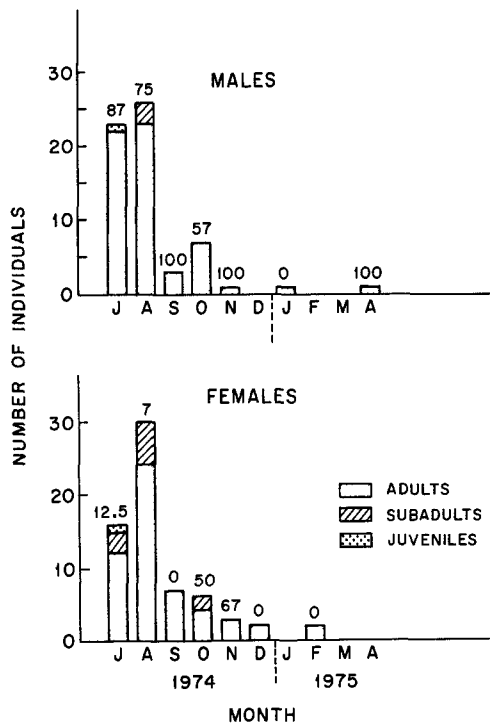


Fig. 4. Number of male and female *Reithrodontomys* captured per month at Devereux. Numbers above histograms indicate percent that were reproductively active

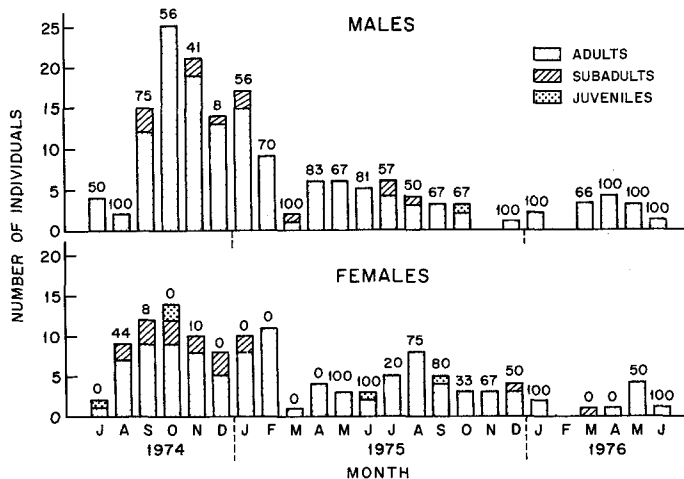


Fig. 5. Number of male and female *Reithrodontomys* captured per month on Goleta Slough grid 1. Numbers above histograms indicate percent that were reproductively active

To determine the importance of reproduction and recruitment in local *Reithrodontomys* populations, I analyzed these parameters in detail.

Reproduction

At Devereux in October, 1974, only 57% of the males were reproductively active and in January, 1975 the only male captured was in non-reproductive condition. In all other months the majority of the males captured were reproductively active (Fig. 4). Pregnant females were captured in July, August, October and November, 1974.

On Goleta Slough grid 1, reproductively active males were found in all months during which males were captured (Fig. 5). Beginning in August 1974, the proportion of reproductively ac-

tive males declined steadily, reaching a low of 8% in December. A gradual increase began after December and reached a peak by March, 1975. From March, 1975 through October, 1975, 50% to 83% of the males captured per month were reproductively active. From November, 1975 through June, 1976 almost all the few males captured were reproductively active. Reproduction in male *Reithrodontomys* did not follow a distinct seasonal pattern from year to year. Although almost all males captured from November, 1975, through June, 1976 were reproductively active, this was not the case for males during the same months of the previous year. During the high population density phase (July, 1974–February, 1975) 42 of 93 males captured were scrotal, whereas 37 of 51 males captured during the low density phase were scrotal. These proportions are significantly different ($\chi^2 = 9.83$, d.f. = 1, $P < 0.01$) indicating that there was a larger proportion of sexually active males at low densities.

Only 6 of 76 females captured were sexually active during the high population density phase whereas 27 of 48 females were sexually active at low densities (Fig. 5). These proportions differ significantly ($\chi^2 = 34$, d.f. = 1, $P < 0.001$) indicating that breeding was more common at low densities. In 8 of the 15 low density months, the majority of females captured were either pregnant or lactating. There were no real trends in female reproductive activity from year to year. However, there was a preponderance of sexually active females in August.

Females came into breeding condition on Meserve's (1972) more southerly study area about one month before (April) females on the Goleta Slough grid (May). Males on Meserve's (1972) plot showed rather distinct reproductive periods. He found no scrotal males in the Goleta Slough in all months. A large proportion were scrotal from October through February (Fig. 5).

The relatively large *Reithrodontomys* population on the Lagoon Central and Goleta Slough grid 2 showed very little reproductive activity. Only 20% of the males were reproductively active on the Lagoon Central grid. No males were reproductively active on Goleta Slough grid 2. No females were reproductively active on either grid. Thus, where *Reithrodontomys* densities were relatively large (Lagoon Central grid, Goleta Slough grid 2 and the high density phase on Goleta Slough grid 1) reproduction was low. However, reproductive individuals were relatively abundant at Devereux when populations were dense.

Age Classes

Relatively few young *Reithrodontomys* were captured at Devereux (Fig. 4). Only 13% of the July population and 16% of the August population were composed of young animals. These peaks in percent young coincided with the overall population peaks. After October, no young animals were captured.

During the high population density phase on Goleta Slough grid 1, a mean of 3.0 young (subadults and juveniles) were captured per month as compared with a mean of only 0.56 young captured per month during the low density phase (Fig. 3) ($t = 3.81$, d.f. = 7, $P < 0.01$, Welch-Aspin test) indicating that there were more young recruited per month at high population densities. I further analyzed this relationship by separately comparing the number of adult and young females and males captured per month at high and low population densities. The overall proportion of young and high densities was not significantly different from the proportion of young at low densities. But the proportion of young females per female adults at high densities, 18/76, was significantly greater than the proportion of young females per adult at low densities, 4/48 ($\chi^2 = 3.88$, d.f. = 1, $P <$

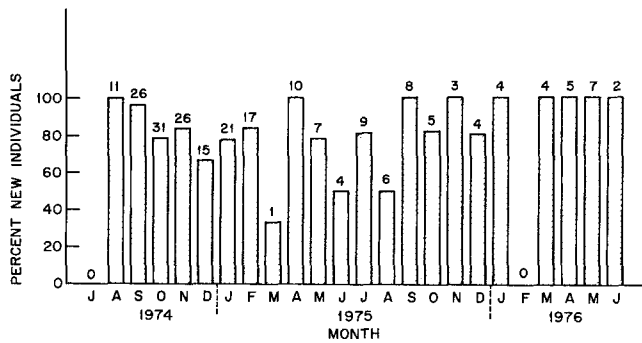
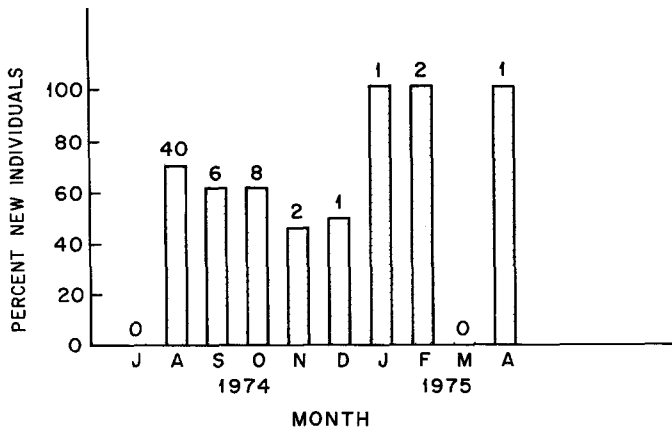


Fig. 6. Percent new individuals entering the Devereux (top) and Goleta Slough (bottom) grids per month. Numbers above histograms indicate total number of new individuals captured

0.05). However, the proportion of young males per male adult was not significantly different at high as compared with low population densities. The proportions of young males to adult females at high and low densities were also not significantly different from one another. Young animals were captured in all months except February, April and May. All *Reithrodontomys* captured on the Lagoon Central and on Goleta Slough grid 2 were adults.

Recruitment

Recruitment is difficult to assess in small mammal populations. To obtain a crude estimate of recruitment rates I analyzed the number of new individuals entering the population per month at Devereux and on Goleta Slough grid 1. There was a gradual decline in the number of new individuals entering the Devereux population from August through December 1974 (Fig. 6). After October, very few unmarked individuals entered the population. On Goleta Slough grid 1 from August through December, 1974 there was a gradual decline in the proportion of new individuals captured per month (Fig. 6). After an increase in the recruitment rate in January and February, 1975, this decline continued with only one new individual captured in March, 1975. Although the number of new individuals entering the population per month fluctuated, a period of relatively low recruitment existed from October, 1974 through August, 1975, when the mean percent of new individuals entering the population per month was 75% as compared with a mean percent of 85% for the month following this time period.

I analyzed whether the proportion of new individuals entering the population per month was greater during the low density

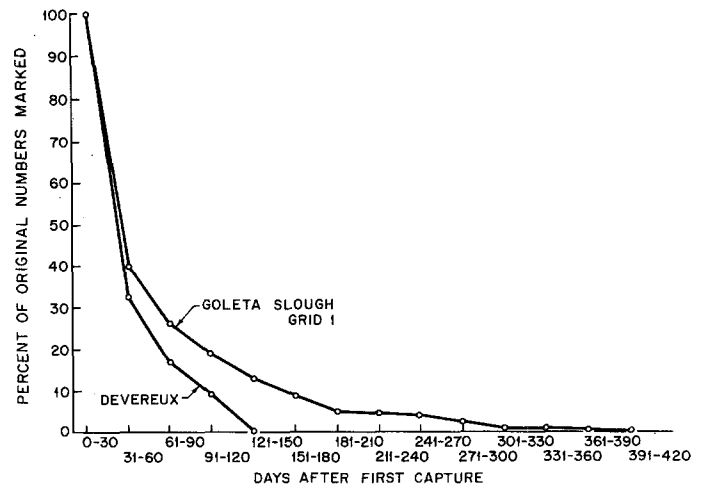


Fig. 7. Percentages of individual adult *Reithrodontomys* recaptured at various times after their first capture. The last six months of the study were not computed for *Reithrodontomys* from the Goleta Slough. $N=168$ for the Goleta Slough. $N=98$ for Devereux

as compared with the high density population phase, and found no significant difference between these rates. However, there were fewer new animals entering the population per month during the last 8 months of the study when the population was quite low ($\bar{X}=3.87$ new animals per month, $SD=2.58$) compared with the number of new animals entering the population per month during the months of highest density (September, 1974–February, 1975; $\bar{X}=22.5$ new animals per month, $SD=6.65$; $\chi^2=7.76$, d.f. = 1, $P<0.01$).

Survival Rates

Within grid comparisons showed virtually identical patterns of survival for females and males. Therefore, survivorship curves are combined for both sexes (Fig. 7). However, differences in survivorship existed between *Reithrodontomys* on Goleta Slough grid 1 and at Devereux. At Devereux, only 33% of the individuals were captured more than 30 days after their initial capture and no individuals were on the grid for more than 120 days (Fig. 7). In the Goleta Slough, the majority of individuals were not captured a second time. However, 40% of the animals did persist for more than one month. Several individuals remained for more than 5 months and one female lived for more than a year. The survivorship curves were significantly different for Goleta Slough 1 and Devereux populations ($P<0.025$, F value = 4.57, d.f. = 3, 13, regression analysis).

In summary, the structure and dynamics of each local *Reithrodontomys* population was different. These differences were in age class structure, recruitment, survivorship, and reproductive potential.

Predators

As the Devereux *Microtus* population increased from February to August, 1974, the number of predators also increased. In February, the only predators observed during eight trapping days at Devereux were one White-tailed Kite (*Elanus leucurus*), one striped skunk (*Mephitis mephitis*) and two dogs (*Canis familiaris*). In July, in three trapping days, four kites were observed. This increased to six kites in three trapping days by August. Also seen at Devereux in July were two skunks, several dogs, Kestrels (*Falco sparverius*), a Cooper's Hawk (*Accipiter cooperii*)

and two gopher snakes (*Pituophis melanoleucus*). Feral cats (*Felis catus*) were common and one long tailed weasel (*Mustela frenata*) was captured in one of the trap station Sherman traps in July. In contrast, after the rodents declined, only one kite was observed in October and November after which no predators of any type were seen. Presumably, the predators left the area after their food supplies were depleted.

White-tailed kites, kestrels and feral dogs were seen intermittently in the Goleta Slough. Other predators were not observed and there was no noticeable increase in the number of predators in the Goleta Slough at any time during the study.

Discussion

Population fluctuations on the Devereux and Goleta Slough grids were asynchronous. Populations of *Reithrodontomys* and *Mus* crashed during the first four months at Devereux, but both species were relatively abundant in the Goleta Slough during the same period. Since climatic conditions on both grids were virtually identical (Blaustein 1978), either the rodents at each site responded differently to the same climatic conditions, or, rodent populations were influenced by other factors that were unique to each study site. Predation and/or competition may have contributed to the population declines of *Reithrodontomys*.

Population crashes at Devereux were probably related to low reproduction rates and predation pressure. Although rodent reproductive activity was also low in the Goleta Slough, the population declines there cannot be easily explained, especially since an increase in predation was not observed.

Reproductive failure of *Reithrodontomys* at Devereux was a proximate factor contributing to its demise. Reproductive failure may have been related to the presence of a potential rodent competitor, the California vole (*Microtus californicus*). There is a significant negative correlation between the presence of voles and reproduction in *Reithrodontomys* in several areas near Santa Barbara, California (Blaustein 1980). *Microtus* may indirectly affect reproduction in *Reithrodontomys* by destroying vegetation in which *Reithrodontomys* make nests. *Microtus* may directly affect the rate of population increase in *Reithrodontomys* by entering its nests and disrupting weaning behavior or by eating young *Reithrodontomys* (see DeLong 1966 and Lidicker 1966). Reduction in food may have also contributed to the demise of *Reithrodontomys*. Studies by Lidicker (1966) and Batzli and Pitelka (1971) in central California suggest that *Microtus* prefers leaves and stems of grasses in winter but switches its food preference to grass seeds in summer. Since *Reithrodontomys* at Devereux is primarily a seed eater (Blaustein personal observation), competition with *Microtus* for seeds in summer may have adversely affected these species. Competition between *Microtus* and *Reithrodontomys* is discussed in detail elsewhere (Blaustein 1980).

Predation pressure upon *Reithrodontomys*, due to the presence of *Microtus* may have led to the ultimate decline of *Reithrodontomys* at Devereux. When a large *Microtus* population existed on the Devereux grid it supported an increasing predator population (Blaustein 1978). When the *Microtus* population declined from July to August, the *Reithrodontomys* population rose from about 65 to more than 90 per ha. A similar increase in *Reithrodontomys* numbers after populations of potentially competing rodents declined occurred during Chandler's (1979) study in Chaparral near Los Angeles. As *Microtus* became rare, predators may have switched to eating the numerous *Reithrodontomys*, causing the subsequent reduction of the *Reithrodontomys* population at Devereux.

Pearson (1963, 1964, 1971) has shown that mammalian predators such as raccoons, foxes, cats and skunks can greatly reduce mouse populations. Carnivores on Pearson's study sites preferred *Microtus* to *Mus* and *Reithrodontomys* but as *Microtus* became rare, predators ate proportionately more *Mus* and *Reithrodontomys*. Pearson tentatively indicated that predation pressure was greatest near the end of a *Reithrodontomys* crash and noted that predators remained on the study sites until virtually no mice were available to them. My limited observations (Blaustein 1978) on predators at Devereux conform to those by Pearson (1964, 1971). Increased predation in the Goleta Slough was not apparent.

Several studies, in a wide range of habitats, have shown that *Reithrodontomys* populations are subject to periodic crashes and extinctions (see for examples, M'Closkey 1972; O'Farrell 1973; Whitford 1976) as was the case at Devereux. Explanations for these crashes were generally not provided, but Whitford (1976) correlated a *Reithrodontomys* population crash in New Mexico with dry conditions. An abnormal dry spell was not apparent prior to the summer extinction of rodents at Devereux and population decline of rodents in the Goleta Slough (Blaustein 1978). However, 1975–1977 were severe drought years in southern California (see Blaustein 1978, and Chandler 1979 for details). Persistent drought conditions probably delayed recovery of rodents by natality after their populations crashed. Life history information supports this. There was a large proportion of reproductively active *Reithrodontomys* on Goleta Slough grid 1 during the drought (Fig. 5), yet recruitment of young was low, inferring poor reproductive success. Although reproduction was low in *Reithrodontomys* during the high density phase in the Goleta Slough, the population remained high for eight months. Recruitment via immigration was important in maintaining high densities during this time. However, as was previously mentioned, the proportion of new recruits during the months with highest population densities was significantly lower when compared with the proportion of recruits at low densities (Fig. 6). This may reflect the establishment of territories or formation of strong hierarchical relationships of the animals on the area at high densities. Newly entering animals probably found it difficult to colonize the study area at this time.

Immigration then, was the main source of recruitment in *Reithrodontomys* populations. Movement from two known *Reithrodontomys* populations (Lagoon Central and Goleta Slough grid 2) to Goleta Slough grid 1 is well within the dispersal capacity of *Reithrodontomys* (Fig. 1; see Brant 1962 and Blaustein 1978 for home range estimates). However, Devereux is not close to any known potential source areas for *Reithrodontomys* or *Peromyscus*. *Reithrodontomys* dispersers could reach Devereux from the Lagoon Central or other extant populations. However, the closest known population of *Peromyscus* is about 3 miles (4.8 km) from Devereux. This is a longer distance than *Peromyscus* generally travel (see Stickel 1968 for review). The *Peromyscus* population at Devereux may not recover for a long time. *Mus* occurs in homes near Devereux and may recolonize quickly. *Microtus* probably follows a cycle and its populations should recover (see Krebs and Myers 1974).

Although the literature suggests that juveniles and males tend to disperse most frequently in certain rodent species (see Fleming 1979; Lidicker 1975 for reviews), this was not the case of *Reithrodontomys*. Adults of both sexes were recruited into the populations. Jule and Cameron (1975) found no sexual differences in their study of *Reithrodontomys* dispersal. Furthermore, *Reithrodontomys* generally travels in heterosexual pairs (Blaustein and Rothstein 1978; Petersen 1975). It would be advantageous for

an individual to travel with a mate if it is the member of a species that is frequently subject to disturbances. This social system would allow individuals to reproduce swiftly once they colonize a new area since there would be no effort involved in finding a mate (see Bekoff 1977).

Several attributes of *Reithrodontomys* probably allow it to exist as a fugitive species. It quickly colonizes disturbed areas such as those subject to flooding (Goleta Slough grid 1, Blaustein 1978). Its climbing ability (Meserve 1976) probably enhances its survival during floods. *Reithrodontomys* quickly colonizes areas vacated by potential competitors (Blaustein 1980), and its numbers may increase as potential competitors decrease in abundance (this study; Chandler 1979). It can utilize dew efficiently and may enter daily torpor in response to osmotic stress, water deprivation or lowered temperatures (Fisler 1965; Coulombe 1970; MacMillen 1964; Reaka and Armitage 1976).

Populations of *Reithrodontomys megalotis* are not persistent when they are sympatric with a large number of other potentially competing rodent species (Brant 1962; M'Closkey 1972; Meserve 1972; O'Farrell 1973; Whitford 1976). The interspecific behavioral subordination of *Reithrodontomys* (Meserve 1972; Blaustein 1980) may make this species extremely susceptible to agonistic interactions with other species. The Goleta Slough population may be persistent because individuals can exist in this disturbed area where other species cannot become established.

Although good correlations of abiotic factors with population irruptions of rodents exist (see for example Pearson 1963 and citations within), there is no general agreement as to the causes of rodent crashes (Lidicker 1966; Pearson 1963). However, that such extinctions and fluctuations occur is important. The simultaneous mass extinctions of several species, as occurred at Devereux is a phenomenon not well documented in the literature. The frequency of such occurrences is necessary to ascertain. These population changes seem to be stochastic events and are difficult to explain.

The information pertaining to *Reithrodontomys* supports the Andrewartha and Birch (1954) model of population regulation to the extent that local population extinctions among *Reithrodontomys* occurred, and that immigration rather than reproduction within certain demes is the most important source of recruitment. The data also support the prediction of Lidicker (1978) that demographic diversity is expected among different populations of the same species. I have documented a declining population (Goleta Slough grid 1), a population that became extinct (Devereux) and populations that were relatively dense (Lagoon Central, Goleta Slough grid 2) during the same time span. *Reithrodontomys* may go extinct locally yet persist globally due to its fugitive species strategy and non-equilibrium ecological events.

Andrewartha and Birch (1954) suggested that environmental heterogeneity may reduce the chance of extinction. In their model some populations are increasing while others are declining towards extinction and still others are remaining relatively stable. Each local population may go extinct but propagules from surviving populations will eventually recolonize the vacated sites. Evidence supporting this non-equilibrium view is accumulating from field studies of sessile organisms, particularly those conducted in the marine intertidal (see Sousa 1979 for review). As the dynamics of local populations of terrestrial vertebrates are studied in greater detail, it is likely that many of these populations will be observed to be in a non-equilibrium state. Although immigration and breeding of *Reithrodontomys* in the present study seem to be affected in a density dependent fashion in the Goleta Slough, this does not preclude a non-equilibrium state. Density dependent population regulation may be evident

on a local scale. However, when viewed on a global scale, the non-equilibrium nature of the populations becomes clear. Density dependent population processes and non-equilibrium states are not mutually exclusive. It is not clear whether density dependent or density independent population regulation is the overriding force influencing the small mammal population changes. The importance of density independent mechanisms in vertebrate population regulation should not be overlooked. Populations of small mammals may not be stable (Krebs and Myers 1974; Southern 1979), and small mammals may be more "insect-like" than is generally supposed.

Acknowledgments. I wish to express my appreciation to Steve I. Rothstein for all his help during the study. My interactions with Joe Connell, Barbara DeWolfe, Sally Holbrook, Armand Kuris, Sam Sweet, and Bob Warner were most helpful and very stimulating.

Field assistance was provided by Sharman Blaustein, Gary Fugle, Harold Haider, and Rebecca Jensen. Dick Broder and Dale Smith kindly assisted me in identifying plant species.

I wish to especially thank Sharman Blaustein for all her help, patience and encouragement throughout the study.

Discussions about population dynamics with Michael Gaines, Charles Krebs, William Lidicker and Bruce Menge helped to improve the manuscript. I wish to especially thank Wayne Sousa for all his time and patience in helping me to formulate my ideas on population and community dynamics. Early drafts of the manuscript were read by J.H. Connell, B.B. DeWolfe, M.S. Gaines, S.J. Holbrook, M.J. O'Farrell, S.I. Rothstein, H.S. Shellhammer and the OSU Ecology Group.

The present draft was greatly improved by the critical readings of Charles Krebs and William Lidicker.

Partial financial support was provided by Sigma Xi and the O.B.B. of S.P.D.

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Received August 9, 1980