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Desmodillus.
Gerbillurus paeba
Rhabdomys

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Gorrasis -

COMPARATIVE DEMOGRAPHY OF THREE NAMIB DESERT RODENTS: RESPONSES TO THE PROVISION OF SUPPLEMENTARY WATER

DONALD P. CHRISTIAN 1979

ABSTRACT.—This study was designed to test the hypothesis that increased dietary water intake is a critical factor in desert rodent reproduction. Populations of three Namib Desert rodent species (*Desmodillus auricularis*, *Gerbillurus paeba*, and *Rhabdomys pumilio*) were monitored by mark-and-recapture live-trapping on two study areas, one of which served as a control. On the other, rodents were continuously provided with sources of drinking water. Populations of *G. paeba* and *R. pumilio* grew rapidly following rains in early 1974, and reached peak population sizes in September or October 1974. Reproduction in both of these species on the control area showed marked declines during the hot, dry months of September to December, January, or February. Both *G. paeba* and *R. pumilio* showed marked responses to the increased availability of water on the experimental area, as evidenced by a greater number of pregnancies and higher proportions of lactating females, and an extension of the breeding season longer into the hot, dry portions of the year. The effect of increased water availability on these species was most pronounced during times of the year when water stress might be expected to be greatest.

Population growth in *D. auricularis* proceeded in a much less seasonally restricted manner than in the other two species, and peak population sizes were not reached until February or March 1975. Breeding intensity in this species on the control area declined only slightly during portions of the year when *R. pumilio* and *G. paeba* were relatively inactive reproductively. On the experimental area, *D. auricularis* showed no consistent reproductive or numerical response to increased water availability. The relationship between response to the experimental provision of water in these species and the seasonality of demographic patterns is discussed.

Reproductive activity in a number of desert rodent species is positively correlated with rainfall and the resulting primary production (Beatley, 1969, 1976; French et al., 1974; McCulloch and Inglis, 1961; Reynolds, 1958, 1960). A number of hypotheses, most of them relating to changes in either the quantity or quality of available food, have been advanced to account for increased rodent reproduction following rainfall. French et al. (1974) suggested that these reproductive changes may be a consequence of increased energy availability, with reproduction occurring only when available energy supplies exceed those needed for maintenance. Many desert rodents shift from a diet composed primarily of seeds to one that includes higher proportions of green vegetation following plant growth, and this change in diet has been correlated with increased reproduction (Bradley and Mauer, 1971; Reichman and Van De Graaff, 1975; Van De Graaff and Balda, 1973). Proposed explanations for this reproductive response to the ingestion of green vegetation include increased dietary water intake (Beatley, 1969, 1976; Bradley and Mauer, 1971) and the stimulative effects of substances found in germinating vegetation (Pinter and Negus, 1965; Negus and Berger, 1977; Negus et al., 1977).

Several studies have presented evidence that water plays an important role in the reproductive physiology of small rodents (Baverstock and Watts, 1975; Breed, 1975; Lindeborg, 1950; Smith and McManus, 1975; Soholt, 1978; Yahr and Kessler, 1975). The results of these and other studies indicate that an increased water intake (relative to nonreproductive maintenance needs) may be necessary for the successful completion of reproduction in rodents and is especially important in the reproductive phys-

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Desmo - aseasonal breeder, no response to extra water physiologically better adapted to arid condts

G. paeba - f. seasonal, some response to water

Rhabdo. v. seasonal, hig response to water provisn

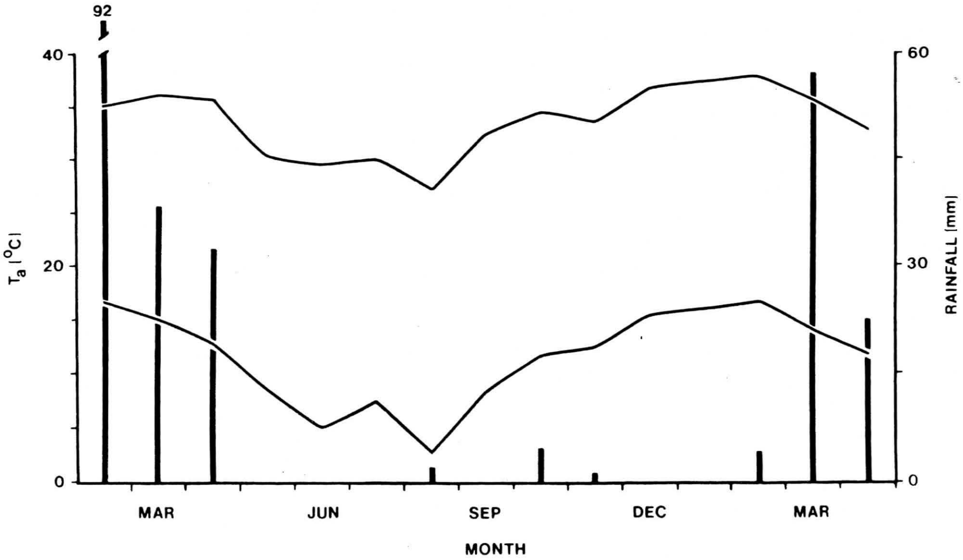


FIG. 1.—Mean monthly rainfall (vertical bars) and mean daily maximum and nightly minimum air temperatures (T_a) during 1974–1975 at Gorrasis (25°18′S, 15°55′E), South West Africa (Namibia).

iology of females. A strong relationship may thus exist between local water availability and reproduction in desert rodents.

The present study was designed to examine the effects of increased dietary water intake on reproduction in populations of desert rodents. The premise upon which this study was based is that if dietary water represents a critical resource for reproduction in these animals, it should be possible, by increasing water availability, either to increase breeding intensities during the rainy season or to extend the breeding season longer into the dry season. Parameters of particular interest include differences in time-specific breeding intensities, in the seasonality of breeding activity, and in consequent demographic performance.

STUDY AREA

This study was conducted between February 1974 and May 1975 at Gorrasis (25°18′S, 15°55′E), a nonworking sheep ranch approximately 120 km inland from the Atlantic coast in southern Africa. This ranch is at the extreme western edge of the pro-Namib subdesert transition zone (Coetzee, 1969), and thus borders the coastal Namib Desert.

The climate of this region is strongly seasonal. Monthly means of daily maximum and nightly minimum air temperatures (recorded about 1 m above the ground surface with a Taylor maximum-minimum thermometer) and total monthly rainfall during the study (an average of three conical rain gauges, one at the ranch headquarters and one at each of the two study areas described below) are shown in Fig. 1. The rainy season coincides with the hottest months of the year. Mean annual rainfall in this area is less than 100 mm; rainfall in 1974 (at least 165 mm) was the heaviest in the area in many years, with some rain occurring before I arrived in late January 1974. Rainfall in 1973 was low (as little as 12 mm falling on some neighboring areas).

Two study areas, one serving as an experimental area, were located 1 km apart on the floor of a broad intermontane valley. Soil at these sites was loose sand and gravel which overlaid a layer of partially exposed calcrete. Vegetation consisted primarily of annual and perennial grasses (*Aristida adscensionis*, *Enneapogon* sp., *Schmidtia kalahariensis*, and *Stipagrostis* sp.), various forbs, and low, sparse bushes (*Rhigozum trichotomum*). Vegetative growth had begun at the start of the study in early February 1974, and seed production took place before April of that

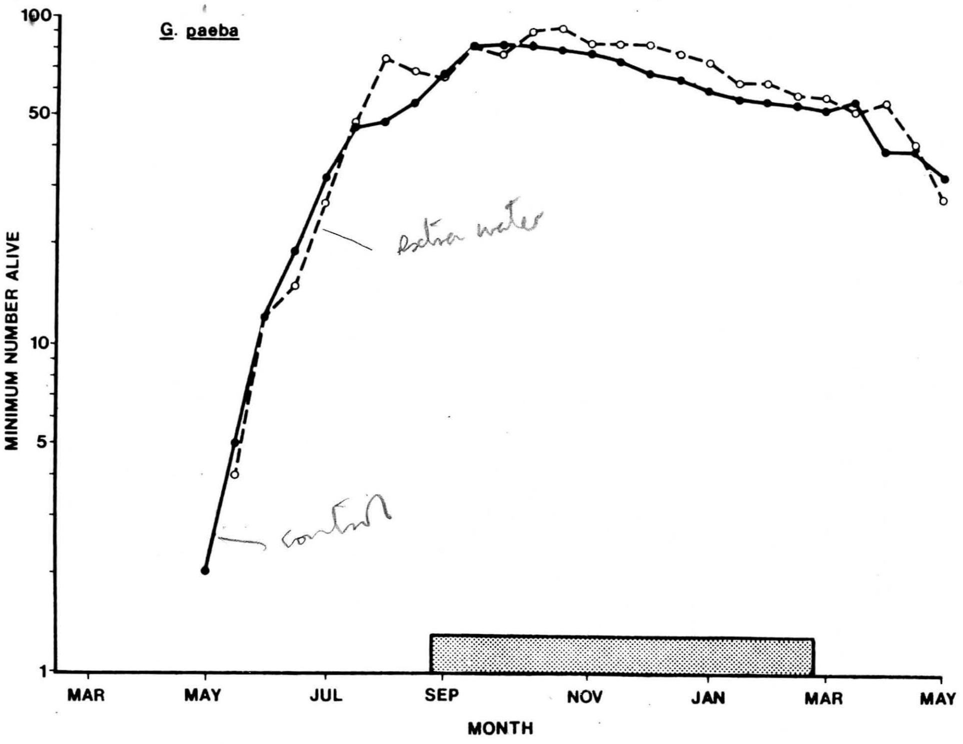


FIG. 2.—Minimum number of *Gerbillurus paeba* known alive in each trap period on control (solid lines, closed circles) and experimental (dashed lines, open circles) areas. Shaded area represents hot, dry portion of the year.

year. From May 1974 until after the 1975 rains, grasses were dry and seeds abundant on the ground surface. Rainfall in 1975 was later than normal, with heavy rain not falling until March. Seed production was completed and the grasses dry and yellow by the termination of the study in early May 1975.

The two study sites differed only slightly in vegetation. Eighteen plant species were found in common on the two areas (21 species collected on the control and 19 on the experimental area), and plant density, heights, and distribution were comparable. The calcrete layer averaged 6.6 cm below the soil surface on the control area and 5.2 cm on the experimental (1,210 depth readings on each grid). Seasonal distribution of rainfall was similar on the two areas, with nearly equal amounts falling on each during the study (157 mm on the control, 140 on the experimental area).

MATERIALS AND METHODS

Demographic data were obtained by mark-and-recapture live-trapping on two grids on the areas described above. Each 2.7-ha grid consisted of 144 trap stations at 15-m spacing in a 12 by 12 pattern. Each trap station was marked with a wooden stake and one folding Sherman live-trap (23 by 9 by 7.5 cm) was placed within 0.5 m of each stake. Trapping was conducted for three nights at 2-week intervals from early March 1974 through April 1975. Traps were set and baited (using a peanut butter and rolled oats mixture) within 2 h before dark, checked and closed generally within 1 h after daylight, and baited and re-set the following evening. Each trap period ended when traps were closed on the third morning. During the winter, traps were re-baited concurrent with the morning check, left open, and checked throughout the day to increase captures of the largely diurnal *Rhabdomys pumilio*. At these times, bait was replenished in the

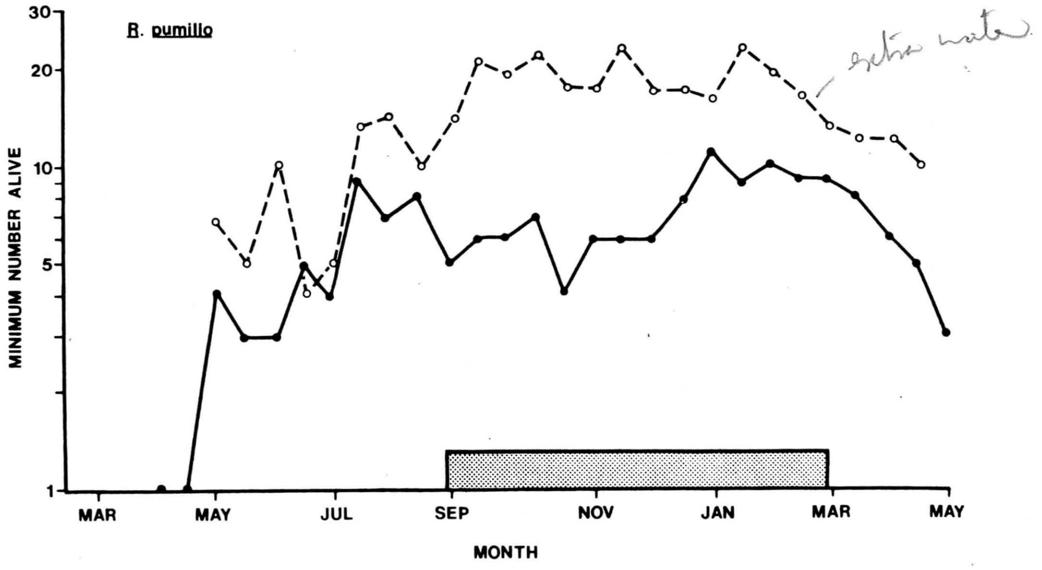


FIG. 3.—Minimum number of *Rhabdomys pumilio* known alive in each trap period on control and experimental areas. Symbols as in Fig. 2.

evening. Rectangular pieces of cardboard were placed on top of the traps to protect captured animals from the sun.

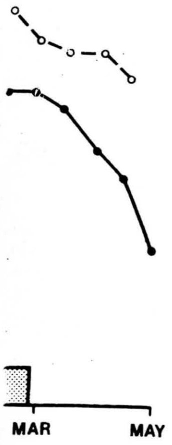
Upon first capture, each animal was toe-clipped for individual identification. At first capture in each trap period, the data recorded for each animal included its identification number, species, sex, reproductive status, location on the grid, and body weight to the nearest g (measured with a 100-g capacity Pesola scale). At subsequent captures within each trap period, only the animal's identification number and its location on the grid were noted. Reproductive activity was assessed by the position of the testes (scrotal or abdominal) in males and the condition of the vaginal opening (perforate or nonperforate) and the size of the nipples (small, medium, or large) in females. Females with bulging abdomens were noted as being pregnant, except *Desmodillus auricularis,* whose normally rotund shape obscured changes in shape that accompanied pregnancy.

Supplementary water was provided on the experimental area in 80 watering devices arranged in an 8 by 10 grid pattern (15-m spacing) superimposed over the live-trap grid. Each watering device consisted of a flat pan, 8 to 10 cm in diameter and 2 to 3 cm deep, partially buried in the ground at the base of a trap station stake. A 750-ml brown glass bottle filled with water was inverted into each pan and attached to a stake with a loop of wire. Each pan was partially filled with small stones to support the bottle at the proper height and to minimize evaporation by reducing the exposed water surface area. The drinking surface area provided at each waterer was roughly 6–10 cm^2. The water bottles were filled as needed to maintain drinking water levels in the pans.

During three trap periods near the end of the study (20–22 March, 2–4 and 11–13 April, 1975) I checked water usage on the experimental grid with a dye (a 0.5% solution of Rhodamine B) which, following ingestion, flouresces in fecal material under long wavelength ultraviolet light. Fecal pellets from live-trapped animals were collected and placed in labelled envelopes until analyzed. The identification numbers of animals showing pink stains on the mouth and face were also recorded.

Occasional trapping with snap-traps was conducted (at least 1.5 km from the grids) to obtain animals for analysis of food habits and litter size and for use as voucher specimens for species identification.

Demographic data were analyzed on the Michigan State University Computer Laboratory CDC-6500, using a computer package written by Walt Conley, New Mexico State University.



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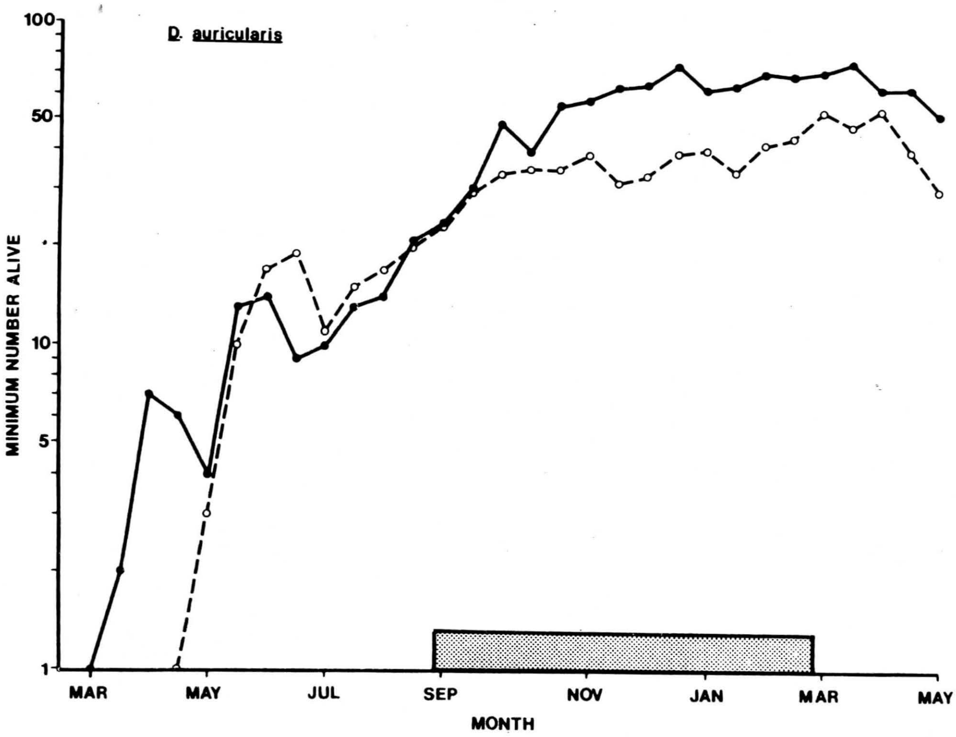

FIG. 4.—Minimum number of *Desmodillus auricularis* known alive in each trap period on control and experimental areas. Symbols as in Fig. 2.

Population sizes were estimated as the minimum number known alive using the direct enumeration technique (Krebs, 1966).

RESULTS

General.—The three most abundant mammal species on each of the two grids were two nocturnal gerbilline rodents, *Gerbillurus paeba* and *Desmodillus auricularis*, and a diurnal murine rodent, *Rhabdomys pumilio*. Thirty 3-night trap periods were recorded on each of the two grids. On the control grid 3,778 captures were made of 229 *D. auricularis*, 222 *G. paeba*, and 42 *R. pumilio*. On the experimental area 191 *D. auricularis*, 284 *G. paeba*, and 97 *R. pumilio* were captured 3,440 times.

During the three trap periods near the end of the study when water utilization on the experimental area was measured, a minimum of 33% of the *D. auricularis*, 29% of the *G. paeba*, and 71% of the *R. pumilio* known alive at those times drank from the experimental waterers, as evidenced by either the presence of dye in the feces or pink stains around the mouth.

Population growth.—Population sizes of *G. paeba*, *R. pumilio*, and *D. auricularis* on the two areas are shown in Figs. 2–4. In early March 1974, rodent populations consisted of only a few widely scattered individuals. Populations of *G. paeba* on both areas grew rapidly during the winter months of May through September (Fig. 2) and reached peak numbers in September (control) or October (experimental). Similarly, population growth in *R. pumilio* on both areas was seasonal, with little or no growth occurring after September (Fig. 3). Populations of these two species exhibited finite rates of increase greater than 1.0 (indicating an increase in population size) in only

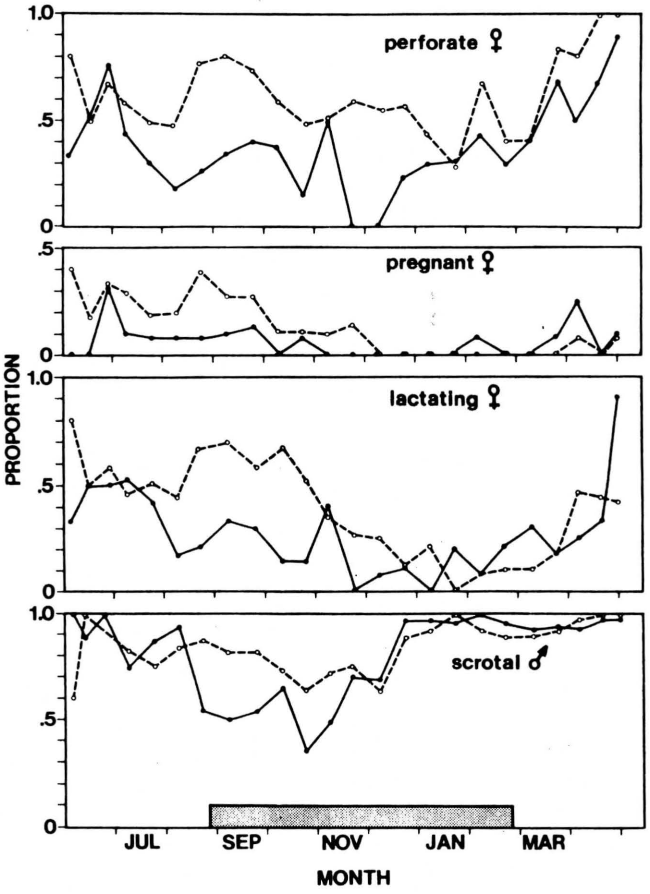

FIG. 5.—Breeding measures in *Gerbillurus paeba* on control (solid lines, closed circles) and experimental (dashed lines, open circles) areas. Data shown are proportions of females that were perforate, lactating, or pregnant and of males with testes in scrotal position, computed on the basis of total numbers of each sex captured in each trap period, without regard to age. Sample sizes and results of statistical tests of differences in each trap period are shown in Table 1. Shaded area represents hot, dry portion of the year.

0.33–0.37 of the trap periods. In contrast to these species, populations of *D. auricularis* on both grids grew relatively continuously throughout most of the study (finite rates of increase above 1.0 in 0.63–0.67 of the trap periods) and did not attain maximum population size until February or March 1975 (Fig. 4). While the qualitative patterns of population growth were similar on control and experimental areas, there were numerical differences between respective population sizes, at least in *R. pumilio* and *D. auricularis* (Figs. 3 and 4).

Reproduction.—Reproduction in *G. paeba* on the control area showed marked seasonal variation (Fig. 5). Proportions of control *G. paeba* females with perforate vaginal openings dropped below 0.4 in late July 1974 and remained low until about mid-March 1975, when the proportion in breeding condition again increased. A similar seasonal decline was observed in the proportion of control *G. paeba* females that were pregnant or lactating. Proportions of *G. paeba* males on the control area with testes in a scrotal position were high through mid-August, when they showed a marked

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TABLE 1.—*Results of* χ^2 *tests for differences in breeding intensity in control (C) and experimental (E) populations of* Gerbillurus paeba. *Tests were computed using data on numbers of breeding and nonbreeding animals in each trap period. Trap periods when there were no significant differences are blank; in others, the probability of significant difference and the population with highest breeding intensity are indicated.*

		Females					Males		
		N					N		
	Month	C	E	Perforate	Pregnant	Lactating	C	E	Scrotal
1974	June	6	5				4	5	
		8	6				8	9	
		16	12				14	13	
	July	21	24	E***			19	22	
		24	37				21	32	
	Aug.	24	25	E***		E*	14	29	
		24	21	E****	E**	E****	35	28	E***
	Sep.	30	30	E****		E****	40	36	E***
		23	33	E****		E*	38	27	E**
	Oct.	22	33			E****	28	29	
		28	27	E***		E****	34	41	E*
	Nov.	15	20				29	24	
		7	22	E***			23	23	
	Dec.	15	20	E****			26	35	
		9	16				26	32	
1975	Jan.	7	14				23	32	
		10	7				19	18	
	Feb.	12	12				24	22	
		14	10				19	17	
	Mar.	10	10				13	19	
		12	6				30	11	
	Apr.	4	15				12	27	
		9	9				25	22	
		10	12			C**	24	17	

* $P < 0.05$; ** $P < 0.025$; *** $P < 0.01$; **** $P < 0.005$.

decline and remained relatively low until mid-December, at which time they again increased and remained above 0.9 for the duration of the study. These seasonal declines in breeding percentages of *G. paeba* occurred during the hottest, driest portion of the year.

Corresponding to its relatively consistent pattern of population growth throughout the year, reproduction in control *D. auricularis* was less seasonally restricted than in *G. paeba* on the same area (Fig. 6). The proportion of male *D. auricularis* with scrotal testes was high until about October, when it dropped to around 0.4 and leveled off for the remainder of the study. Proportions of perforate female *D. auricularis* on the control area showed no consistent changes throughout the study, and there was only a slight decline in the proportion lactating during the hot, dry season.

To examine reproductive responses to increased water availability in these two species, differences between the two areas in numbers of breeding and nonbreeding animals were tested by chi-square. Results of these tests are indicated in Table 1 for *G. paeba* and in Table 2 for *D. auricularis*. In 8 of 11 trap periods between mid-July and early December, the proportion of *G. paeba* females that had perforate vaginas was significantly higher on the experimental area than on the control. Similarly, the proportion of lactating females was significantly higher in six consecutive trap periods (10 weeks) between early August and mid-October. In only one trap period was the proportion of pregnant *G. paeba* females significantly higher on the experimental area. The proportion of lactating *G. paeba* was significantly higher on the control area

TABLE 2.—*Results of chi-square tests for differences in breeding intensity in control (C) and experimental (E) populations of* Desmodillus auricularis. *Symbols as in Table 1.*

		Females				Males		
		N				N		
	Month	C	E	Perforate	Lactating	C	E	Scrotal
1974	June	2	6			11	8	
		2	7	E*		5	10	
		3	2			4	4	
	July	5	5			6	8	
		6	3			7	8	
	Aug.	8	6		C*	11	9	
		13	6			8	12	
	Sep.	9	9			18	16	C*
		15	14			26	17	
	Oct.	11	13			20	18	C**
		22	15			29	17	C*
	Nov.	21	11			32	23	
		24	10			31	18	
	Dec.	25	10		E*	34	19	
		26	16			41	18	C**
1975	Jan.	25	14			28	24	C****
		26	11			30	21	C*
	Feb.	27	17			34	25	
		23	14			39	29	
	Mar.	24	21			39	31	
		25	16			44	27	
	Apr.	21	23	C***		36	28	
		25	20			36	16	
		20	11			33	20	C***

* $P < 0.05$; ** $P < 0.025$; *** $P < 0.01$; **** $P < 0.005$.

than on the experimental grid in the last trap period; this was the only significant difference in that direction in both sexes of this species during the study. In addition to these differences in the seasonality of breeding in female *G. paeba* on the two areas, there were marked differences in the total occurrence of pregnancies in this species, 22 on the control area and 58 on the experimental grid.

The proportion of male *G. paeba* with scrotal testes was significantly higher on the experimental area than on the control in four of five trap periods between late August and mid-October (Table 1). These differences in breeding intensity between control and experimental populations of *G. paeba* occurred during the period of lowered reproduction on the control area in the hottest, driest months of the year.

Results of chi-square tests for differences in numbers of breeding and nonbreeding *D. auricularis* on the two areas (Table 2) indicate no consistent differences between control and experimental females that were lactating or had perforate vaginas. The proportion of male *D. auricularis* with scrotal testes was significantly higher on the control than on the experimental grid in seven trap periods.

Because sample sizes of *R. pumilio* were small, it is impossible to make time-specific comparisons of breeding intensities between control and experimental areas. However, several criteria indicate a reproductive response to increased water availability in this species. While there were no marked differences in overall mean breeding proportions in this species between the two areas, there were striking differences in overall reproductive output and its seasonal occurrence. Obviously pregnant females were observed in six trap periods on the control area versus 10 on the experimental area, and over twice as many pregnancies were seen on the experimental area

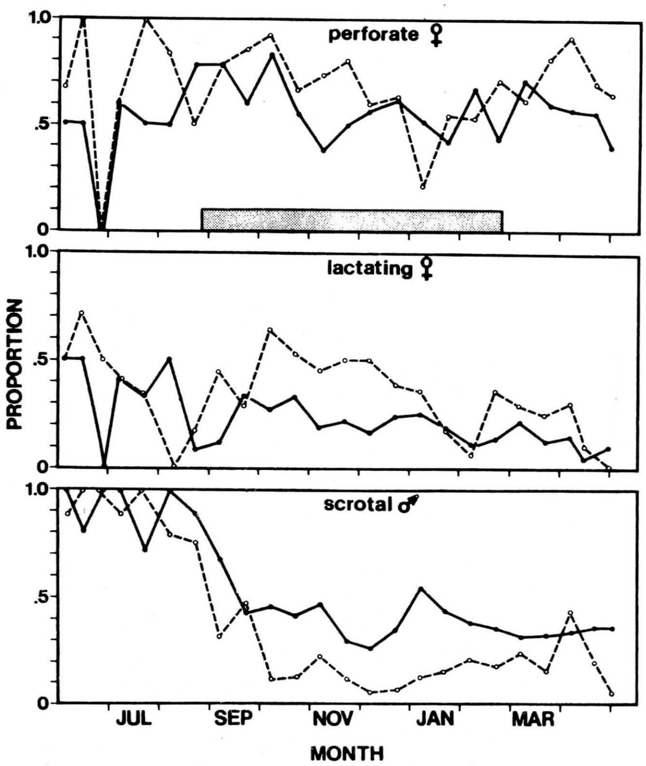

FIG. 6.—Proportions of *Desmodillus auricularis* females that were perforate and lactating and of males with testes in scrotal position on control and experimental areas. Computation of proportions and symbolism as described for Fig. 5. Sample sizes and results of statistical tests of differences in each trap period are shown in Table 2.

(22) as on the control (9). No pregnant female *R. pumilio* was observed on the control area between mid-October 1974 and the end of March 1975, while seven pregnant females were observed on the experimental area during that period. Similarly, lactating *R. pumilio* were observed in 22 trap periods on the experimental area and in only 11 on the control. These reproductive differences were reflected in the numbers of animals that were obviously juveniles when captured for the first time on the control area (11) and on the experimental area (36), and probably explain the greater abundance of *R. pumilio* on the experimental grid.

Survivorship.—Two-week survival rates and the life-table values for the expectation of further life (e_x) were computed from data obtained by direct enumeration of marked animals (Krebs, 1966). Overall mean two-week survival rates of both sexes of all species on the control area were relatively high ($\geq$0.72), with *G. paeba* having the highest mean rates ($\geq$0.84). Life expectancy values indicate that *R. pumilio* is the shortest lived of the three species (mean e_x from first capture about 7 weeks). Values of expectation of further life at the time of first capture for *D. auricularis* and *G. paeba* are similar (about 9–11 weeks), although the maximum e_x for animals still alive 8 to 14 weeks after first capture is considerably higher in *D. auricularis* (39 weeks) than in *G. paeba* (23 weeks).

The life expectancy of animals of both sexes of *G. paeba* and *D. auricularis* entering the experimental populations between March and July 1974 was much lower than for animals captured for the first time on the control area during that period. This difference was especially pronounced in male *D. auricularis*. After July 1974, only slight differences in life expectancy were observed between areas, species, and sexes.

The differences in life expectancy between the two areas during the early months of the study had a marked effect on the subsequent weight distribution in the experimental population of *D. auricularis*. While there were no significant differences between the two populations in mean body weights or in weight distributions through early October 1974, the experimental population of *D. auricularis* consisted of animals of significantly lower body weights throughout the remainder of the study (*t*-test, $P < 0.01$). The correspondence between the demographic differences (i.e., in population size and male reproduction) between control and experimental populations and body weight differences suggests that the poorer demographic performance of *D. auricularis* on the experimental area was related in some way to differential mortality between the two areas during the early months of the study. Unfortunately, data on the sources of that mortality are not available. Life expectancy differences between control and experimental *G. paeba* produced no noticeable effect on body weight distributions or mean body weights.

Discussion

Population patterns of small rodents in the desert environment where this study was conducted appear to be related to seasonal climatic variations. The timing of rainfall in this environment is reasonably predictable, but its effectiveness in producing resources is highly unpredictable (see Low, 1976, for a discussion of various types of environmental predictability). Water becomes available in this area at the onset of rains between December and April; green vegetation is available for several weeks following the rains. During the ensuing months of May or June to late August, potential evaporation is relatively low (Schulze, 1969), temperatures are cool, and condensation occurs regularly. Beginning in late August or early September, conditions become increasingly more arid until alleviated by the following rainy season.

Presumably as a result of the almost complete failure of rains in 1973, the year prior to the start of this study, rodent populations in early 1974 were reduced to extremely low levels. Following the 1974 rains, populations of *Gerbillurus paeba* and *Rhabdomys pumilio* on the control area increased rapidly, showing little or no population growth after September or October 1974. Reproduction in both of these species occurred primarily before September or October, at which time there was a sharp reduction in breeding percentages in *G. paeba* and the beginning of a five-month period when no pregnant *R. pumilio* was observed on the control area. *Desmodillus auricularis*, while also apparently responding to the rainfall and/or plant growth that occurred at the start of the study, exhibited a much more aseasonal demographic pattern, with reproduction and population growth continuing relatively consistently throughout most of the study.

The major objective of this research was to examine the effects of the experimental provision of drinking water on reproduction and demography in desert rodents. The response by each species to this experimental treatment was correlated with the seasonal nature of its demographic pattern on the control area. Breeding proportions in the relatively aseasonal *D. auricularis* were not increased on the experimental area. The demographically more seasonal *G. paeba* and *R. pumilio* showed appreciable reproductive, and, in the case of *R. pumilio*, numerical, responses to the experimental provision of water. Results for these two species support the contentions of several authors (Beatley, 1969, 1976; Bradley and Mauer, 1971) that increased water availability is at least one of the factors controlling reproduction in desert rodents, and provide an experimental demonstration of that effect in these animals.

An important consequence of the experimental treatment was an apparent extension of the breeding season into the hot, dry months of the year in *G. paeba* and *R. pumilio*. That is, differences in reproductive activity between control and experimental populations of these two species were most striking during a portion of the year when, because of climatic factors, water stress might be most expected. This indicates that the dry season breeding declines observed in these species on the control area may have been due, at least in part, to water shortage. These results suggest a strong relationship between seasonal changes in water availability and the seasonality of demographic patterns in at least some desert rodent species. A similar relationship has been suggested for other small rodents inhabiting less arid areas (Bradford, 1974; Newsome et al., 1976).

Gerbillurus paeba and *R. pumilio* exhibited seasonally restricted breeding patterns and rapid population responses to favorable conditions. This type of demographic response to seasonal events has been documented for a number of vertebrates inhabiting unpredictable arid environments (French et al., 1974; Keast, 1959; Low, 1976). The response to increased water availability by these species, and the relationship of that response to population patterns, while perhaps expected results for desert rodents, are certainly not inconsequential, particularly when the lack of response by *D. auricularis* is considered. It could not be demonstrated that this species responded to the seasonal availability of water, and its demographic pattern appears to be qualitatively different than those exhibited by the other two. Thus, while the population patterns of *G. paeba* and *R. pumilio* are explicable in terms of their responses to seasonal changes in water availability, a different explanation must be given for the demographic pattern of *D. auricularis*. *D. auricularis* is physiologically more capable of conserving water than are *G. paeba* and *R. pumilio*, which have similar free water requirements. Elsewhere (Christian, 1977, 1979), I have presented data on water conserving abilities of these species, and suggested a physiological basis for differences among the three in (1) response to increased water availability and (2) seasonality of demographic patterns.

The provision of supplementary water had little apparent effect on the general patterns of population growth between the control and experimental areas. In only one of the two species (*R. pumilio*) that showed reproductive responses to supplementary water did the increased reproduction result in marked numerical differences between control and experimental populations. In the experimental *G. paeba* population, reproduction continued over a longer part of the year and 28% more animals were captured than on the control area, but only a slightly larger peak population was produced. This indicates that the numerical consequences of increased reproduction were apparently offset by increased mortality or emigration. Thus, while reproduction was partly under the control of water availability, other factors, at least during this year of abundant resources, appear ultimately responsible for regulating population size in this species.

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