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[FINAL]

EFFECT OF DENSITY ON THE POPULATION DYNAMICS OF *PEROGNATHUS FORMOSUS* AND ITS RELATIONSHIPS WITHIN A DESERT ECOSYSTEM

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ABSTRACT

In April 1973 the populations of *Perognathus formosus* in Plot C in Rock Valley were artificially increased. Herb and seed production were very high in 1973 and the introduced mice survived and reproduced, building up a peak density of 49 mice/ha in August. These populations were censused during 1974 and in April 1975, in both the experimental half of Plot C with sheet metal barriers (southern) and the control half (northern). In March 1974, densities in Plot C were 33.6/ha (S) and 33.9/ha (N), and an estimated 2/ha in Plot A, which has never been manipulated. Although some mice became sexually active in the spring in Plot C, no pregnant females or young animals were captured. In the absence of reproduction, densities declined to 19.6 (S) and 23.5/ha (N) in August 1974 and 6.1 (S) and 7.2/ha (N) in April 1975. In April, 90% of males and 57% of females were sexually active; 27% of females were pregnant. In Plot A each female produced about nine young in 1974. Herb production was 23.3 kg/ha in the spring of 1974, compared to 4.5 kg/ha in 1972, when pocket mouse reproduction was good, and 802 kg/ha in 1974 when reproduction was very high. Mean monthly body weights were significantly lower every month in 1974 than in 1972. The accumulated data for Rock Valley indicate that the reproductive success of *P. formosus* is principally limited by population density at the beginning of the breeding season, in an inverse fashion. Whenever spring densities have been higher than 27/ha, there has been no reproduction. The quantity of herb production seems to have little effect except when it is exceptionally high. Very high herbage production apparently mitigates density effects and permits good reproduction. The test of the hypothesis that the density-dependent effect is the result of behavioral interactions of pocket mice was inconclusive.

INTRODUCTION

In 1972 certain density-dependent relationships were found for *Perognathus formosus* that were manipulated so as to have initially low, medium and high densities in 4.4- and 8.9-ha enclosures (Chew et al. 1973). Within this year of low herbage and seed production, the incidence and duration of sexual activity, the number of young weaned per successful pregnancy and survival were inversely related to density. In 1973 the populations in the two, 4.4-ha enclosures were increased to very high densities at the start of the season, and one enclosure was modified by the addition of 60 sheet metal barriers 15.2 m long x 32 cm high, installed in a semigrid pattern. We wished to test the hypothesis that the barriers would reduce intraspecific interactions, consequently resulting in a higher equilibrium density in the enclosure with barriers than in the one without barriers. Extraordinary herbage and seed production occurred in 1973 (Chew and Nelson 1975, Turner et al. 1974), and the high mouse densities were not only maintained, but they expanded. Reproduction was high and mortality was low. There was no significant difference in the growth curves of the two populations; neither declined to an equilibrium level (Chew and Turner 1974). Consequently, the hypothesis was not tested. In the area with barriers, male home range was reduced and males showed more and longer reproductive activity. This could be interpreted as due to the male pocket mice being under less stress as a consequence of reduced movement and contact with each other. However, females were sexually more active in the nonbarrier enclosure. It was decided to prolong the period of testing of the hypothesis through 1974 since it was unlikely that herb production would again be exceptionally high, although there could be a residual beneficial effect of seed reserves built up in 1973.

OBJECTIVE

The objective was to continue to test the hypothesis that the carrying capacity of the enclosure ecosystems for *Perognathus formosus* is limited by density, through behavioral interactions, instead of by food resources.

METHODS

In 1974 the *P. formosus* populations were not manipulated, but were subject only to periodic censusing. The methods of census and analysis were the same as in 1972 and 1973 (see Chew et al. 1973), except that the interval of sampling was increased from every two weeks to 21 to 33 days (Table 1). Also, since there were lower mouse densities in 1974, we were able to weigh the first 30 *P. formosus* captured each census in each enclosure. The tests of hypothesis remained as in 1973 (Chew and Turner 1974).

RESULTS

POPULATION SIZES

Table 1 summarizes the numbers of individuals in the two populations at sampling times from September 11, 1973, to April 11, 1975. Mice are categorized according to sex and plot. The southern side of enclosure C is the experimental plot with sheet metal barriers, the northern side is the control. Each plot is about 4.43 ha. The numbers of males, sample by sample, are significantly different in the two plots ($\chi^2 = 23.6$, $\chi^2_{0.05(n=8)} = 15.5$, but the numbers of females and total numbers are not different.

PATTERN OF MORTALITY

Mortality rates were calculated for each category in Table 1. Caculations are for three "seasons"; overwinter 1973-74, active season 1974 (March 12 to August 12) and overwinter 1974-75. The lambda values (decline in numbers per head per day) are given in Table 2. Analysis of variance of the lambda values shows a significant effect of season; mortality was lower during the active season than overwinter when the mice generally stay below ground. The effect of season also significantly depends upon sex and plot. Male mortality was lower than female overwinter but was higher than female during the active season. Mortality in the southern

Table 1. Number of *P. formosus* alive on successive sampling dates, according to sex and plot: southern plot is the experimental plot with barriers, northern is the control (A3UCC01)

Category			Field Season of 1974							
Sex	Plot	Sept. 11, 1973	March 12, 1974	April 3, 1974	April 25, 1974	May 19, 1974	June 12, 1974	July 15, 1974	Aug. 12, 1974	April 11, 1975
♀	S	194	61	56	51	49	48	43	39	11
♀	N	243	74	69	68	65	61	57	54	15
♂	S	221	88	72	65	61	55	52	48	16
♂	N	223	76	71	66	61	57	55	50	17

plot was less than in the northern during the active season; the two plots were almost the same in the overwinter periods.

The mice were also categorized, within sex and plot, according to their source in the 1973 populations, i.e., whether they were introduced into the plots from outside as adults or juveniles, or born in the plots early in the year (April-June), in midseason (July) or late (August-October). These categories are given in Table 3. Analysis of variance was done for sex x plot x birth time, within the overwinter period 1973-74 and within the active season 1974. Overwinter there was a significant effect of category on mortality rate ($P < 0.05$); mice that were born late in 1973 had lower survival. There was no significant effect within the active season.

REPRODUCTIVE ACTIVITY

The percentages of individuals that were sexually active in the period March to August 1974, are summarized in Table 4. No female was observed to be pregnant or lactating and no young animal was captured. Anova shows a significant effect of sex on sexual activity; more males were active than females. The probability of a plot effect is between 5 and 10%.

BODY WEIGHT

Body weights of adults are summarized in Table 5. The weights are clearly lower in 1974 than in 1972 and 1975. The means for each month in 1974 are significantly different from those in 1972 and 1975.

DISCUSSION

The 1974 field season was very different from 1972 and 1973. There was a limited level of sexual activity; no pregnancy or young were registered in Plot C. The population of *P. formosus* in Plot C simply survived through the year, with modest mortality, to resume reproduction the next spring. Of the 156 male and 135 female *P. formosus* registered in March 1974, all of breeding age, 98 males and 93 females were alive in August 1974 (66%), and 33 males and 26 females (20%) were alive and sexually active in April 1975.

Table 2. Mortality rates of *P. formosus* according to sex, season and plot. Mortality rates (lambda values) are percentage loss per day during each season, where $\lambda = (\ln n_1 - \ln n_2)/\text{days}$

		Lambda X 10^5		
		Overwinter	Active season	Overwinter
Sex	Plot	1973-1974	1974	1974-1975
♀	S	632	292	521
♀	N	650	206	527
♂	S	503	396	452
♂	N	588	274	444

Significant effects: Season $P < 0.005$

Sex X Season $0.01 < P < 0.05$

Sex X Plot $P < 0.05$

Table 3. Mortality rates ($\lambda \times 10^5$) of *P. formosus* according to age category, sex and plot during overwinter 1973-74 (A3UCC01)

		Age categories			
Sex	Plot	Introduced	Born early	Born mid-season	Born late
♀	S	506	587	533	831
♀	N	648	516	481	979
♂	S	532	222	548	1028
♂	N	513	473	379	1073
Average		550	450	485	978

Significant effects: Age category $0.01 < P < 0.05$

Table 4. Percentage of *P. formosus* that were reproductively active on successive dates. There was no activity in 1974 after May 19 (A3UCC01)

Sex and reproductive state	March 12, 1974	April 3, 1974	April 25, 1974	May 19, 1974	April 11, 1975
♂ scrotal tested	42.3	38.5	24.4	2.5	90.0
♀ vulva enlarged or cornified	0	22.4	3.4	0	30.8
♀ pregnant or lactating	0	0	0	0	26.9

Table 5. Body weights of adult *P. formosus*, males and females combined, mean and (in parentheses) 95% confidence limits (A3UCC01)

Month	1972	1974	1975
March	19.26 (18.56-19.96)		
April	20.66 (19.99-21.32)	18.67 (17.81-19.52)	19.79 (19.32-20.27)
May	21.16 (20.34-21.98)	17.94 (14.32-21.57)[a]	
June	20.71 (19.88-21.54)	17.23 (16.60-17.60)	
July	20.02 (19.16-20.88)	18.30 (17.69-17.63)	
August	19.94 (19.17-20.71)	17.43 (17.11-17.75)	

Animals of northern and southern plots were significantly different:

N 18.34 (17.80-18.89), S 17.50 (16.93-18.07)

Some limiting condition prevented reproduction in 1974 but the population easily survived one year without reproduction and was of sufficient size to regrow from its April 1975 density of 6.7 *P. formosus* per hectare. Probably a second year of depletion at the same rate could have been survived, since the projected density for April 1976 is 1.34/ha and the population of Plot A in April 1972 grew successfully from a spring density of 1.13/ha to 4.97/ha in July. French et al. (1974) reported similar failures of reproduction in the Rock Valley enclosures: "The rodents virtually failed to reproduce in the study enclosures in 1962, 1963 and 1967." Their Table 12, however, reports that 50.8% of females bred in 1963.

French et al. (1974) pointed out that *P. formosus* has a long life span in the field (for a small rodent); for their populations, mean life expectancy at the time of weaning was 11-14 months (Table 7). Long life, coupled with long reproductive capability (four-year-old mice were breeding in French's populations), is important in times of declining population size "and may be interpreted as an adaptation to fluctuating environmental conditions" (p. 70).

Noy-Meir (1973) described desert ecosystems as a trigger→pulse of growth→reserve system. For plants, the trigger of adequate rainfall occurs in discrete events that have a highly random component; the rainfall results in a pulse of plant reproduction, the plants then survive until the next trigger event on their reserves of seeds, or of water and energy in roots and stems. Stability of the system is conferred by the reserve, and conservative use of the reserve. It is tempting to fit *P. formosus* neatly into this format. That is, to suppose that pocket mice wait for a triggering event before commencing reproduction; the trigger could be the pulse of annual and/or perennial growth. The plant growth could be simply a signal that seed production is to be expected, and/or it may provide essential energy, nutrients and/or water for the processes of reproduction. Pocket mice are adapted to "pay for" their conservatism in waiting for a "signal" by their longevity and prolonged reproductive life. Pocket mice conservatively use their reserves of their own tissues and the reserves of their plant food by resorting to heterothermism, particularly in the winter, reduced activity (remaining underground from October through February, in general) and reduced home range in periods of low plant production (French et al. 1974). However, as yet, the facts do no easily allow one to make this neat fitting of *P. formosus* into the system; the regulation of *P. formosus* reproduction and population growth is complex.

Table 6. Herb biomass in spring and relative reproduction (RP) of *P. formosus* in Rock Valley enclosures

$$\text{RP} = \frac{\text{no. young registered during year}}{\text{no. adult females at start of breeding season}}$$

All numbers are normalized to an area of 9ha

Year	Herb biomass (kg/ha)	Data source	Relative reproduction of *P. formosus*			Ave. RP	Source
1963	3.8	(1)					
1964	5.7	(2)	6/22= 0.27	97/54= 1.80	34/14= 2.43	1.50	(3)
1965	0.24	(2)	79/7= 11.3	492/26=18.9	149/20=7.45	12.55	(3)
1966	185	(4)	133/31=4.29	273/79=3.46	182/48=3.79	3.85	(3)
1967	45	(4)	24/47= 0.51	0/174= 0	0/135= 0	0.17	(3)
1968	247	(4)	73/23= 3.17	130/38=3.42	105/12=8.75	5.11	(3)
1971	6.4	(5)					
1972	4.5	(5)	45/7= 6.42	168/38=4.42	146/106=1.38	4.07	(6)
1973	802	(5)	27/4= 6.75	824/104=7.92	622/104=5.98	6.88	(7)
	234	(8)					
1974	23.3	(5)	74/8= 9.25[a]	0/148=0	0/121=0	3.08	(9)

a/ The population of Plot A was not censused in 1974, however the numbers of mice in 1974 could be estimated from the censuses of October 1973 and March 1975.

Sources of data

(1) Beatley (1969a) for unspecified location in Rock Valley
(2) Beatley (1969b:Table 1) Rock Valley, Beatley plots 3 and 4
(3) French (personal communication), Rock Valley enclosures A, B and C respectively
(4) Wallace and Romney (1972) Rock Valley enclosures
(5) Zone 20, Validation Site, Validation Site Reports of Turner (1972), Turner (1973) and Turner and McBrayer (1974)
(6) Chew et al. (1973) Plot A, Plot C north, and Plot C south (low, medium and high density) respectively.
(7) Chew and Turner (1974) Plot A, Plot C north, Plot C south (low density, super high density without barriers, super high density with barriers) respectively
(8) Chew and Nelson (1975) Plot C
(9) Present report

FACTORS AFFECTING REPRODUCTION

Table 6 summarizes information on herb production and pocket mouse reproduction in Rock Valley over a decade. Values of herb production are not normally distributed, even when transformed to logarithms. Values are skewed to the left (low production) and also have a tendency to bimodal distribution. Table 7 categorizes the values of relative reproduction of pocket mice into low, medium and high categories of herb and rodent reproduction. Relative

Table 7. Categorization of relative reproduction values for *P. formosus* (from Table 6) according to low, medium and high herb production and number of females at start of breeding season

	No. ♀♀ at start of season			
Herb production kg/ha	Low 4-14	Medium 20-79	High 104-174	Category average
Low, 0.24-6.4	2.43 11.3^a 6.42	0.27 1.80 18.9^a 7.45^a 4.42	1.38	6.04 2.79^c
Medium, 23-45	9.25	0.51	0 0 0 0	1.63
High, 185-802	8.75 6.75^b	4.29 3.46 3.79 3.17 3.42	7.92^b 5.98^b	5.28 4.80^d
Category average	7.48 6.72^c	4.68 2.79^c	2.18 0.28^d	

a/ values for 1965

b/ values for 1973

c/ average omitting 1965 values

d/ average omitting 1973 values

reproduction values of five or more indicate breeding by young of the year and/or multiple litters by adult females. Table 7 suggests that, with some exceptions, relative reproduction is inversely related to density of *P. formosus* at the start of the breeding season and that this effect is greater than the effect, if any, of the quantity of herbage produced. Years 1972 and 1974 are particularly suggestive. In 1972, a year of low herb production, relative reproduction of mice ranged from 6.42 to 1.38, inversely with the spring density of the population. In 1974, when herb production was about five times greater than in 1972, mouse reproduction was high in the low-density population, but was zero in the two high-density populations. In 1967, when herb production was about twice that in 1972, there was also zero reproduction in the two populations that began the year with high density. In all cases where the spring density was greater than 120 females per 9 ha (or about 27 males and females per ha) reproduction completely failed. Turner and Chew (in press) found that production of *P. formosus* is negatively related to spring densities. Table 7 suggests that there is no effect of the quantity of herbage, except that very high herb production (as in 1973) can negate the high rodent density effect and permit high relative reproduction.

The year 1965 is very anomalous; herb production was the lowest recorded, whereas relative reproduction was the highest. Beatley (1969b) reported for this year (p. 265-266): "The critical rain failed to come in the autumn of 1964 . . . and through the winter months into early spring the winter annuals were totally absent in most areas. However, mid-March to mid-April was a period of extremely heavy [unseasonal] rainfall . . . During early April there was an out-of-season germination of the winter annuals . . . certain species were represented by numbers of seedlings comparable to [those of] autumn germination. The seedlings grew slowly . . . remained small . . . many not matured . . . at time of onset of summer temperatures." It is tempting to see this unseasonal germination as the trigger to exceptional rodent reproduction, particularly since the herbage biomass was so small.

Elimination of the high values of rodent reproduction of 1965 and 1973 from the averages for categories in Table 7 does not affect the inverse relationship of spring rodent density and level of rodent reproduction; the modified values do provide some basis for seeing a direct relationship of herb production and relative rodent reproduction.

The rankings of herb biomasses and of average relative reproduction of pocket mice (Table 6) were compared by the Kendall rank correlation coefficient. The rankings are not significantly correlated. If all eight pairs are used, N = 4, when $N_{0.05(n=8)} = 36$; if 1965 is omitted from the rankings, N = 18, $N_{0.05(n=7)} = 30$.

REVIEW OF PREVIOUS WORK

Since there has been reference in the literature to a coincidence or relationship between rodent reproduction and herb production in desert ecosystems, I have examined several sources of these conclusions to see if I can come to the same conclusion.

Beatley (1969a) commented (p. 721): "When the rain critical to autumn germination came, winter annuals were present during autumn-to-spring, and there was spring reproduction in the rodents (as indicated by summer densities) [i.e., only a postreproduction census of rodents was taken]. When the critical rain failed to come, winter annual populations were negligible and the rodents did not reproduce in the spring." My statistical analysis of the data given by Beatley (1969a, Table 1), using the Kendall rank correlation test, shows that for 15 sites measuring over five consecutive years (1963-1968), the ranking of density of winter annuals in spring (excluding introduced species) is significantly correlated ($P < 0.001$) with the total number of rodents captured in a grid of 7 x 7 Sherman traps, on a 50-foot interval, set for two nights in July, August or September. On the average, most of the rodents were *Dipodomys merriami* (36%) and *Perognathus longimembris* (37%). Beatley's inference that spring reproduction of rodents was correlated with winter annual density could be confounded several ways, but it is probably reasonable.

The study of Van De Graaff and Balda (1973) was limited to one comparison, but it directly measured reproduction of rodents. They reported on two populations of *D. merriami*, 57 km apart, which existed in contrasting states of vegetative growth; one in the absence of winter annuals and the other in a habitat with annuals and other signs of vegetative growth. In the "absence" of winter annuals, only 15% of the adult males and no adult female *D. merriami* were reproductively active; in the presence of annuals, 95% of males and 92% of females were active. By chi-square test, the difference is significant at the 99% level.

The Reichman monograph (in press) provides abundant data, for a time span of two years, on rainfall, annual density and coverage, and reproduction of five species of heteromyids on sites in the Sonoran Desert near Tucson, Arizona. The number of animals involved is beyond that of any other study. Certain of the conclusions drawn are: a) in "dry years, like the first year of this study, . . . breeding was curtailed, and involved only a small percentage of the population." b) "During the second year . . . the desert received more than double the amount of rainfall of the first year and the subsequent contrasts in vegetation, rodent activity, and reproduction were striking . . . more greenery, more reproductive animals, longer breeding seasons, more polyestrous females." c) "There is a broad association between the number of rodents with green vegetation in their stomachs and the percent of the population in reproductive condition." d) "Among all . . . species there was a significantly higher percentage of individuals reproductive during the second year than during the first. Apparently abundant green vegetation in the second year was an important factor in increased reproduction."

In my analysis I find: a) The rainfall is greater the second year of the study, but less so on the permanent plots than at the Weather Bureau Stations referred to. A difference can be more clearly seen if one considers the months with greater than 25 mm of rainfall (which is the critical, germination-inducing amount in Rock Valley, Nevada). In the permanent plots in 1970-71 there are only three such months, whereas in 1971-72 there are five, and one marginal (22 mm). The curtailment of reproduction by rodents in 1970-71 is definite; in *Perognathus* spp. there was little or no reproductive activity after August and only *D. merriami* had any winter or spring sexual activity. For *D. merriami*, the average monthly percent of active females was 23.3±SE 6.6 in 1970-71 and 66.7±5.9 in 1971-72. b) However, an effect of rainfall on herbaceous vegetation is not apparent in the data given. Density of annuals/100 m^2 on the permanent plots was greater in 1970-71 (dry year) than in 1971-72. For October through May the average density was 3939 ± SE 720 in 1970-71 and 1320 ± 135 in 1971-72. The percentage of ground "dominated by herbaceous plants" was not significantly different in the two years (4.7 ± 0.7% vs. 4.05 ± 1.21% on rocky hills; 4.68 ± 1.10% and 6.61 ± 1.97% on creosote flats). c) There is a "broad association," which can't be statistically tested, between the level of reproduction by females and the greenery content of their stomachs. In *D. merriami* for June-August 1970 the incidence of reproduction was 66.8, 38.6 and 17.1% in consecutive months, while the stomach contents were 3.5, 7.5 and 9% greenery. However, in the winter of 1970 there were 34 and 25% greenery in the stomachs, but no reproduction. In the summer of 1971, *D. merriami* increased up to 97% reproductive activity in females, with only modest greenery intakes (2-12% of stomach contents) in previous months. But, there were then seven months of sustained high reproduction (65-85% of females active) coincident with high intake of greenery (25-66% of stomach contents). In *Perognathus amplus* there was a coincidence of reproduction and greenery intake in August-October 1971 and again in March-May 1972. d) It can only broadly be inferred that green vegetation was a factor in increased reproduction in 1970-72.

In summary, the collective information is not completely supportive of a quantitative relationship of annual production and rodent reproduction. One can infer from the information what one wishes. There is no basis for deciding whether the vegetation is a trigger to reproduction, or for what it is necessary (water, minerals, vitamins, energy).

BODY WEIGHTS

Reduced vigor of the pocket mice in 1974 is clearly seen in their low body weights. Mean monthly body weights in 1974 were significantly less than weights in 1972 (Table 5), which was a year of good reproduction. Weights in 1974 were significantly less than weights of the survivors in April 1975. Unfortunately, in 1974 no weights were taken for the low density population. All weights in Table 5 are for mice in the very high density populations.

PATTERNS OF MORTALITY

In 1974 mortality of *P. formosus* was greater overwinter than during the active season, for both sexes and plots (Table 2). This is not always true. My analysis of French's data (pers. comm.) for mortality of cohorts of young-of-year through successive seasons in enclosures A and C, shows that in 4 of 9 cases winter mortality was greater than during the active season, and in 5 of 9 cases the reverse was true.

In 1974 females had a greater overwinter mortality than males, but females had lesser mortality during the active season. Only a mixed comparison can be made with earlier years. In 1972 and 1973 there were too few resident adults at the start of the year for an analysis of mortality. In 1973 most of the adults in the populations had been introduced from outside the enclosures. However, these introduced animals showed the same pattern as in 1974. Introduced females had a lower mortality than males during the active season ($\lambda_{♀}$ 0.00378 vs. $\lambda_{♂}$ 0.00513). In the overwinter period, introduced females had a greater mortality than males ($\lambda_{♀}$ 0.00556 vs. $\lambda_{♂}$ 0.00517).

I can imagine some basis for a sexual difference in mortality of this sort. Male *P. formosus* have a larger home range than females (Chew et al. 1973); consequently males could have more stress from interactions with other individuals than do females. The broader-ranging males might, however, have larger seed stores than females at the start of the overwinter period. The greater winter mortality of females may be a delayed result of stresses of gestation and lactation and/or the result of smaller seed stores. During the winter period, when the mice are underground, seeds are the only available food (plus, possibly some arthropods); in the active season vegetative parts of plants can supplement seeds.

Table 8. Comparison of selected parameters of *P. formosus* populations in the experimental (southern) and control (northern) plots. a/sigma ± 95% confidence limits

Year	Parameter	Experimental	Control	Level of significance
1973	Home range before June 20			
	introduced ♂♂	17.42 ± 2.30^a	23.87 ± 3.40^a	>95%
	introduced ♀♀	12.94 ± 2.65^a	12.68 ± 2.28^a	n.s.
	% sexually active adults	100	100	n.s.
	No. young-of-year ♂♀	311	412	>95%
	Max. no. sexually active			
	young-of-year ♂♂	48	0	>95%
	young-of-year ♀♀	15	44	>95%
	No. pregnant young ♀♀	2	14	>95%
1974	No. mice/9 ha in March			
	♂♂	61	74	n.s.
	♀♀	58	76	n.s.
	Mortality (λ) March to	♂♂ 0.00396	♂♂ 0.00274	n.s.
	August	♀♀ 0.00292	♀♀ 0.00206	n.s.
	Reproductive activity			
	♂♂	38/76 = 0.50	26/73 = 0.356	>95%
	♀♀	22/56 = 0.39	6/96 = 0.087	>95%

COMPARISON OF EXPERIMENTAL AND CONTROL PLOTS

Table 8 lists some parameters of the populations of *P. formosus* in the experimental (southern) and control (northern) plots. Reduced home range of males in the experimental plot may be a response to the sheet metal barriers. Reduced range and presumably reduced interactions of mice may be the basis for increased sexual activity in the south. Greater range of males in the north may be the basis for greater impregnation of young females in 1973 in the northern population. Such a consequence could not be seen in 1974, since no sexually active female became pregnant in either plot. In 1974 mortality values were lower for southern mice than northern, but this had no significant effect on the numbers of males and females alive at the end of the season in the two plots.

CONCLUSIONS

The accumulated evidence supports the hypothesis that the reproductive success, population growth and production of *P. formosus* in Rock Valley enclosures are inversely related to population density at the beginning of the breeding season. Population control thus has a density-dependent basis. The evidence does not support the hypothesis that density-dependence is due to behavioral interactions of the mice. The data for Rock Valley imply that the quantity of herbage of winter annuals in the spring is not decisive in affecting reproduction of *P. formosus*, except that when herb production is exceptionally high (1973) it may mitigate any rodent density-dependent effects.

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