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# REPRODUCTION AND POPULATION STRUCTURE OF POCKET GOPHERS (Thomomys bottae) FROM IRRIGATED ALFALFA FIELDS.

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ABSTRACT: Pocket gophers were collected from irrigated alfalfa fields (IRR) and non-irrigated fallow fields (NIRR) in Davis, California, for 2 years. Reproduction was continuous in IRR fields with very little seasonal variation in reproductive activity. In contrast, reproduction in NIRR fields occurred primarily during the rainy season (winter and spring). Females in IRR fields produced approximately twice as many litters per year (3.6-3.9) as females in NIRR habitats (1.7). The high reproductive potential of adult females in IRR fields coupled with the early age of sexual maturity among young females suggests that population recovery after control measures is likely to be relatively rapid in irrigated alfalfa fields. Immigration into the optimal habitat of irrigated alfalfa fields is also likely to add to rapid recovery if gopher populations in nearby areas are not controlled as well.

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## INTRODUCTION

The burrowing and foraging of pocket gophers (Family Geomyidae) can have large impacts on both natural (e.g., Tilman 1983, Hobbs and Mooney 1985, Cantor and Whitham 1989) and managed (e.g., Crouch 1971, Foster and Stubbendieck 1980, Luce et al. 1981) ecosystems. On agricultural fields, ranges, and forest regeneration areas, the removal, burial, and/or damage to vegetation caused by pocket gophers can cause significant economic loss (Chase et al. 1982). For example, pocket gophers can significantly reduce the amount of forage for livestock on rangeland (Foster and Stubbendieck 1980) and damage and removal of seedlings in pine plantations can cause greater than 65% mortality within 3 to 5 years (Crouch 1971, Hooven 1971). Pocket gophers in alfalfa fields can significantly reduce alfalfa yields and cause a significant increase in weedy species (Luce et al. 1981). Thus, control of pocket gophers may often be necessary to maintain productivity.

Several applicators, toxicants, baits, and traps have been developed to control pocket gophers in various habitats (Storer 1958, Marsh and Cummings 1977). In most agricultural situations, damage control is accomplished through a reduction in pocket gopher numbers. Thus, effective and efficient control necessitates a thorough understanding of the ecology and biology of pocket gophers, particularly pocket gopher population dynamics and the effect of both biotic and abiotic factors on various population parameters.

This paper presents data on several components of the overall birth rates of pocket gophers (Thomomys bottae navus) in irrigated alfalfa fields and in nearby non-irrigated fallow fields in Davis, California. Specifically, the seasonal timing of reproduction, litter size, number of litters per female per year, and the age structure of the population are examined. The reproductive patterns of pocket gophers from the two habitat types are compared, and the importance of considering the reproductive patterns of pocket gophers in alfalfa fields as well as in surrounding areas in models of pocket gopher population control is discussed.

## METHODS

The study was conducted on the University of California, Davis campus. The area is characterized by a Mediterranean climate with cool, rainy winters and hot, dry summers. Pocket gophers were collected from two habitat types: 1) irrigated alfalfa fields (IRR), and 2) non-irrigated fallow fields (NIRR). Alfalfa fields were cut and flood irrigated every 3 to 4 weeks from May through September. Alfalfa was by far the dominant plant in IRR fields but other plant species such as barley (Hordeum spp.), white lawn clover (Trifolium repens), mallow (Malva neglecta), curly dock (Rumex crispus), and morning glory (Convolvulus arvensis) were also in these fields. NIRR fields received only natural precipitation which occurred from mid-October through April in 1979-80 and from late December through mid-April in 1980-81. Total rainfall was 63.7 cm in 1979-80 and 28.7 cm in 1980-81. During winter and spring NIRR fields were dominated by weedy annuals such as barley (Hordeum spp.), wild oats (Avena fatua), fiddleneck (Amsinckia intermedia), mallow (M. neglecta), miner's lettuce (Montia perfoliata), chickweed (Stellaria media), and redstem storksbill (Erodium cicutarium). Yellow star thistle (Centaura solstitalis) and morning glory (C. arvensis) were the dominant species during summer.

Pocket gophers were collected monthly from both habitat types from July 1979 through June 1981. Trapping began at the beginning of each month and continued until at least 30 pocket gophers had been collected from each habitat (trapping usually took 2 to 3 weeks). Gophers were collected by placing Macabee kill-traps in burrow systems that showed signs of recent gopher activity (fresh mounds or earth plugs). All captured gophers were placed in plastic numbered bags and returned to the laboratory for processing. Gophers were weighed on a triple beam balance and standard measurements were taken.

Reproductive condition of all animals was determined as follows. Males with epididymides containing large distinct tubules were classed as capable of reproducing whereas those with small opaque epididymides were classed as nonreproductive (Tryon 1947). Females were classed as lactating if the mammary glands showed development, the nipples were enlarged, and the fur around the nipples was licked away. The uterus was removed and examined macroscopically for the presence of embryos and placental scars. Placental scars, viable embryos, and resorbing embryos were counted and recorded. The crown-rump length of all embryos was measured with dial calipers and the average crown-rump length of viable embryos was used as a measure of embryo size. The pubic symphysis gap of all females was measured if it had begun to form.

Males were classed as adult if they weighed $\geq$ 110 g (Miller 1946, Gunther 1956). Females were classified as adult or subadult based on the size of the pubic symphysis gap. The pubic symphysis in female pocket gophers is permanently dissolved at sexual maturity to allow for the passage of young (Hisaw 1924). Most females in this study with a pubic symphysis gap of 6 mm or greater showed evidence of past or present reproductive activity. Females with a pubic symphysis gap of less than 6 mm either showed no signs of past or present reproductive activity or showed signs of approaching sexual maturity (e.g., a somewhat enlarged uterus with a greater degree of vascularization than that seen in females with a closed symphysis). Hence, females were classed as adults if the pubic symphysis gap was $\geq$ 6 mm. In addition 12 females had a closed or only partially opened pubic symphysis but were definitely of adult size (greater than 110 g). These females were also classed as adults.

For analysis, data were grouped by season: summer (July-September), fall (October-December), winter (January-March), and spring (April-June). $\underline{X}^2$ contingency tests were used to test for differences in reproductive activity and age structures of the populations between seasons within habitats and between habitats. Student's $\underline{t}$-tests were used to compare litter sizes between years within habitat types and between habitats. Because embryo resorption increases with embryo size, the best estimates of litter size at birth are obtained from larger sized embryos (Loeb and Schwab 1987). Thus, only medium (10 - 20 mm crown-rump length) and large (> 20 mm crown-rump length) sized viable embryos were used to estimate litter size at birth. Means $\pm$ 1 S.E. are presented.

## RESULTS

A total of 1,457 pocket gophers were collected from the two habitats over the 2 years of the study: 728 from IRR fields and 729 from NIRR fields. Trapping success in IRR fields in 1979-80 was 48.0% which did not differ significantly ($\underline{X}^2$ = 0.52, $\underline{\text{d.f.}}$ = 1, $\underline{P}$ > 0.05) from trapping success in NIRR fields (46.1%). However, in 1980-81 trapping success in IRR fields (44.0%) was significantly higher ($\underline{X}^2$ = 11.60, $\underline{\text{d.f.}}$ = 1, $\underline{P}$ < 0.001) than in NIRR fields (36.4%). The age and sex composition of the samples are reported in later sections.

### Reproduction and Population Structure -- IRR fields.

Reproductive activity in IRR fields was essentially continuous throughout the study (Fig. 1a and 1b). At least 50% of the adult males were in reproductive condition during every season and the proportion of adult males in reproductive condition did not vary significantly among seasons in either 1979-80 ($\underline{X}^2$ = 4.57, $\underline{\text{d.f.}}$ = 3, $\underline{P}$ > 0.05) or 1980-81 ($\underline{X}^2$ = 2.96, $\underline{\text{d.f.}}$ = 3, $\underline{P}$ > 0.05). In 1979-80, however, 77.5% (124/160) of the adult males were in reproductive condition whereas in 1980-81 only 62.6% (104/174) of the adult males were in reproductive condition. The difference was statistically significant ($\underline{X}^2$ = 8.72, $\underline{\text{d.f.}}$ = 1, $\underline{P}$ < 0.003).

Reproductive activity of females from IRR fields exhibited more seasonal variation than that of males (Fig. 1b). In 1980-81, the proportion of adult females in reproductive condition (pregnant and/or lactating) varied significantly among seasons ($\underline{X}^2$ = 9.01, $\underline{\text{d.f.}}$ = 3, $\underline{P}$ < 0.05) with the highest level of reproductive activity occurring during the spring and summer months (Fig. 1b). Spring and summer were also the periods of highest reproductive activity in 1979-80 but variation among seasons was not significant ($\underline{X}^2$ = 6.56, $\underline{\text{d.f.}}$ = 3, 0.10 > $\underline{P}$ > 0.05).

Despite some seasonal variation in the reproductive activity of females from IRR fields, reproduction in these fields can still be considered continuous. At least one pregnant female was collected from these fields in 23 of the 24 months, and in no season were less than 50% of the females in reproductive condition. Overall, 64.4% (103/160) of the adult females from IRR fields were in reproductive condition in 1979-80 and 69.7% (101/145) were in reproductive condition in 1980-81; the proportion of adult females in reproductive condition did not differ significantly between years ($\underline{X}^2$ = 0.95, d.f. = 1, $\underline{P}$ > 0.05).

Estimated litter size at birth was 5.23 $\pm$ 0.50 ($\underline{n}$ = 26, range 2-12) in 1979-80 and 4.25 $\pm$ 0.42 ($\underline{n}$ = 20, range 1-8) in 1980-81. The difference between years was not significant ($\underline{t}$ = 1.45, $\underline{P}$ > 0.05). When data for both years are combined the estimated litter size at birth is 4.80 $\pm$ 0.34. The number of litters per female per year was estimated by the method of Scheffer (1933, 1938). In 1979-80, adult females from IRR fields produced an average of 3.9 litters and in 1980-81, females produced an average of 3.6 litters. Production of young averaged 20.4 per female in 1979-80 and 15.3 in 1980-81.

Seasonal age structure of the population is shown in Fig. 2. Only 12.8% of the population in 1979-80, and 11.6% of the population in 1980-81 were subadults. Age structure (the proportion of subadults in the population) did not differ significantly between years ($\underline{X}^2$ = 0.23, $\underline{\text{d.f.}}$ = 1, $\underline{P}$ > 0.05) or among seasons in either 1979-80 ($\underline{X}^2$ = 0.24, $\underline{\text{d.f.}}$ = 3, $\underline{P}$ > 0.05) or 1980-81 ($\underline{X}^2$ = 5.46, $\underline{\text{d.f.}}$ = 3, $\underline{P}$ > 0.05).

### Reproduction and Population Structure--NIRR Fields.

In contrast to IRR fields, reproduction in NIRR fields was highly seasonal (Fig. 1c and 1d). The proportion of adult males in reproductive condition in NIRR fields varied significantly among seasons in both 1979-80 ($\underline{X}^2$ = 40.65, $\underline{\text{d.f.}}$ = 3, $\underline{P}$ < 0.0001) and 1980-81 ($\underline{X}^2$ = 39.21, $\underline{\text{d.f.}}$ = 3, $\underline{P}$ < 0.0001). In both years, the proportion of adult males in reproductive condition was low in summer, increased during fall, reached a peak of almost 100% in winter, and declined again in the spring (Fig. 1c). The proportion of adult males in reproductive condition was 70.3% (111/158) in 1979-80 and 59.4% (76/127) in 1980-81. The difference between years was marginally significant ($\underline{X}^2$ = 3.38, $\underline{\text{d.f.}}$ = 1, $\underline{P}$ = 0.07). The proportion of adult males in reproductive condition did not differ significantly between IRR and NIRR fields in either 1979-80 ($\underline{X}^2$ = 2.16, $\underline{\text{d.f.}}$ = 1, $\underline{P}$ > 0.05) or 1980-81 ($\underline{X}^2$ = 0.24, $\underline{\text{d.f.}}$ = 1, $\underline{P}$ > 0.05).

Reproductive activity among females from NIRR fields was also highly seasonal and followed a similar pattern to that of the males (Fig. 1d). There was significant variation in the proportion of adult females in reproductive condition among seasons in both 1979-80 ($\underline{X}^2$ = 13.98, $\underline{\text{d.f.}}$= 3, $\underline{P}$ < 0.005) and 1980-81 ($\underline{X}^2$ = 14.95, $\underline{\text{d.f.}}$ = 3, $\underline{P}$ < 0.005). In 1979-80, reproductive activity was low during the summer, increased during the fall, reached a peak in winter and declined again in spring. Reproductive activity continued to decline through the summer and fall of 1980-81 and did not increase until winter. There were no pregnant or recently parous females captured from these fields during August, September, November, or June of 1979-80, nor from August through January 1980-81, although some females appeared to be lactating during some of these months. In 1979-80, 52.3%

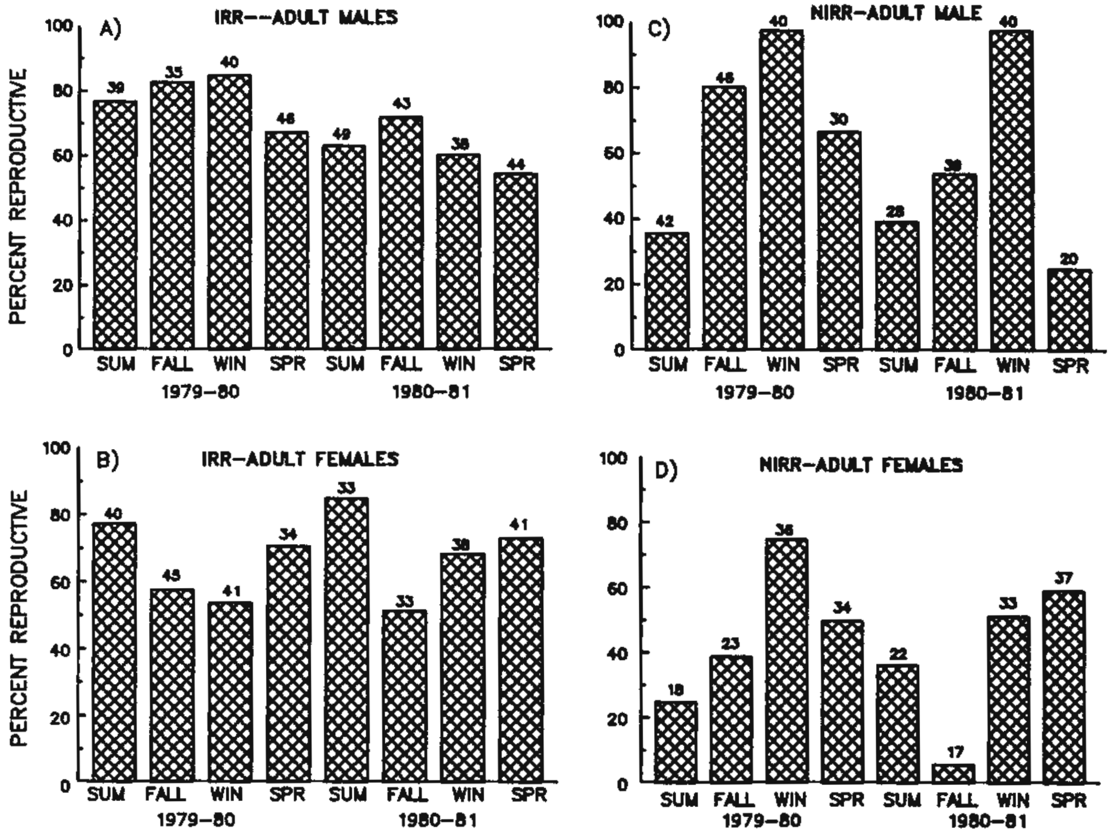


Fig. 1. The proportion of adult pocket gophers in reproductive condition from irrigated alfalfa fields (IRR) and non-irrigated fallow fields (NIRR). Females were considered reproductive if they were either pregnant or lactating. Numbers above histobars denote the total number of adults captured during the season.

(57/109) of the adult females from NIRR fields were in reproductive condition and in 1980-81, 44.0% (48/109) were in reproductive condition. The proportion of adult females in reproductive condition did not differ significantly between years ($X^2$ = 1.49, d.f. = 1, $P > 0.05$). However, the proportion of adult females in reproductive condition was significantly lower in NIRR fields than in IRR fields in both 1979-80 ($X^2$ = 3.89, d.f. = 1, $P < 0.05$) and 1980-81 ($X^2$ = 16.75, d.f. = 1, $P < 0.001$).

Estimated litter size at birth was 4.25 $\pm$ 0.62 ($n$ = 8, range 2-8) in 1979-80 and 3.71 $\pm$ 0.57 ($n$ = 7, range 2-6) in 1980-81. The difference between years was not significant ($t$ = 0.63, $P > 0.05$) and the estimated litter size at birth for both years combined was 4.00 $\pm$ 0.41. Estimated litter size at birth did not differ significantly between NIRR and IRR fields in either 1979-80 ($t$ = 1.01, $P > 0.05$), 1980-81 ($t$ = 0.69, $P > 0.05$), or for both years combined ($t$ = 1.25, $P > 0.05$). The estimated number of litters per year for females from NIRR fields was 1.7 in both 1979-80 and 1980-81. The production per female averaged 7.2 young in 1979-80 and 6.3 young in 1980-81.

In 1979-80, subadults made up 27.5% of the population from NIRR fields and 34.6% of the population in 1980-81. There were significantly more subadults in the population in 1980-81 than in 1979-80 ($X^2$ = 4.40, d.f. = 1, $P < 0.05$). The proportion of subadults in the population also varied significantly among seasons in both 1979-80 ($X^2$ = 9.83, d.f. = 3, $P < 0.05$) and 1980-81 ($X^2$ = 14.38, d.f. = 3, $P < 0.005$). In both years, the proportion of subadults was highest in the summer, decreased in the fall, was lowest during winter and increased again in spring (Fig. 2b). There were significantly more subadults in NIRR fields than in IRR fields in both 1979-80 ($X^2$ = 24.49, d.f. = 1, $P < 0.0001$) and 1980-81 ($X^2$ = 53.66, d.f. = 1, $P < 0.0001$).

## DISCUSSION

Dixon (1929) and Scheffer (1938) suggested that pocket gophers probably reproduce throughout the year in irrigated fields in central and southern California but they lacked sufficient data from summer months to document it. However, in a 14-month study conducted in Davis, California, Miller (1946) showed that reproduction in irrigated alfalfa fields occurred throughout the year. The present study further substantiates year-round reproduction in irrigated alfalfa fields in central California.

Year-round reproduction in IRR fields is likely due to the constant availability of nutritious green forage brought about by irrigation during the summer. A comparison of reproductive patterns of pocket gophers in IRR and NIRR fields illustrates the importance of precipitation and green forage for pocket gopher reproduction. Pocket gopher reproduction in NIRR fields was restricted to the periods of natural rainfall, i.e., the winter and spring months. During the dry summer months little green forage was available but soon after the onset of the winter rains, there was a flush of green vegetation as the winter annuals germinate. In both years, the peak in breeding in NIRR fields began approximately 1 to 1-1/2 months after the initiation of the winter rains. Reproduction essentially ceased during late spring and summer after the annuals had set seed and died.

In contrast, spring and summer were the periods of highest reproductive activity in IRR fields.

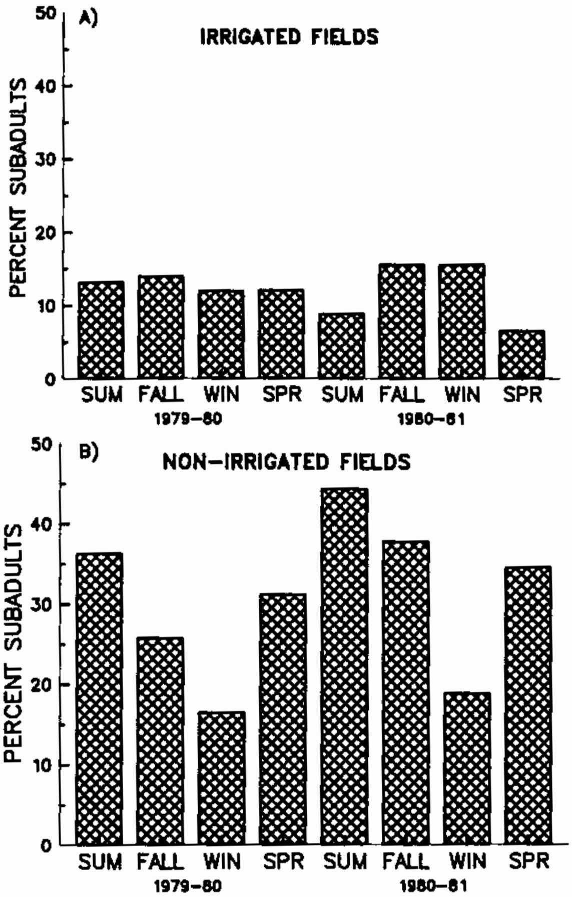


Fig. 2. Proportions of the populations collected from irrigated alfalfa fields and non-irrigated fallow fields that were subadults.

Females in IRR fields produced approximately twice as many litters per year as females in NIRR fields. Furthermore, the largest potential litter size of a female from IRR fields was 12, whereas the largest potential litter size of a female from NIRR fields was 8. Patton and Brylski (1987) found that litter sizes of pocket gophers in an eastern California desert habitat were significantly larger in irrigated alfalfa fields than in nearby non-irrigated natural habitats. Thus, in some situations irrigation in alfalfa fields may not only increase the number of litters produced per female but also the number of young in each litter.

Despite the high reproductive potential of pocket gophers in IRR fields resulting in reproductive rates 2 to 3 times greater than in NIRR fields, the proportion of subadults in IRR fields was significantly lower than in NIRR fields. The lower proportion of subadults in IRR fields may be due to several factors including increased subadult mortality, increased emigration, decreased adult mortality and/or increased growth rates of gophers in IRR fields. The consequences of these factors, in terms of population growth, are quite different. For example, if the low number of young in IRR fields is due to high mortality rates and/or emigration of young, then the population is likely to remain stable even with the high rates of reproduction. In contrast, if the low number of young in the population is due to high growth rates and early maturity, then the population is likely to be increasing. Thus, it is important to determine which factor(s) contribute most to observed age ratios.

Increased mortality--The high rate of reproduction in IRR fields and the significantly larger body size of pocket gophers from IRR fields than NIRR fields (Loeb 1981) suggests that females had sufficient body stores and energy for lactation. Thus, increased pre-weaning mortality in IRR fields relative to NIRR fields is unlikely and, if subadult mortality was greater in IRR fields, it most likely occurred after weaning.

Pocket gophers are solitary, territorial animals and young disperse from the natal burrow sometime after weaning to take over an existing burrow system or establish a new system (Howard and Childs 1959, Williams and Cameron 1986). Dispersal by pocket gophers is primarily above-ground (Howard and Childs 1959), making dispersing animals more vulnerable to above ground predators such as hawks and owls. Pocket gopher densities in IRR fields are many times higher than in NIRR rangeland (Howard and Childs 1959) and may reach as high as 50/acre (Miller 1957). Thus, the high densities in IRR fields might mean that young pocket gophers in IRR fields would have to disperse farther than young gophers in the less dense NIRR fields to find a vacant burrow system or an area in which to establish a new burrow system. Longer dispersal distances (relative to young in NIRR fields) would increase chances of predation resulting in higher mortality rates. While no data are presently available to support this hypothesis, some evidence is available to refute it, at least in part. Due to the high quality and quantity of forage in IRR fields, pocket gopher burrow systems in IRR fields are only 40% the size of burrow systems in non-irrigated rangelands (Howard and Childs 1959). Reduced territory size would serve to reduce the distance to vacant systems or areas, despite the high densities. Also, during the present study, IRR fields did not appear to be saturated with active pocket gopher burrows and there were many areas within these fields where pocket gophers were either sparse or nonexistent. Thus, although mortality rates of young pocket gophers may have been higher in IRR fields than in NIRR fields, it is unlikely that they were high enough to explain the disparate age ratios between the populations.

Increased emigration--Due to high densities of pocket gophers in IRR fields, young pocket gophers may have to emigrate out of these fields to suboptimal habitats such as NIRR fields. Emigration would not only decrease the number of young in IRR fields, but also increase the number of young in NIRR fields. No data are presently available on dispersal distances of young pocket gophers in IRR fields and/or movement between habitats. Thus, it is not possible to determine the importance of emigration to the age structure of the populations in the two habitats.

Increased adult survival--No data are presently available which compares survival of pocket gophers from IRR and NIRR fields. The higher nutritional plane and larger body size of pocket gophers in IRR fields suggests that adults in these fields may have greater survival rates than adults in NIRR fields (e.g., less vulnerable to predation or poor weather and food conditions). However, survival of adult male pocket gophers is not related to body weight (Daly and Patton 1986) which suggests that survival may not differ greatly between the two habitats.

Differential growth rates--Pocket gophers in irrigated alfalfa fields have faster growth rates than pocket gophers in non-irrigated natural habitats (Patton and Brylski 1987). The increased growth rate of young in IRR fields is likely due to the year-round availability of green forage, the high nutritional value of alfalfa, and year-round optimal burrowing conditions. Thus, no matter when pocket gophers are born in IRR fields, they will experience optimal conditions for growth. In contrast, in NIRR fields most of the young are born in late winter and spring and are probably weaned during late spring and early summer. Late spring and summer are the periods of little or no rainfall. It is unlikely that pocket gophers in NIRR fields can obtain sufficient energy and nutrients for rapid growth at this time, and much of their growth is probably delayed until after the onset of the winter rains as illustrated by the seasonal age structure of the population (Fig 2b). Thus, while young animals in IRR fields can enter the adult population within a few months of weaning no matter when they are born, the majority of young in NIRR fields do not enter the adult population until late fall or early winter (at approximately 6 to 9 months of age). I suggest that differential growth rates are responsible, in large part, for the low number of young in IRR fields relative to NIRR fields, despite the high reproductive rates.

An accelerated growth rate and earlier age at reproduction will have important consequences for the growth of populations in IRR fields. The instantaneous rate of increase, $r$, is highly sensitive to the age at first reproduction (Cole 1954, Stearns 1976). Decreasing the age at first reproduction can greatly increase the population rate of increase. It is not known whether males who reach 110 g at an early age can reproduce in IRR fields. However, because one male can breed with several females (Patton and Feder 1981), the age of sexual maturity of females is the most critical. In seasonally breeding populations of pocket gophers young females born early in the breeding season may often breed in the year of their birth (Howard and Childs 1959, Daly and Patton 1986). In IRR fields, the breeding season is continuous, thus it is likely that most females in IRR fields breed in their first year.

In summary, irrigated alfalfa fields provide excellent conditions for pocket gopher population growth and maintenance. The high nutritional quality of alfalfa, the year-round availability of green forage, and year-round optimal burrowing conditions brought about by irrigation practices result in a continuously breeding population as well as early recruitment of young into the breeding population and possibly increased litter sizes.

### Control Implications

One of the largest problems in pocket gopher control is maintaining the population at a low level after the initial control effort. The results of the present study suggest that this may be very difficult in irrigated alfalfa fields. The high rate of reproduction due to year-round breeding and the early recruitment of young into the breeding population mean that the remaining population is likely to recover relatively rapidly. Because the population density will be reduced after control, any increased mortality due to longer dispersal distances is also likely to be reduced, resulting in higher survival of young. Further, population reduction will result in many vacant burrow systems. While little is still known about pocket gopher dispersal, it is likely that many of these burrow systems will be occupied by pocket gophers dispersing from surrounding areas. If surrounding areas are not irrigated, the greatest influx in dispersing young is likely to occur in early spring and summer and reinvasion should be monitored closely at this time. If surrounding areas are other irrigated alfalfa fields, reinvasion is likely to occur at a steady rate throughout the year. Thus, maintenance of low gopher populations in irrigated alfalfa fields will likely necessitate repeated control operations in the fields themselves and periodic control operations in surrounding areas. The periodicity of control in surrounding areas will depend on the types of habitats surrounding the alfalfa fields.

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