COMPARATIVE DEMOGRAPHY AND WATER METABOLISM IN THREE NAMIB DESERT RODENTS

Dissertation for the Degree of Ph. D.
MICHIGAN STATE UNIVERSITY
DONALD PAUL CHRISTIAN
1977

This is to certify that the

thesis entitled

COMPARATIVE DEMOGRAPHY AND WATER
METABOLISM IN THREE NAMIB DESERT RODENTS

presented by

DONALD PAUL CHRISTIAN

has been accepted towards fulfillment
of the requirements for

Ph. D. degree in Zoology

Major professor

Date August 5, 1977

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ABSTRACT

COMPARATIVE DEMOGRAPHY AND WATER METABOLISM IN THREE NAMIB DESERT RODENTS

By

Donald Paul Christian

This research was designed to examine the role of dietary water in the population biology of small desert-dwelling rodents. Reproduction and population growth in desert rodents are closely associated with rainfall and the ensuing plant growth. The field portion of this study tested an hypothesis that increased dietary water intake is a primary factor in the reproductive response of these rodents to rainfall/plant growth.

I tested this hypothesis in a 14-month field study in the Namib Desert of southern Africa. Populations of two nocturnal gerbilline rodents, *Gerbillurus paeba* and *Desmodillus auricularis*, and a diurnal murine rodent, *Rhabdomys pumilio*, were monitored by mark-and-recapture live-trapping on two areas. One of these areas served as a control, and on the other drinking water was continuously provided in 80 self-filling watering devices. Reproductive condition of live-trapped animals was assessed by external criteria, and demographic parameters were estimated from data obtained by direct enumeration of marked animals.

The major results of this field study may be summarized as follows: 1) The provision of supplementary drinking water was sufficient to increase reproductive output in *G. paeba* and *R. pumilio*, but *D. auricularis* showed no consistent reproductive or numerical response to the experimental treatment. 2) Breeding intensities of *G. paeba* and

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R. pumilio on the control area declined during the hot, dry months of the year; a major effect of the provision of water was an extension of the breeding season longer into the dry season on the experimental area, suggesting that the lowered breeding intensities on the control area at that time were due in part to low water availability. 3) Differences in the responses of these three species to the experimental treatment paralleled the degree of seasonality of their demographic patterns on the control area, with G. paeba and R. pumilio being highly seasonal and D. auricularis being relatively aseasonal; this relationship suggests that G. paeba and R. pumilio may require more water than D. auricularis, and that, as a result, the former two species are restricted to breeding primarily during portions of the year when water availability is greatest.

The hypothesis suggested by result 3) was tested in a series of laboratory experiments designed to compare water conservation in these species. Daily food consumption and fecal production, minimum evaporative water loss at three humidities, minimum fecal water content, and maximum urine osmotic, urea, and chloride concentrations were measured. These data were used to estimate daily metabolic water production and minimal total daily water loss. An estimate was obtained of the daily preformed water intake that animals of each species would need to remain in water balance. The preformed water requirements were expressed as a minimum necessary proportion of free water in the diet.

At all three humidities, G. paeba and R. pumilio would require diets of very similar water content to maintain water balance. Desmodillus auricularis could maintain water balance on a diet

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containing 0.62 to 0.67 as much free water (on a g water per g dry food basis) as needed by the other two species. These results thus provide support for the hypothesis that physiological differences among coexisting species in environments where water availability varies strongly with season may indeed have important demographic consequences.

An argument is presented that, due to its greater ability to conserve water, *D. auricularis* experiences a more predictable environment (relative to water availability) than *G. paeba* and *R. pumilio*. Differences among these three species in several correlates of life history patterns that are generally associated with differences in environmental predictability support this contention, and suggest that this view may represent a reasonable interpretation of some of the ecological consequences of the physiological differences among these three species.

COMPARATIVE DEMOGRAPHY AND WATER METABOLISM IN THREE NAMIB DESERT RODENTS

By

Donald Paul Christian

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Zoology

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ACKNOWLEDGEMENTS

I wish to thank members of my guidance committee, Rollin H. Baker (Chairman), Marvin H. Hensley, Richard W. Hill, and Earl E. Werner, of Michigan State University, Walt Conley, New Mexico State University, and C. G. Coetzee, State Museum, Windhoek, South West Africa, for their encouragement and assistance during this research.

Field work was supported by a grant from the Jens Touborg Fund to The Museum, Michigan State University. Computer time was provided through an NSF RANN Analysis of Ecosystems grant, no. GI-20, and was made available through the courtesy of William E. Cooper. The Department of Zoology and the College of Natural Science provided funds for key punching. Additional financial support and use of equipment was provided by the Department of Zoology and The Museum, Michigan State University. Walt Conley generously allowed the use of his computer package for demographic analysis. Numerous calculations were made on the Wang 600-14 calculator in the Michigan State University Museum.

The cooperation of the South West Africa Department of Nature Conservation is gratefully acknowledged. Mike Müller of the South West Africa Department of Agriculture Herbarium kindly identified plant specimens. I want to thank C. G. Coetzee, Michael Penrith, and Mary Lou Penrith, of the State Museum, Windhoek, South West Africa, for their assistance and hospitality. I am deeply appreciative of the support and encouragement offered by Jens K. Touborg. I wish to express

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my sincere appreciation to Thys and Antoinette Louw and their family, whose friendship, generosity, and assistance contributed to the project in countless ways.

Finally, I would like to thank my wife, Sandy, for her assistance and support during the field, laboratory, and writing stages of this research.

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I. FIELD EXPERIMENTS

INTRODUCTION

Deserts are typically characterized as extreme and highly variable environments, with large daily and seasonal temperature fluctuations and rainfall that is low, unpredictable, and often confined to a few months of the year (Cloudsley-Thompson, 1975). The nature of the environmental problems with which small desert rodents contend seems reasonably well understood. First, they probably are periodically faced with shortages of food, water, cover, and other critical resources. The various physiological and behavioral attributes of desert rodents that allow them to survive these extreme conditions have been well documented (e.g., Brown and Bartholomew, 1969; Eisenberg, 1963; Hudson, 1964; Schmidt-Nielsen, 1964). An additional feature with which animals must deal is the temporal variability or unpredictability of desert environments (Low, 1976; Conley _et al_., 1977). Associated with this environmental variability is great seasonal and year-to-year variation in reproductive performance among desert rodents (see especially French _et al_., 1974). This demographic pattern has been discussed in recent contributions in terms of shifts between relative r- and relative K-strategies (Conley _et al_., 1977; Nichols _et al_., 1976).

This variability in reproductive activity has been correlated with variation in rainfall and the resulting primary production (French _et_

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al., 1974; Beatley, 1969; McCulloch and Inglis, 1961; Reynolds, 1958, 1960). Not only do rodents breed primarily following rainfall/plant growth, but also the intensity of reproduction appears to vary with the quantity of available food. For example, French et al. (1974) observed correlations between available food supply and not only breeding intensity but also litter size, reproduction by young-of-the-year, and survival of newborn in Perognathus formosus populations. 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. In addition to these quantitative effects, there are a number of possible qualitative changes in food following rainfall that might influence rodent reproduction. 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 shift has been correlated with increased reproduction (Bradley and Mauer, 1971; Reichman and Van De Graaff, 1975). Proposed explanations for this reproductive response to the ingestion of green vegetation include increased dietary water intake (Beatley, 1969; Bradley and Mauer, 1971) and the stimulative effects of estrogenic or gonadotrophic substances found in germinating vegetation (Pinter and Negus, 1965; Bodenheimer and Sulman, 1946). All of these hypothesized mechanisms attempting to explain the association between desert rodent reproduction and rainfall/plant growth remain to be well demonstrated.

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Of the proposed rainy-season or post rainy-season resources that are critical for reproduction in desert rodent populations, an increased dietary water intake attracts particular interest because of 1) the universality of aridity as a characteristic of desert environments (Cloudsley-Thompson, 1975), and 2) the attention given the water relations of small desert rodents in the literature. The hypothesis that increased dietary water intake is a primary factor in the reproductive response of these rodents is easily justified on physiological bases.

Reproductive functions involving both males and females, as well as functions pertaining only to females can be envisioned as entailing increased water costs. First, successful reproduction requires finding a mate, courting, and copulating. Although little information is available on the natural history of these activities in free-living desert rodents, we know that they are, at least in part, performed above-ground (Kenagy, 1976). Rodents in burrows are exposed to high ambient humidities and experience minimal evaporative water loss (Schmidt-Nielsen, 1964). Changes in the schedule of burrow and above-ground activity (Kenagy, 1973; French et al., 1966) that presumably accompany reproductive activities in these rodents would result in their spending more time in low humidity environments and sustaining higher evaporative water losses (Baudinette, 1972; Schmidt-Nielsen, 1964). We might therefore expect that breeding rodents of both sexes would need higher water intakes to balance the increased losses incurred in above-ground activity.

In addition to these humidity effects, activity per se may result in markedly higher evaporative water losses (Chew and Dammon, 1961;

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Wunder, 1970). A critical question that remains unanswered in this regard is whether or not the increased water losses associated with activity are balanced by the greater production of metabolic water. Wunder (1970), in a study of the energetics of activity in *Eutamias merriami*, found that the ratio of evaporative water loss to oxygen consumption in running animals was at least twice that in resting animals, suggesting that the higher losses were not balanced by the greater metabolic water production. On the other hand, Raab and Schmidt-Nielsen (1972) reported only slight effects on the evaporative-water-loss-to-oxygen-consumption ratio with activity in *Dipodomys spectabilis*, and concluded that activity would have little effect on water balance in these animals. The latter authors, however, ignored the increased fecal production (and probably water loss via that route) and greater formation of metabolic wastes (thus either increasing urinary water loss or necessitating increased urine concentrations) that would accompany higher metabolism.

The reproductive functions of female rodents produce increased water demands (Chew, 1965). Dice (1922) measured water consumption increases of 217 and 171 percent in, respectively, pregnant and lactating *Peromyscus maniculatus bairdi*, and 360 and 370 percent in *Peromyscus leucopus novaboracensis*. In addition, he observed increased water intakes of 140 percent in nursing *Microtus ochrogaster*. Lindeborg (1950) found that the water intake of female *P. m. bairdi* increased by 35 percent during the final 10 days of gestation, by 111 percent of the 14th day of nursing, and by 158 percent at weaning. Smith and McManus (1975) found that the increased water needs of lactating *Mus musculus* during the last week of gestation were proportional to litter

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size. In a study of Australian rodents, Baverstock and Watts (1975) found that the water intake of females nursing small litters was only slightly elevated in four out of five species. With larger litters, water intake progressively increased over time during lactation. In two species (*Notomys alexis* and *Mus musculus*), restriction of water intake below *ad libitum* levels did not alter survival of the young, but did lead to reduced growth rates, especially in larger litters. Complete water deprivation in two nursing *N. alexis* led to eventual death of the young, with some being killed by the mother.

In another study of *N. alexis*, Breed (1975) noted that water deprivation had a variety of detrimental effects on female reproductive physiology. The length of the estrous cycle was greater due to an increase in the diestrous phase. Uterine atrophication, impairment of normal follicular development, and an increased frequency of unluteinized follicles were also observed. While the generality of these phenomena is unknown, the similarity of reproductive functions in various rodent species would suggest that water is of similar importance for most rodent species. The available data indicate that there may be strong pressures for desert rodents to reproduce only when adequate water supplies are available.

The present study was designed to examine the effects of increased dietary water on reproduction in populations of desert rodents. The premise upon which this study was based is that if dietary water represents a critical rainy season resource for these animals, it should be possible, by increasing water availability, to either increase breeding intensities during and immediately following the rainy season or to extend the breeding season longer into the dry season. The

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paradigm used was to provide experimental populations of free-living rodents with an artificial water supply and compare responses of members of those populations with controls. In a manner similar to other recent studies (Bradford, 1975; Newsome *et al*., 1976), water was provided via drinking. Parameters of particular interest included differences in time-specific breeding intensities, in the seasonality of breeding activity, and in consequent demographic performance (especially population growth, recruitment, and survivorship).

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STUDY AREA

This study was conducted between February 1974 and May 1975 at Gorrasis (25°18'S, 15°55'E), a non-working sheep ranch approximately 120 km inland from the Atlantic coast in southern Africa. This ranch is at the extreme western edge of the proNamib subdesert transition zone (Coetzee, 1969), and thus borders the coastal Namib Desert. Prior to 1971, when all domestic animals were removed from the ranch, Gorrasis had been used for about 15 years for raising karakul sheep.

The climate of this region is strongly seasonal. The summer months of December through about March are hot; during the winter months (May to September) nighttime temperatures often drop to near or below freezing. Monthly means of daytime maximum and nighttime minimum air temperatures during this study, recorded about 1 m above the ground surface with a Taylor maximum-minimum thermometer, are shown in Figure 1. Maximum air temperature recorded during this study was about 44°C. Day and night air temperatures frequently differed by as much as 28-32°C.

The rainy season coincides with the hottest months of the year. Mean annual rainfall in this area is less than 100 mm. Total monthly rainfall during each month of this study (an average of three conical rain gauges, one at the ranch headquarters and one at each of the two study areas described below) is shown in Figure 2. Rainfall in 1974 (at least 165 mm) was the heaviest in the area in many years, with some rain occurring before the author's arrival in late January 1974. Rainfall in 1973 was low, with as little as 12 mm falling on some neighboring ranches.

Figure 1. Monthly mean daytime maximum and nightime minimum air temperatures during the study.

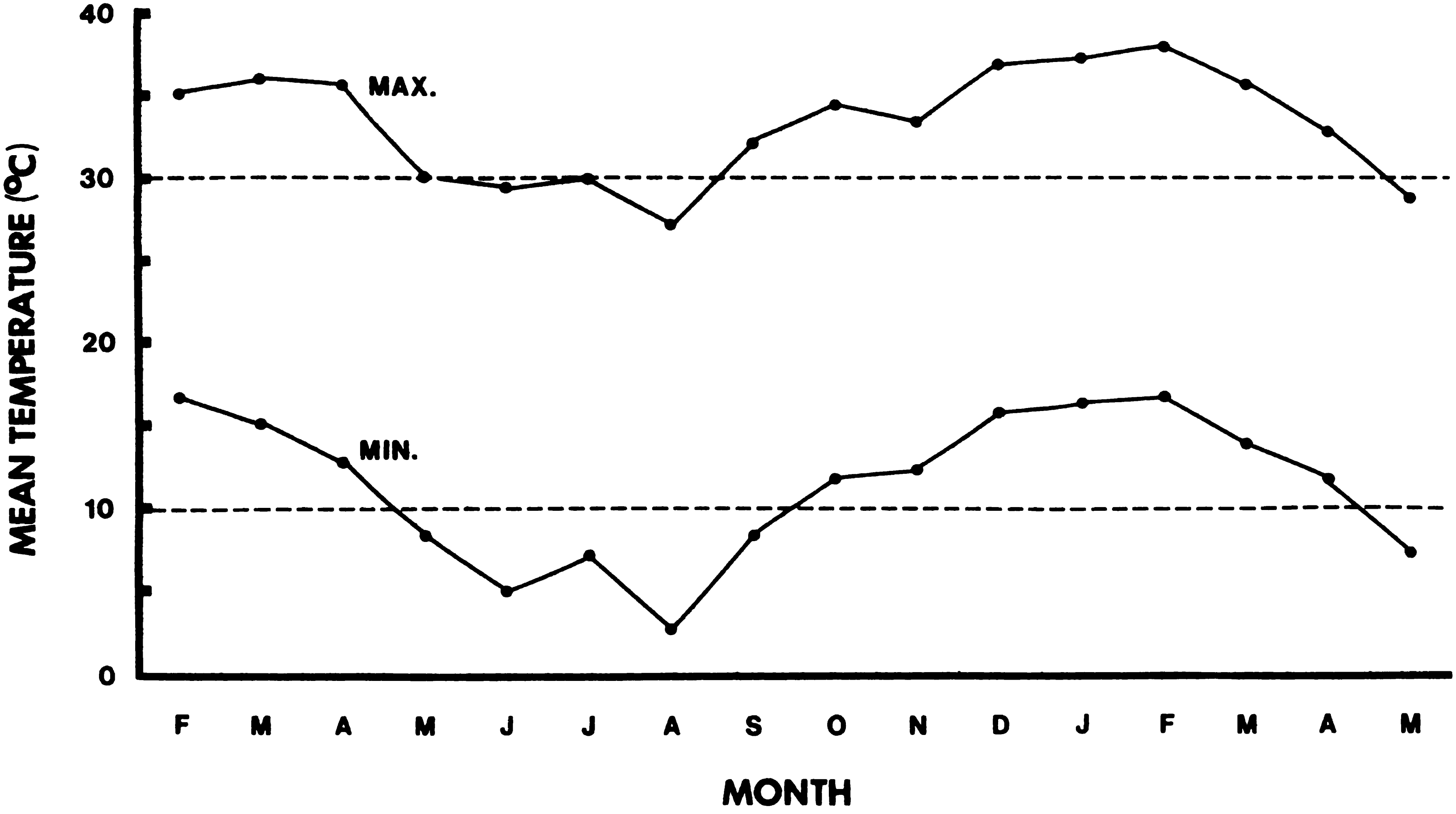
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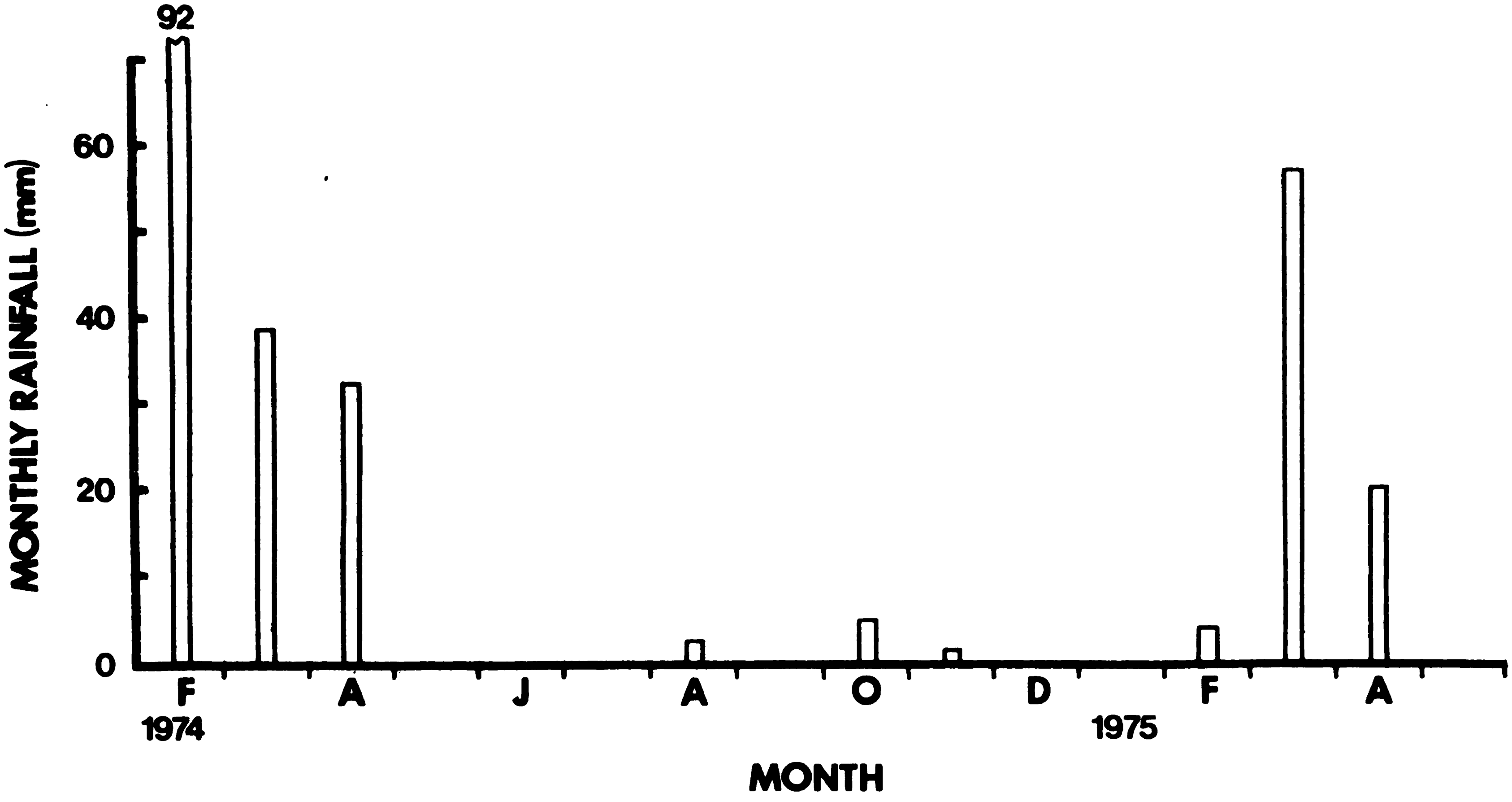
Figure 2. Monthly rainfall during the study.



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Fog serves as a water source for some Namib Desert animals (Seely and Hamilton, 1976; Louw, 1972), and occurs up to 40 days a year in portions of the Namib close to the Atlantic coast (Schulze, 1969). At Gorrasis, however, fog is rare, occurring during this study on only a few days during the winter months following a disturbance of prevailing winds (generally easterly between midnight and noon, and westerly between early afternoon and midnight). Dew is frequently present early in the morning, but only during the winter. Although I have no information on evaporation, Schulze (1969) presents data on potential evaporation for two localities in South West Africa (Gobabeb, 23°24'S, 15°03'E, in the Namib Desert 56 km from the Atlantic coast; and Windhoek, 22°34'S, 17°06'E, on a high inland plateau). Evaporation from a free water surface in a class A evaporation pan at each of these localities is about 3500 mm per year, with minimum evaporation occurring between May and September and maximum amounts between October and January.

Two study areas, one serving as an experimental area, were located 1 km apart on the floor of a broad intermontane valley. Soil at this site was loose sand and gravel, and overlaid a layer of partially exposed calcrete. Vegetation consisted primarily of annual and perennial grasses, various forbs, and low, sparse bushes (_Rhigozum trichotomum_). A list of plants collected on each area and their relative abundance is shown in Table 1. Vegetative growth had begun at the start of the study in February 1974, and seed production took place before April of that year. From May 1974 until after the 1975 rains, grasses were dry, and seeds were abundant on the ground surface. Rainfall in 1975 was later than usual, with heavy rain not falling until March. Seed production was completed and the grasses dried and

Table 1. Plants collected on each live-trapping area. Asterisks indicate relative abundance, rare (*), minor (**), common (***), and abundant (****). An (x) indicates presence in 1974 only.

FAMILY	SPECIES	CONTROL GRID	EXPERIMENTAL GRID

Table 1. Plants collected on each live-trapping area. Asterisks indicate relative abundance, rare (*), minor (**), common (***), and abundant (****). An (x) indicates presence in 1974 only.

FAMILY	SPECIES	CONTROL GRID	EXPERIMENTAL GRID
Acanthaceae	Monechme desertorum	*	*
Aizoaceae	Trianthema triquetra	** (x)	** (x)
Amaranthaceae	Calicorema capitata	*	*
Bignoniaceae	Rhigozum trichotomum	****	****
Chenopodiaceae	Salsola aphylla	*	*
Compositae	Hirpicum gazanoides	***	***
Cucurbitaceae	Cucumis sp.	*** (x)	*** (x)
Gramineae	Aristida adscensionis	****	****
	Enneapogon scaber	**	
	Enneapogon sp.	** (x)	** (x)
	Eragrostis sp.	* (x)	* (x)
	Schmidtia kalahariensis	****	****
	Stipagrostis ciliata	***	***
	S. obtusa	***	***
	S. uniplumis	***	***
Leguminoseae	Crotalaria sp.	***	***
	Cyamopsis serrata	* (x)	
	Tephrosia dregeana	* (x)	**
Martyniaceae	Sesamum capense	***	
	S. triphyllum		***
Rubiaceae	Kohautia caespitosa	***	***
Scrophulariaceae	Aptosimum spinescens	*	
Zygophyllaceae	Tribulus sp.	**** (x)	**** (x)
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Only minor differences existed between the two study sites. As seen in Table 1, plant species composition on the two areas was similar. The calcrete layer averaged 6.6 cm below the soil surface on the control grid and 5.2 cm on the experimental (1210 depth readings on each grid). Censuses of Rhigozum trichotomum bushes on each grid showed an average height of about 40 cm on each. The average density of these bushes on the control area was 3.5 per 100 m^2, compared with 4.3 per 100 m^2 on the experimental area. 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 area, 140 mm on the experimental).

Small mammal predators observed on or near the study areas included two owls (Bubo africanis and Tyto alba), a variety of small carnivores (Vulpes chama, Canis mesomelas, Felis libyca, Ictonyx striatus, and Genetta genetta), and at least two reptilian predators, puff adders (Bitis arietans) and yellow cobras (Naja nivea). Grazing animals using the study areas were hares (Lepus capensis and L. saxatilis), steenbok (Raphicerus campestris), and, infrequently, gemsbok (Oryx gazella), springbok (Antridorcas marsupialis), and ostriches (Struthio camelus).

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METHODS AND MATERIALS

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 x 12 pattern. Each trap station was marked with a short wooden stake (maximum above-ground height about 30 cm), and one folding Sherman live-trap (23 x 9 x 7.5 cm) was placed within 0.5 m of each stake. Traps were baited with a mixture of rolled oats and peanut butter. Trapping was conducted for three nights at two week intervals, beginning in early March 1974 and continuing through April 1975. Traps were set and baited 0.5 to 2 hours before dark, checked and closed generally within one hour 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 concurrently with the morning check, left set, and checked throughout the day to increase captures of the diurnal *Rhabdomys pumilio*. At these times, traps were again baited in the evening. Rectangular pieces of cardboard were placed on top of the traps to protect captured animals from the sun. At the end of each trap period, any remaining bait was shaken from the traps and traps were washed as necessary. The traps were removed every 2-3 trap periods for use on other live-trap areas, thus effecting randomization of placement of specific traps.

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Upon first capture, each animal was marked with a toe-clipped number (constraint of two toes clipped per foot). At first capture in each trap period, the data recorded for each animal included its identification number, species, sex, location on the grid, and body weight to the nearest g (measured with a 100 g capacity Pesola spring 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 following criteria: for males, the position of the testes (scrotal or abdominal); for females, the condition of the vaginal opening (perforate or nonperforate), and the relative size of the nipples (small, medium, or large). In addition, females with bulging abdomens were noted as being pregnant.

Supplementary water was provided on the experimental area in 80 self-filling watering devices arranged in an 8 x 10 pattern (15 m spacing) superimposed over the live-trap grid. Each waterer consisted of a flat pan, 8-10 cm in diameter and 2-3 cm deep, partially buried in the ground at the base of a trap station stake. Into each pan was inverted a 750 ml brown glass bottle which was filled with water and attached to the stake with a loop of wire. Each pan was partially filled with small stones to support the bottle at the proper height and reduce the exposed water surface area, thereby minimizing evaporation. 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 made a check on water usage on the experimental grid using Rhodamine B, a dye which, following ingestion, flouresces

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flouresces in fecal material under long wavelength ultraviolet light. A 0.5 percent solution of Rhodamine B in water was placed in the waterers at these times, and fecal pellets from live-trapped animals were collected and placed in labelled envelopes until analyzed. In addition, the identification numbers of animals showing pink stains on the mouth and face were 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. Population sizes were estimated using the direct enumeration technique (Krebs, 1966). Other methods of data analysis are discussed in appropriate sections under Results.

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RESULTS

General

The three most abundant species on each of the two grids were two gerbilline rodents, Gerbillurus paeba and Desmodillus auricularis, and a murine rodent, Rhabdomys pumilio. Less common species captured were (numbers on control and experimental areas, respectively) Gerbillurus vallinus (2,1), Malacothrix typica (16,12), Mus (=Leggada) minutoides (3,23), Steatomys pratensis (3,4), and the insectivore (Family Macroscelididae) Macroscelides proboscideus (0,2). Subsequent analyses will deal only with populations of G. paeba, D. auricularis, and R. pumilio.

Representative morphological and litter size data for these species are shown in Table 2. Body weights are from live-trapped animals on the control grid; body measurements and litter sizes were obtained from snap-trapped animals. In captivity, R. pumilio have litters as large as 10-12; maximum observed litter size in captive D. auricularis is three. Rhabdomys pumilio's activity pattern is largely diurnal (Christian, 1977), while the gerbils are strictly nocturnal.

Thirty 3-night trap periods were recorded on each of the two grids for a total of 12,960 trap-nights on each. On the control grid, 3,778 captures were made on 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.

Table 2.

Weight (g),
Mean adult
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Litter size

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Table 2. Representative body weights, adult body measurements, and litter sizes of _D. auricularis_, _G. paeba_, and _R. pumilio_. Sample sizes are shown in parentheses.

	D. auricularis	_G. paeba_	_R. pumilio_
Weight (g), observed range*	23-80	10-31	11-59
Mean adult body weight (g)*	46-60	24-28	45-53
Mean total length (mm)	195.5 (23)	196.0 (47)	229.6 (26)
Mean tail length (mm)	89.0 (23)	109.9 (47)	118.5 (26)
Mean hind foot length (mm)	26.5 (23)	28.4 (47)	25.4 (26)
Litter size (mean, range)	3, 2-4 (17)	4, 2-7 (35)	5, 3-6 (22)

*Pregnant females excluded. Weight range and mean adult body weights are based on statistics from animals captured in each trap period on the control grid.

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The efficiency of the live-trapping procedure in capturing marked animals was assessed by computing the percentages of the minimum number of animals known alive in each trap period that were caught in that trap period. These data, for each species on each area, are presented in Table 3. These results show that the trapping procedure was highly effective for *D. auricularis* (mean of 76-78 percent catch of the minimum number known alive in each trap period). Capture rates of marked *G. paeba* and *R. pumilio* were lower than for *D. auricularis*, but still sufficiently high to allow reasonable estimation of demographic parameters.

Differences in sex ratios from the expected value of 1:1 were tested by χ^2, using data on the numbers of males and females captured in each trap period. In both *R. pumilio* populations, there were no significant deviations from equal numbers of each sex in any trap period. In the gerbils, however, significant differences in sex ratios (with higher proportions of males) were observed in several trap periods, primarily during the second half of the study.

During the three trap periods near the end of the study when water utilization on the experimental area was measured, it was found that a minimum of 33 percent of the *D. auricularis* known alive at those times, 29 percent of the *G. paeba*, and 71 percent of the *R. pumilio* had drunk from the experimental waterers, as evidenced by either the presence of dye in the feces or pink stains around the mouth. Data on the movements of live-trapped animals indicate that the watering devices were within the movement capabilities of all animals resident on the experimental grid.

Table 3. E
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Percent catc number known
91-100
81-90
71-80
61-70
51-60
41-50
40
Mean Percenta

Table 3. Efficiency of live-trapping procedure on the two grids. Data presented are the distributions of percentage catch of the minimum number known alive in each trap period.

Percent catch of minimum number known alive	Number of trap periods					
	G. paeba		*D. auricularis*		*R. pumilio*	
	Contr.	Exper.	Contr.	Exper.	Contr.	Exper.
91-100	1	3	2	6	4	6
81-90	2	4	15	11	1	2
71-80	5	0	3	1	4	5
61-70	3	8	5	4	3	2
51-60	5	3	0	2	3	4
41-50	7	5	1	1	4	3
40	2	4	1	1	8	3
Mean Percentage	62	63	78	76	55	64

Population

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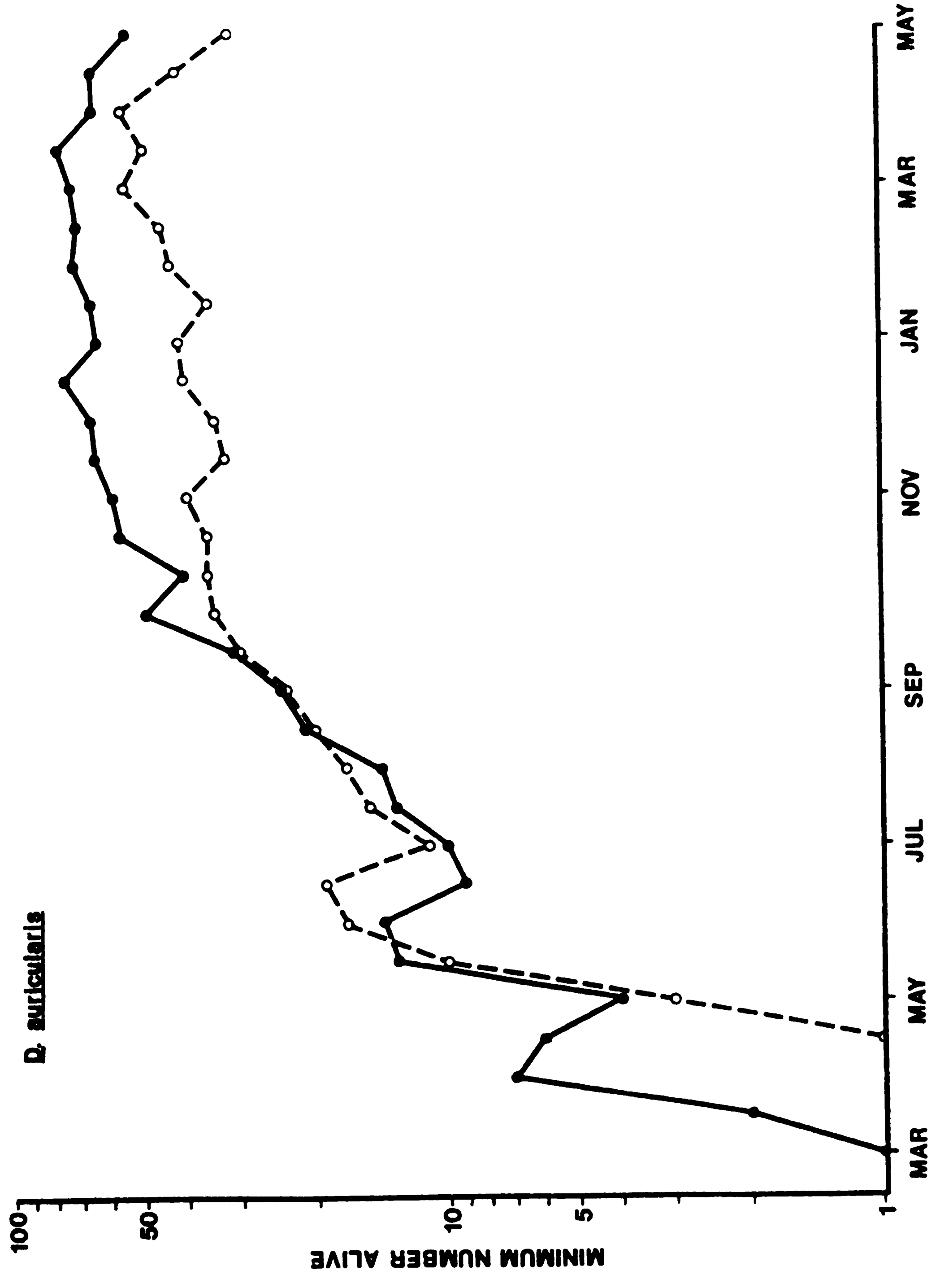
Population Size and Recruitment

Population sizes of D. auricularis, G. paeba, and R. pumilio on the two areas are shown in, respectively, Figures 3, 4, and 5. At the beginning of the study in early March 1974, rodent populations on the two live-trap areas consisted of only a few widely-scattered individuals. Surveys over large areas of the ranch revealed a general scarcity of active rodent burrows. In a study on the same area in February 1973 (R. H. Baker, unpubl. data), small rodents were very abundant, so a large decline occurred sometime during the intervening year. Presumably the previously-mentioned failure of rains in 1973 was at least a contributing factor in this decline. Following rains in January to April 1974, rodent populations began to increase, primarily during May and June of that year.

Populations of these three species exhibited different patterns of increase from low to peak numbers. Gerbillurus paeba populations on both areas increased rapidly during the winter months of May through September, and reached peak numbers in September (control) or October (experimental) (Figure 4). Similarly, R. pumilio on both areas showed little population growth after September (Figure 5). In contrast to these species, D. auricularis did not attain maximum population size until February or March 1975.

Finite rates of increase in population size per two weeks ($\lambda = N_{t+2}/N_t$, t in weeks) from April or May 1974 until the end of the study are shown in Table 4. While there are no striking differences in mean λ's, the distribution of λ's between those less than one (indicating a declining population) and those greater than or equal to one (indicative of, respectively, a growing or stable population) illustrate

Figure 3. Minimum number of D. auricularis known alive in each trap period on the control (●——●) and experimental (○— —○) areas.


D. auricularis
MINIMUM NUMBER ALIVE
100
50
10
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1
MAR
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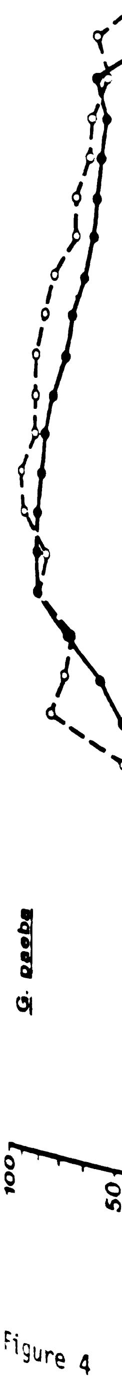
Figure 3

Figure 4. Minimum number of G. paeba known alive in each trap period on the control (●——●) and experimental (○— —○) areas.



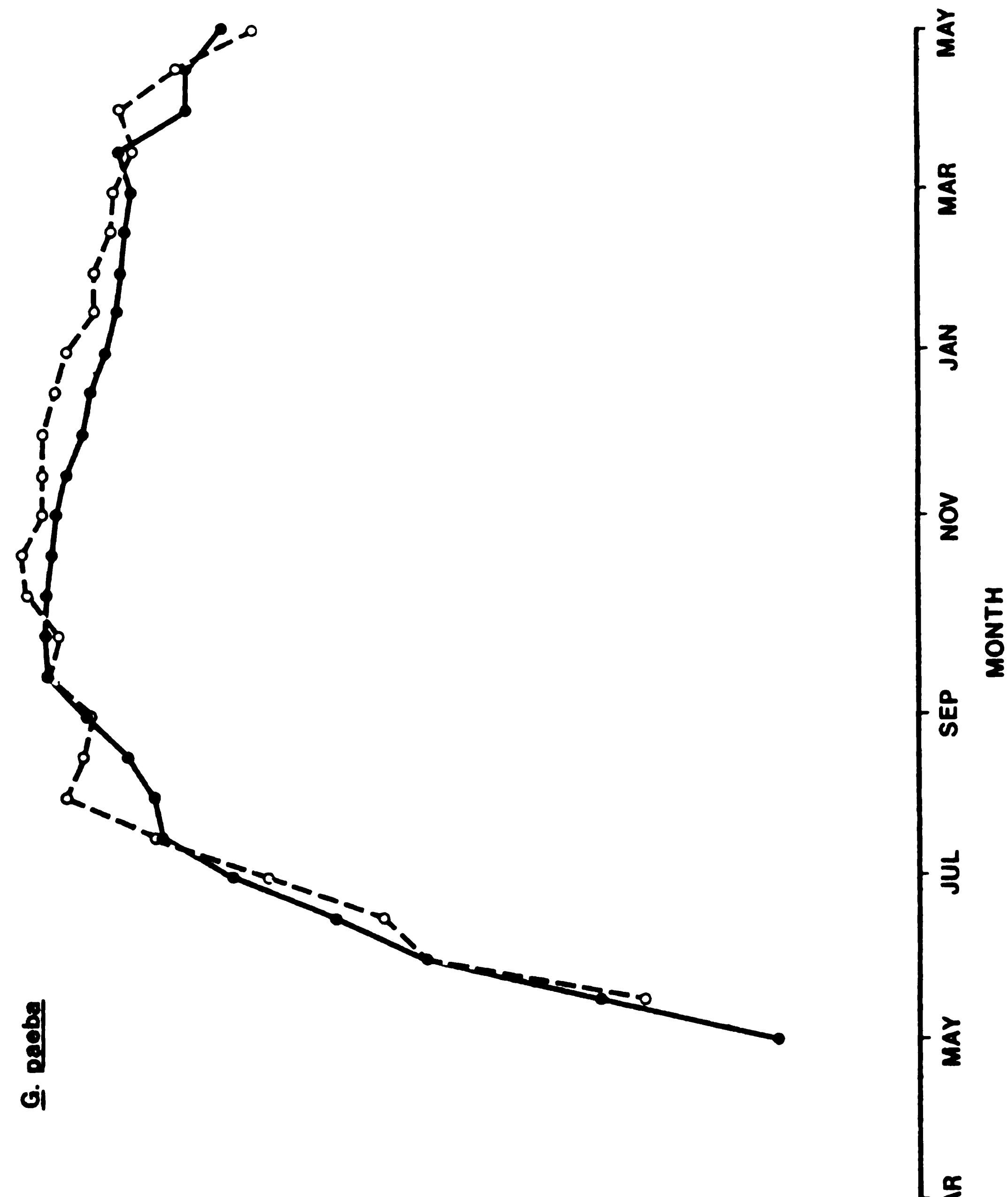

G. paeba
MINIMUM NUMBER ALIVE
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Figure 4

Figure 5. Minimum number of *R. pumilio* known alive in each trap period on the control (●—●) and experimental (○– –○) areas.

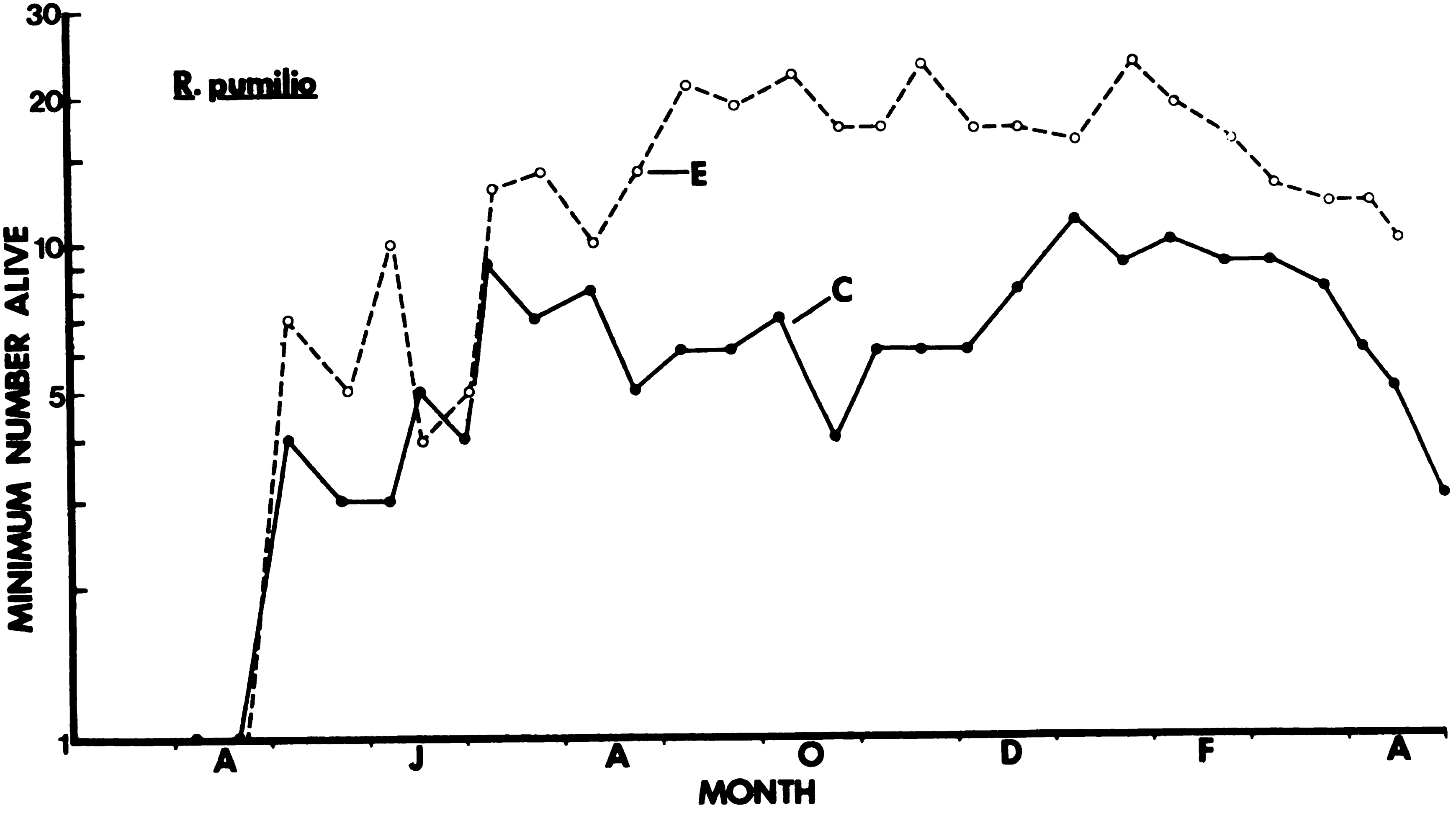

Figure 5

Table 4. F
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Trap Period	Mo
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11	"
12	Au
13	"
14	Se
15	"
16	Oc
17	"
18	No
19	"
20	De
21	"
22	Ja
23	"
24	Fe
25	"
26	Ma
27	"
28	Ap
29	"
Mean	
Number ≥ 1.	
Number < 1.	

Table 4. Finite rates of increase in population size per two weeks (λ) of rodents on the two live-trap areas.

Trap		D. auricularis		G. paeba		R. pumilio	
Period	Month	Contr.	Exper.	Contr.	Exper.	Contr.	Exper.
1	Mar.	----	----	----	----	----	----
2	"	----	----	----	----	----	----
3	Apr.	----	----	----	----	----	----
4	"	0.67	3.00	----	----	----	----
5	May	3.25	3.33	2.50	----	0.75	0.71
6	"	1.08	1.70	2.40	3.00	1.00	2.00
7	June	0.64	1.12	1.58	1.25	1.67	0.40
8	"	1.11	0.58	1.68	1.80	0.80	1.25
9	July	1.30	1.36	1.50	1.78	2.25	2.60
10	"	1.08	1.13	1.02	1.56	0.78	1.08
11	"	1.50	1.18	1.12	0.92	1.14	0.71
12	Aug.	1.14	1.15	1.24	0.96	0.62	1.40
13	"	1.33	1.30	1.22	1.26	1.20	1.50
14	Sep.	1.53	1.13	1.01	0.94	1.00	0.90
15	"	0.82	1.03	0.99	1.13	1.17	1.16
16	Oct.	1.40	1.00	0.98	1.07	0.57	0.77
17	"	1.04	1.11	0.98	0.89	1.50	1.00
18	Nov.	1.10	0.82	0.95	1.01	1.00	1.35
19	"	1.02	1.06	0.92	1.00	1.00	0.74
20	Dec.	1.15	1.18	0.96	0.94	1.33	1.00
21	"	0.84	1.02	0.94	0.94	1.38	0.94
22	Jan.	1.03	0.85	0.94	0.87	0.82	1.44
23	"	1.09	1.23	0.98	1.00	1.11	0.83
24	Feb.	0.99	1.05	0.98	0.91	0.90	0.84
25	"	1.03	1.20	0.96	1.00	1.00	0.81
26	Mar.	1.07	0.91	1.07	0.90	0.89	0.92
27	"	0.83	1.12	0.71	1.08	0.75	1.00
28	Apr.	1.00	0.75	1.00	0.75	0.83	0.83
29	"	0.83	0.76	0.83	0.67	0.60	----
Mean		1.15	1.23	1.18	1.15	1.04	1.09
Number ≥ 1.00		19	20	12	13	14	12
Number < 1.00		7	6	13	11	11	12

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differences in the patterns of population growth in these three species. Desmodillus auricularis populations were stable or increasing in 73-77 percent of the two week intervals, whereas populations of G. paeba and R. pumilio were stable or growing in only 48-56 percent of the time intervals. Differences in these distributions between D. auricularis and each of the other two species were tested in 2 x 2 χ^2 contingency tables. These tests indicate that the distribution of λ's between those greater than or equal to one and those less than one for D. auricularis and G. paeba on both areas are different at $0.5 < P < .10$. The probabilities of these distributions being different for D. auricularis and R. pumilio are $P > .10$ on the control area and $.025 < P < .05$ on the experimental area. Gerbillurus paeba populations on both areas, after reaching maximum numbers in September or October, declined steadily at an average rate of about 5-6 percent per two weeks. Populations of R. pumilio showed no consistent patterns of increase or decline after reaching peak numbers. It should be noted that the apparent rapid declines in all three species during the last three trap periods are probably an artifact of catching less than 100 percent of the minimum number alive in each trap period.

Differences in patterns of population growth among these species were further examined by linear regression of population size (expressed arithmetically rather than logarithmically) on time from the start of the study, using data from trap periods one (designated week zero) through 27 (week 52). This linear regression explained a large portion of the variation in population size in D. auricularis on both areas (coefficient of determination $r^2 = .93 - .94$), indicating that population growth in this species proceeded in a relatively linear fashion during the course (

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These data on finite rates of increase and the linear regressions indicate that population growth in *D. auricularis* during this study progressed in a different fashion and was much less seasonally restricted than in *G. paeba* and *R. pumilio*.

While the qualitative patterns of population growth in each species were similar on the two areas, there were numerical differences between populations on the control and experimental areas. Population sizes of *G. paeba* on the two areas were similar throughout the study, with a peak population size on the control area .89 that on the experimental area. From early October until the end of the study, control population size averaged .91 that on the experimental grid. *Desmodillus auricularis* on the two areas increased in close parallel until September, when the rate of population growth on the experimental area fell behind that on the control grid. From that time until the end of the study, *D. auricularis* population size on the experimental area averaged about 65 percent that on the control. Throughout the study, control *R. pumilio* population size averaged about 52 percent that on the experimental grid. Probable reasons for these differences between control and experimental *D. auricularis* and *R. pumilio* population sizes will be presented later.

Recruitment of new animals was examined by computing the proportion of the total recruitment (that is, of the total number of first

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captures) that occurred in each trap period (Table 5). These data illustrate that the timing of peaks in recruitment was roughly similar for all species on both areas, occurring between trap periods 9 and 18. However, the three species exhibited differing degrees of temporal compression of these peaks. These differences were examined by computing the maximum proportion of the total recruitment that occurred in any one ten-week interval. The magnitude of these proportions parallels the degree of seasonality of population growth, with the more seasonal species, *G. paeba* and *R. pumilio*, having higher proportions of their total recruitment concentrated in these ten-week intervals, and a tendency for peaks to occur sooner than in *D. auricularis*. The latter species on both areas had peak recruitment between trap periods 13 and 18, and these peaks included between .324 and .355 of the total recruitment. Maximum recruitment in a ten-week interval in both *R. pumilio* populations included .413 - .428 of the total recruitment, with maximum recruitment occurring between trap periods 11 and 16. Peak recruitment in both *G. paeba* populations occurred earlier (trap periods 9-14) than in the other species, and included a higher proportion of the total recruitment (.503-.554). These differences in the seasonality of recruitment are further illustrated in Figure 6, for each of the three species on the control area. The proportion of the total recruitment that occurred in each trap period was computed, and these proportions were summed over time to compare differences in the cumulative proportions of total recruitment. The resulting curves (Figure 6) have starting points of 0.0, when no animals had been captured, and end points of 1.0, when all animals had been captured for the first time. An arbitrary level of 0.8 of the total recruitment was chosen to compare

Table 5.

Trap Periods
1-2
3-4
5-6
7-8
9-10
11-12
13-14
15-16
17-18
19-20
21-22
23-24
25-26
27-28
29-30

Table 5. The proportion of the total recruitment occurring per 4 weeks.

Trap	*D. auricularis*		*G. paeba*		*R. pumilio*	
Periods	Contr.	Exper.	Contr.	Exper.	Contr.	Exper.
1-2	.013	.005	.000	.004	.000	.000
3-4	.048	.005	.000	.004	.024	.000
5-6	.056	.053	.023	.011	.095	.072
7-8	.030	.068	.068	.053	.048	.072
9-10	.022	.057	.162	.166	.119	.103
11-12	.066	.058	.135	.179	.190	.093
13-14	.132	.126	.257	.158	.119	.186
15-16	.114	.120	.122	.109	.119	.134
17-18	.109	.078	.077	.092	.048	.031
19-20	.074	.026	.023	.064	.024	.114
21-22	.064	.079	.036	.050	.143	.083
23-24	.061	.052	.027	.021	.024	.072
25-26	.062	.094	.019	.029	.000	.010
27-28	.105	.142	.036	.035	.048	.031
29-30	.034	.036	.018	.029	.000	.000

Figure 6. Cumulative proportion over time of the recruitment of new animals on the control area.

Figure 6

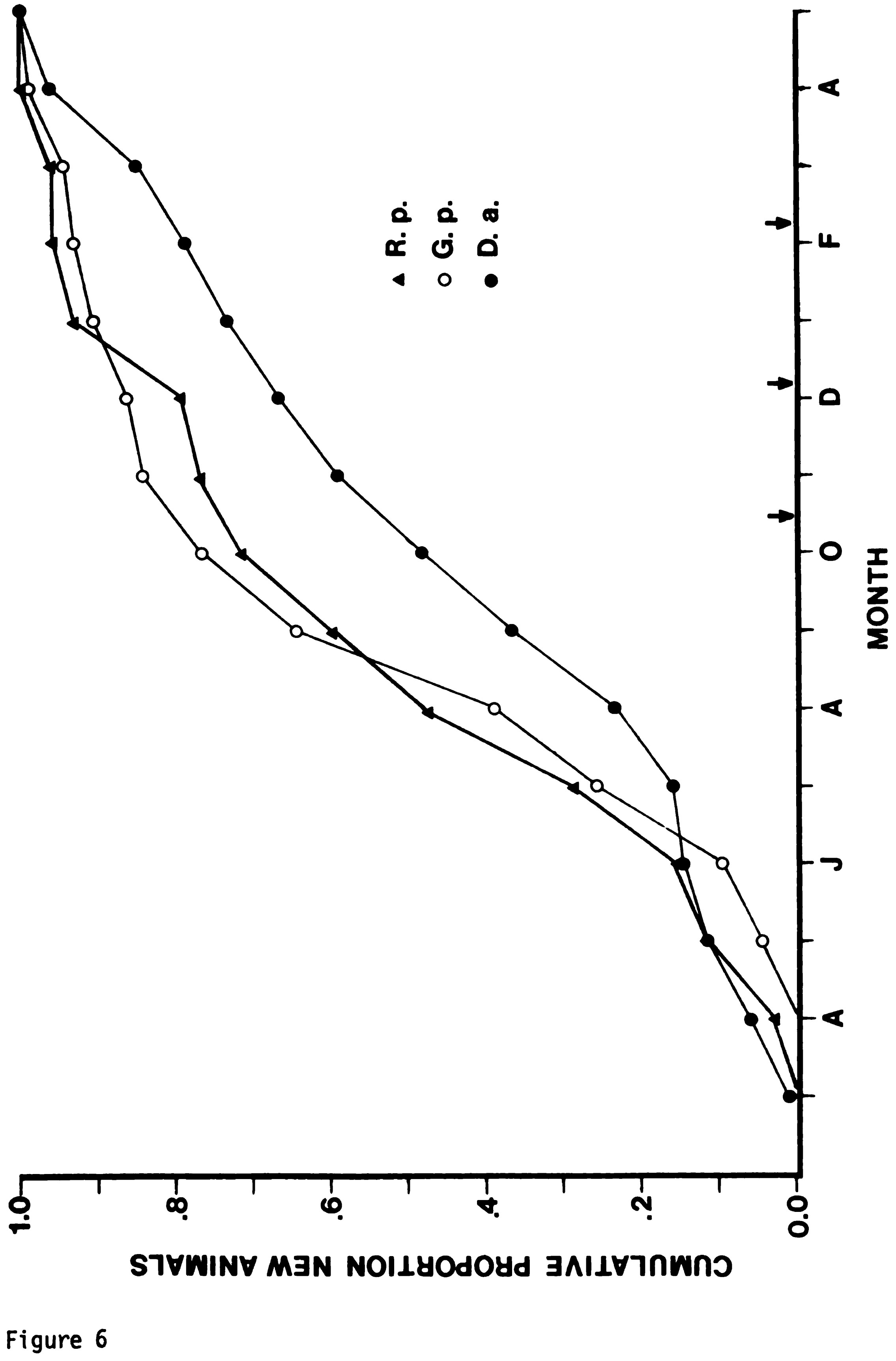
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Figure 6

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species. As indicated by the arrows above the abscissa in Figure 6, control *G. paeba* completed 0.8 of their recruitment in October, *R. pumilio* in December, and *D. auricularis* in February. Experimental populations of these species showed similar patterns of recruitment.

Summarizing these data, two of the three species, *G. paeba* and *R. pumilio*, exhibited relatively seasonal patterns of recruitment and population growth. These species showed little population growth after the onset of hot, dry conditions in September or October, and had high proportions of their recruitment concentrated into a short time period. In contrast, population growth and recruitment in *D. auricularis* was more continuous throughout the study. Numerical differences between control and experimental populations will be discussed further below.

Reproduction

Breeding intensity in small mammal live-trapping studies has typically been expressed as a proportion of breeding animals in the adult population. The only means available for establishing age classes in these species is on the basis of body weight. I have little confidence in these weight-defined age classes for these species and, to avoid introducing artificial biases in estimating breeding intensities, have therefore expressed the numbers of males or females of each species breeding in each trap period as proportions of the total numbers of each sex captured in that trap period, without regard to age. The minimum body weight at which scrotal testes or perforate vaginal openings were observed was 28 g in male and 27 g in female *D. auricularis*, 16 g in male and female *G. paeba*, and 28 g in male and 29 g in female *R. pumilio*. Rarely, except in *R. pumilio*, did animals of lower body weights than these enter traps.

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Sample sizes of *R. pumilio*, particularly on the control area, were small, so that time-specific comparisons of breeding intensities between the control and experimental areas are difficult. There were no marked differences in mean breeding intensity in this species between the two areas, but there were striking differences in overall reproductive output and in its seasonal distribution. Obviously-pregnant females were observed in 6 trap periods on the control area versus 10 on the experimental area, and over twice as many pregnancies (22) were seen on the experimental area as on the control (9). No pregnant *R. pumilio* females were observed on the control area between mid-October 1974 and the end of March 1975, while 7 pregnant females were observed on the experimental area during that period. Similarly, lactating *R. pumilio* females were found in 22 trap periods on the experimental area and in only 11 on the control. These reproductive differences were reflected in differences 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). The reproductive differences seem an obvious explanation for the greater abundance of *R. pumilio* on the experimental grid.

Sample sizes of both the nocturnal gerbils were large enough that breeding percentages in all except the first few trap periods could be compared. Pregnancy was not assessed in *D. auricularis* on the basis of bulging abdomens, since their normally rotund shape obscured changes in body shape accompanying pregnancy.

Breeding percentages of these two species are shown in Figures 7, 8, and 9. I will first discuss differences in the seasonal patterns of breeding in *G. paeba* and *D. auricularis* on the control area, before

Figure 7. Percentage of *G. paeba* males with scrotal testes on the control (●——●) and experimental (○- — -○) areas.

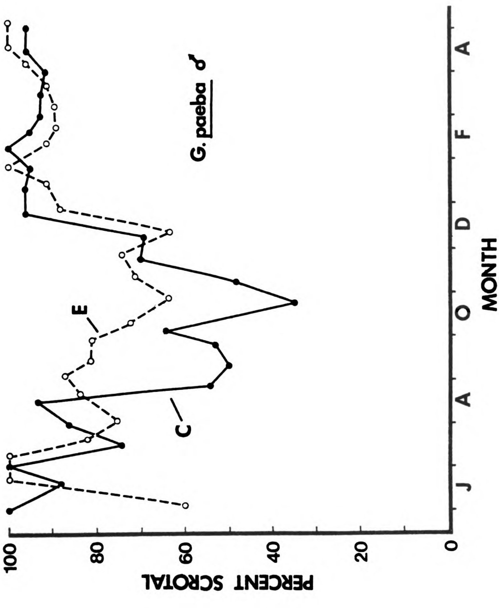

Figure 7

Figure 8. Breeding measures in G. paeba females on the control (●——●) and experimental (○– –○) areas.

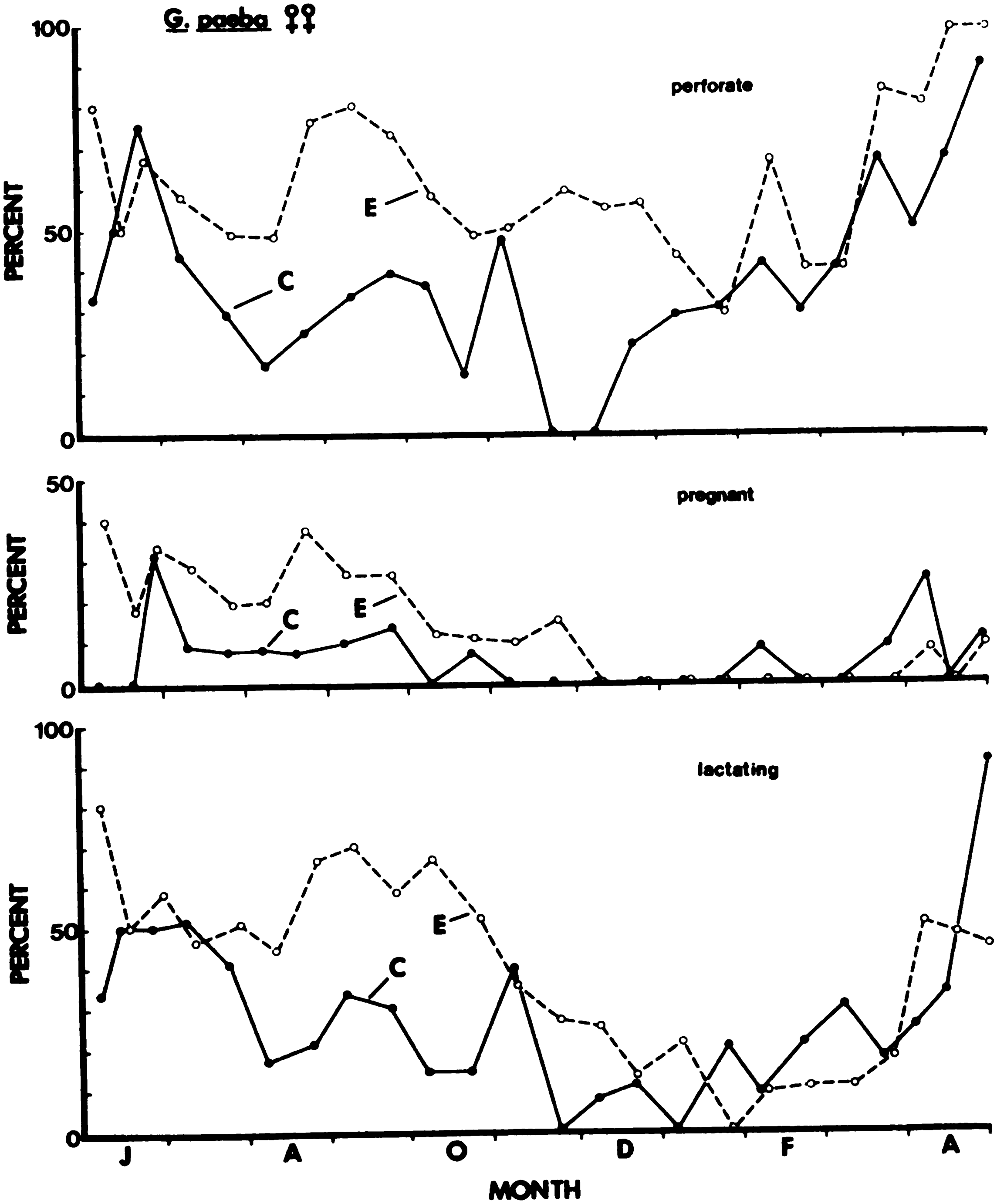
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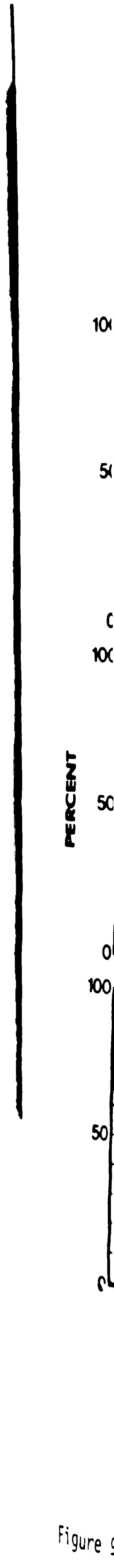
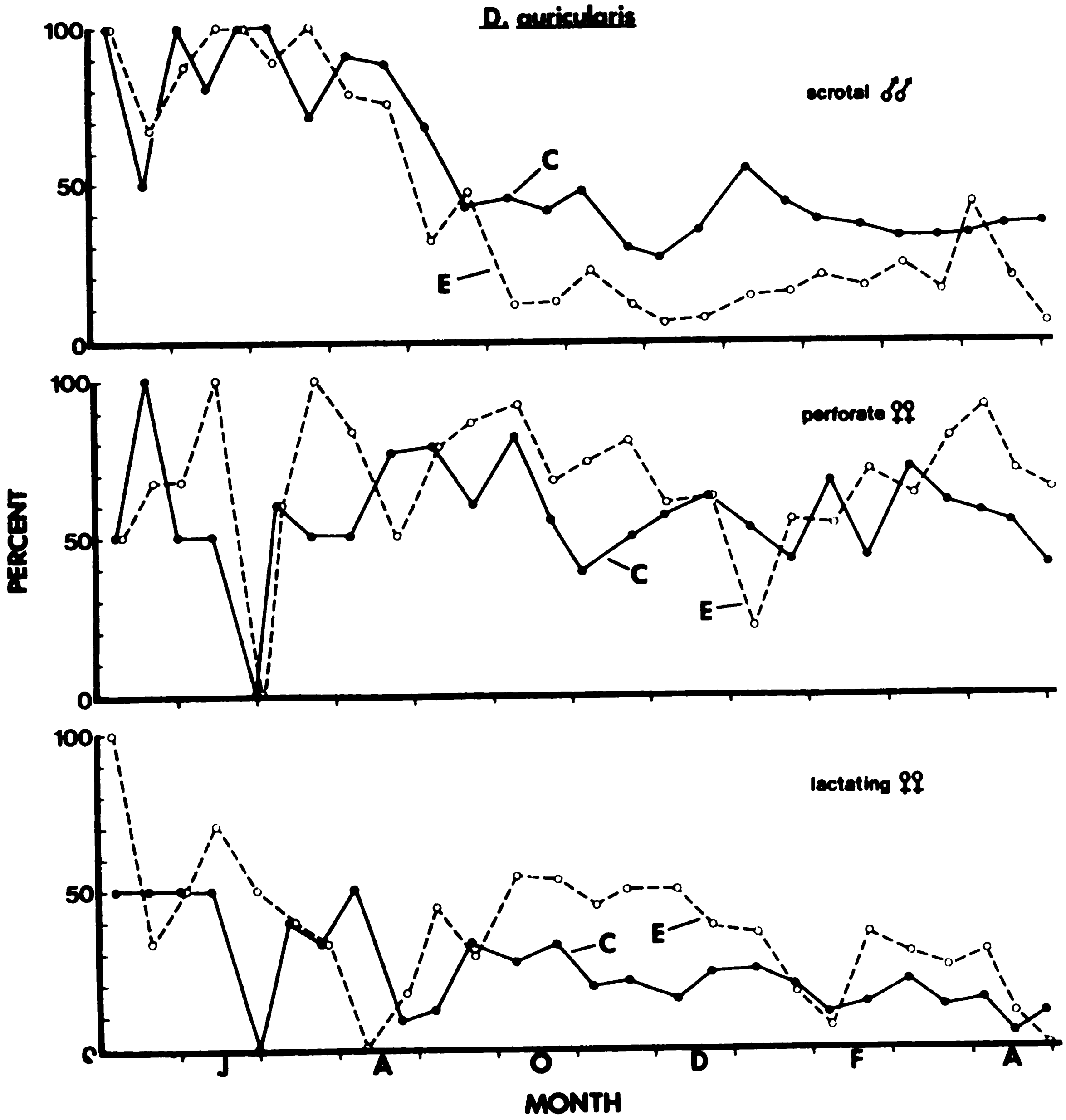
Figure 8

Figure 9. Breeding intensity in male and female _D_. _auricularis_ on the control (●——●) and experimental (○— —○) areas.

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comparing these species on the control and experimental areas. Proportions of males of the former species with testes in a scrotal position on the control area were high (> .7) through mid-August, when they showed a marked decline and remained relatively low (< .7) until mid-December when they again increased and remained above 0.9 for the remainder of the study (Figure 7). Proportions of control _G. paeba_ females (Figure 8) with perforate vaginas 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 lactating. This seasonal decline in _G. paeba_ breeding percentages occurred during the hottest, driest portion of the year.

Corresponding to a 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 (Figure 9). The proportions of _D. auricularis_ males with scrotal testes was high until about October, when it dropped to around 0.3 to 0.4 and leveled off for the remainder of the study. The proportions of perforate _D. auricularis_ females showed no consistent changes throughout the study, and there was only a slight decline in the proportion lactating during the hot, dry season.

Differences in breeding proportions of each species on the two areas in each trap period were tested by χ^2. Obviously, the nature of capture-recapture data precludes independence among samples over time, since some animals are found in several samples. Myers (1974) recognized this problem, and felt it more appropriate to utilize standard statistical tests as an approximation to probabilities rather than

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The results of these χ^2 tests are shown in Table 6 for G. paeba and in Table 7 for D. auricularis. In nine of eleven 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 females lactating 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 G. paeba that were lactating was significantly higher on the control area than on the experimental in the last trap period.

The proportion of G. paeba males with scrotal testes was significantly higher on the experimental area than on the control in four out of five trap periods between late August and mid-October. These differences between control and experimental G. paeba populations occurred during the period of lowered breeding intensity on the control area in the hottest, driest months of the year. Thus, the apparent effect of this reproductive response on the experimental area was an extension of the breeding season further into the dry season.

In addition to these differences in the seasonality of breeding in 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 area. There was also a slight tendency, approaching statistical significance ($.05 < P < .10$, tested by χ^2), for an increased frequency of repeat (two, three, or four times)

Table 6.

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Table 6. Results of χ^2 tests for significant differences in breeding proportions of *G. paeba* on control and experimental areas. Trap periods when there were no significant differences are left blank. In others, the probability and directionality of differences are indicated.

Trap			Females		Males
Period	Month	Perforate	Lactating	Pregnant	Scrotal
6	May				
7	"				
8	June				
9	"				
10	July	<.01, E>C			
11	"				
12	Aug.	<.01, E>C	<.05, E>C		
13	"	<.005, E>C	<.005, E>C	<.025, E>C	<.01, E>C
14	Sep.	<.005, E>C	<.005, E>C		<.01, E>C
15	"	<.005, E>C	<.05, E>C		<.025, E>C
16	Oct.		<.005, E>C		
17	"	<.01, E>C	<.005, E>C		<.05, E>C
18	Nov.				
19	"	<.01, E>C			
20	Dec.	<.005, E>C			
21	"				
22	Jan.				
23	"				
24	Feb.				
25	"				
26	Mar.				
27	"				
28	Apr.				
29	"				
30	"		<.025, C>E		

Table 7.

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Table 7. Results of χ^2 tests for significant differences in breeding proportions of *D. auricularis* on control and experimental areas. Symbolism as described for Table 6.

Period	Month	Females		Males
		Perforate	Lactating	Scrotal
6	May			
7	"			
8	June	<.05, E>C		
9	"			
10	July			
11	"			
12	Aug.		<.05, C>E	
13	"			
14	Sep.			<.05, C>E
15	"			
16	Oct.			<.025, C>E
17	"			<.05, C>E
18	Nov.			
19	"			
20	Dec.		<.05, E>C	
21	"			<.025, C>E
22	Jan.			<.005, C>E
23	"			<.05, C>E
24	Feb.			
25	"			
26	Mar.			
27	"			
28	Apr.	<.01, E>C		
29	"			
30	"			<.01, C>E

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The data in Table 7 indicate that there were no consistent differences in proportions of control and experimental D. auricularis females that were lactating or had perforate vaginas. The proportion of male D. auricularis with scrotal testes was significantly higher on the control area than on the experimental grid in 7 trap periods.

Thus, these three species appeared to show a graded series of reproductive responses to the experimental provision of drinking water. Desmodillus auricularis showed no consistent response to this experimental treatment. There was an increased occurrence of pregnancies in G. paeba on the experimental area, and that population bred longer into the dry season than the same species on the control area. In the experimental R. pumilio population, more than twice as many pregnancies were observed, and over three times as many juveniles were captured as on the control area. In the latter species, a numerical response accompanied this reproductive response.

Mortality

Survivorship was computed from data obtained by direct enumeration of marked animals (Krebs, 1964, 1966). As stressed by Krebs and others, "mortality" calculated from live-trap data by these methods is equated with disappearance from the live-trapping grid, and thus includes not only death but also emigration from the area and trap avoidance. Two measures of survivorship were computed. First, the probability of surviving each two-week interval was calculated as the proportion of the animals known to be alive at time t that were still known to be alive 2 weeks later (after Krebs, 1966). These values provide time-specific estimates of the survivorship of animals alive on an area at a certain time, and, where possible, have been computed separately for each sex. Two-week survival rates were computed separately for all individuals known to be alive on an area at a specific time, and for new "recruits" (i.e., animals captured for the first time) in each trap period. These measures allowed assessment of, first, changes in overall survival, and second, changes in survival rates of animals entering the population.

The second survivorship measure utilized was the life-table calculation for the expectation of further life (e_x). These data, rather than estimating the survival rates of animals in a population at a particular time, summarize the mortality pattern over time of a group of animals entering a population at the same time. In small mammal live-trapping studies, age $x = 0$ is generally equated with the age at first capture, and, typically, only the life expectancy at the time of first capture is presented (see Leslie _et al._, 1955). Additional information, however, may be obtained by computing e_x values for "older" animals, i.e., the expectation of further life for animals still alive x time intervals subsequent to first capture. These measures may be particularly valuable in comparing groups of animals with survivorship (l_x) curves of differing shapes.

In the present study, e_x values were computed, separately for each sex where possible, using data for all animals regardless of weight at first capture, as the relationship between age and weight in these species, as previously mentioned, is unclear. Life expectancy values were computed by grouping at a common origin animals captured for the first time during several consecutive trap periods. These animals were treated as a "cohort", an l_x curve was calculated and, from those data, values of e_x were computed using a linear approximation,

$$e_x \simeq T_x/l_x, \text{ where } T_x = \sum_{x=x}^{\infty} L_x \text{ and } L_x \simeq \frac{l_x + l_{x+1}}{2}$$

Since the shapes of the l_x curves for these populations were often quite different, e_x values expressed only at the time of first capture frequently obscured large differences in life expectancy at times subsequent to first capture. I have thus presented both the e_x at first capture and the highest e_x value calculated for animals alive x weeks after first capture.

Two-week survival rates of all animals, and of "recruits", of the three species on both areas are shown in Table 8. Since sample sizes of R. pumilio on both areas were small, both sexes of that species have been pooled in these calculations. Mean overall survival rates of both sexes of all species were relatively high, and only slightly different from one another, with G. paeba having the highest mean rates. During two early trap periods (2 and 5), experimental G. paeba females had survival rates of 0.0. These values were based on sample sizes of one each, and, when excluded from the calculations of means, a mean survival rate of 0.83 for that group is obtained.

While mean overall survival rates of the three species are not strikingly different, the variances of D. auricularis survival rates were considerably higher (3.1 - 9.9 times) than those for G. paeba. Variances of R. pumilio survival rates were generally intermediate between those of the other two species. The higher variances in D. auricularis survival rates largely reflect differences in the seasonal constancy of survival rates (see Table 8). Survival rates of G. paeba, of both sexes on both areas, were consistently high throughout the

Table 8. Survival rates of rodents on the two areas (per two-weeks).

	OVERALL SURVIVAL										RECRUIT SURVIVAL							
	D. auricularis				*G. paeba*				*R. pumilio*		*D. auricularis*				*G. paeba*			
Trap	Male		Female		Male		Female				Male		Female		Male		Female	
Period	Contr.	Exper.	Contr.	Exper.	Contr.	Exper.	Contr.	Exper.	Contr.	Exper.	Contr.	Exper.	Contr.	Exper.	Contr.	Exper.	Contr.	Exper.
1	---	---	.00	---	---	---	---	---	---	---	---	---	.00	---	---	---	---	---
2	.00	---	.00	.00	---	---	---	.00	---	---	.00	---	.00	.00	---	---	---	.00
3	1.00	---	.17	---	---	---	---	1.00	1.00	---	1.00	---	.17	---	---	---	---	1.00
4	.33	.00	.67	---	---	---	---	1.00	1.00	---	.50	.00	.50	---	---	---	---	---
5	.00	1.00	.33	1.00	1.00	---	1.00	.00	.50	.60	---	1.00	.00	1.00	1.00	---	1.00	---
6	.75	1.00	.40	1.00	1.00	1.00	.50	---	1.00	.67	.75	1.00	.25	1.00	1.00	1.00	1.00	---
7	.45	.80	1.00	.71	1.00	.86	1.00	.67	1.00	.29	.60	.75	1.00	.33	1.00	.80	1.00	.67
8	1.00	.45	.67	.50	1.00	.71	.86	.80	.80	1.00	1.00	.67	---	.50	1.00	1.00	.67	.67
9	1.00	.50	1.00	.50	.85	.58	.79	.55	1.00	.75	---	.00	1.00	.00	.80	.80	.75	.43
10	.71	.89	.67	.80	.74	.94	.65	.83	.57	.67	.00	.83	.00	.67	.50	.90	.50	.76
11	.86	.73	.71	1.00	1.00	.75	.88	.63	.43	.50	.50	.67	.33	1.00	1.00	.83	.80	.56
12	.42	.50	.44	.62	.86	.69	.71	.71	.38	.80	.50	.00	.00	.00	1.00	.55	.78	.33
13	.80	.71	.64	.89	.73	.92	.89	.88	.60	.67	.60	.62	.50	.75	.68	.79	.80	.75
14	.71	.58	.91	.82	.68	.72	.75	.82	.67	.65	.69	.33	.50	.33	.80	.50	.50	.77
15	.74	.72	.83	.81	.88	.95	.78	.92	.67	.72	.50	.71	.62	.57	.90	.80	.60	1.00
16	1.00	.79	1.00	.88	.92	.89	.84	.80	.57	.79	1.00	.33	1.00	1.00	.80	.70	.57	.60
17	.88	.84	.87	.88	.92	.86	.73	.76	1.00	.94	.54	.75	.71	1.00	.50	.71	.67	.60
18	.86	.78	1.00	.88	.91	.92	.88	.88	1.00	.82	.71	.43	1.00	.50	.57	.75	1.00	.00
19	.95	.94	.89	.86	.88	.92	.92	.85	.83	.65	.83	---	.40	---	.00	.33	1.00	.67
20	.92	.90	.96	1.00	.96	.90	.78	.85	1.00	.82	1.00	.67	.67	1.00	.00	1.00	---	.50
21	.74	.95	.90	.74	.89	.80	.90	.87	.88	.65	.18	1.00	.33	.50	.50	.67	.50	.50
22	1.00	.81	.90	.87	.86	.81	1.00	.81	.82	1.00	---	.43	.67	---	.33	.57	1.00	.00
23	.94	.95	.93	1.00	.89	.98	.95	.96	1.00	.83	.50	.00	.67	---	1.00	1.00	1.00	.50
24	.90	.92	.90	.88	.97	.88	.85	.96	.90	.84	.50	.60	.33	.50	1.00	1.00	1.00	.00
25	.88	.93	1.00	.94	.95	.86	.95	.91	1.00	.75	.71	.80	---	.00	1.00	1.00	.50	---
26	.84	.73	.79	.62	.94	.86	.89	.78	.78	.85	.50	.00	.00	.00	.00	.40	---	.00
27	.76	.80	.75	.84	.71	.94	.71	1.00	.62	.83	.33	.17	.00	.83	.57	.67	.00	1.00
28	.92	.66	.96	.78	.93	.68	1.00	.75	.80	.91	1.00	.12	1.00	.29	---	.20	---	.00
Mean	.75	.76	.72	.79	.89	.84	.84	.77	.80	.75	.60	.50	.45	.54	.69	.74	.74	.49
s^2	.0785	.0492	.0904	.0483	.0091	.0119	.0157	.0639	.0413	.0251	.0848	.1217	.1337	.1443	.1200	.0529	.0693	.1180

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study, and showed little or no seasonal change. The decline in *G. paeba* numbers after reaching peak population size was not accompanied by lower survival. In fact, survival rates during that period were slightly higher on both areas than during the phase of rapid population growth. On the other hand, *D. auricularis* survival rates during the first 12 trap periods (March through mid-August) were generally low and/or highly variable. Survival rates of *R. pumilio* on the experimental area showed no consistent seasonal trends. On the control grid, however, individuals of this species survived less well between trap periods 10 and 16 (July to October), the period encompassing a portion of the cool winter months.

Survival rates of animals captured for the first time were lower than the overall rates. Whether this reflects a higher mortality *per se*, rather than dispersal or trap avoidance by some animals after an initial capture, is not known. Differences between sexes and between areas in mean survival rates of first-captured *D. auricularis* were slight. Similarly, except for the much lower mean survival rate of first-captured *G. paeba* females on the experimental area, mean survival rates were similar for the two sexes of this species. The survival rates of "recruits" in some segments of the populations did show marked seasonal variation. In *D. auricularis*, with the exception of control females, which survived less well during the first half of the study (mean recruit survival per two weeks = 0.33) than in the second half (mean rate = 0.57), there was little consistent seasonal variation in survival rates of animals captured for the first time. Certain segments of both *G. paeba* populations showed large differences between the survival of recruits during the early part of the study and after peak population size was reached. These differences, however, are not consistent and are difficult to interpret. Survival rates of first-captured control *G. paeba* females and experimental males were relatively constant over time. Control *G. paeba* males and experimental females survived about half as well if first captured during the second portion of the study than when populations were growing.

Little information is available on the causes of mortality in these rodents. As described earlier, a variety of reptilian, avian, and mammalian predators were observed on or near the study areas. During June 1974 a *Felis libyca* removed an unknown number of trapped animals from the experimental area until it was removed, but no other information is available on predation as a mortality factor. In spite of this lack of data on the causes of mortality, it is of interest to examine two specific aspects of the nature of mortality in these populations: first, the relationship between breeding activity and mortality; and second, the degree of concordance between male and female survival rates. These aspects were analyzed by computing correlation coefficients between breeding percentages and survival rates, and between male and female survival rates for *G. paeba* and *D. auricularis*. These data are shown in Table 9. The data in the first three lines of the table suggest differences in the mortality costs of reproductive activities between species, sexes, and areas. In *D. auricularis* on both areas there was a significant negative correlation between male survival rates and the proportion of males with scrotal testes. The corresponding correlations in *G. paeba* males were not significant. In females of both species on the experimental area, correlations between survival rates and proportions with perforate vaginal openings were not

Table 9. Correlations between survival rates (s) and breeding percentages in each trap period, and between male and female survival rates. Significance levels are probabilities of significant correlation; NS = not significant.

	D. auricularis		*G. paeba*	
	Contr.	Exper.	Contr.	Exper.
♂s vs. scrotal	−.486	−.412	+.329	−.209
	.01<P<.05	.01<P<.05	NS	NS
♀s vs. perforate	−.325	+.080	−.429	−.026
	.05<P<.10	NS	.01<P<.05	NS
♀s vs. lactating	−.735	+.008	−.556	−.551
	P<.01	NS	P<.01	P<.01
♂s vs. ♀s	+.410	+.747	+.234	+.732
	.05<P<.10	P<.01	NS	P<.01

significant. This correlation was significant in control *G. paeba* and approached statistical significance in control *D. auricularis* females. The strongest and most highly significant correlations were between female survival rates and the proportions of lactating females of *G. paeba* on both areas and *D. auricularis* on the control area. These results suggest that increased water availability on the experimental area may have reduced the mortality costs of being reproductively active (perforate) in females of both species, and of lactating in *D. auricularis*, but had no effect on mortality associated with breeding in males of either species. It should be stressed that these measures do not compare survival rates of breeding and nonbreeding animals, but examine the effects of changes in breeding intensity on the survival of all animals of each sex.

The data in the last line of Table 9 indicate that the correlations between male and female survival rates of both species are highly significant on the experimental grid, but not on the control (although the correlation for *D. auricularis* on that area approaches significance). These results suggest that the timing, and perhaps the causes, of mortality on the experimental grid were similar for both sexes, whereas on the control area the relationship between male and female mortality was weaker.

Life expectancy values are shown in Table 10. It should be noted that, because of possible artificial truncation of the survivorship curves near the end of the study, comparison of changes in e_x values over time within a group should be approached cautiously. Comparisons across sexes, species, and areas within each time interval, however, should be valid. These results indicate that life expectancy of animals

Table 10. Life expectancies (e_x) in weeks of rodents living on the two areas. Maximum e_x is the highest e_x value calculated subsequent to e_x at first capture.

		Males				Females			
		e_x at first capture		Maximum e_x		e_x at first capture		Maximum e_x	
Species	Month of first capture	Contr.	Exper.	Contr.	Exper.	Contr.	Exper.	Contr.	Exper.
D. auricularis	March-July	6.6	5.3	30.3	9.7	11.1	9.5	38.7	31.6
	July-Sep.	14.2	9.0	20.3	20.6	11.0	11.9	29.3	20.9
	Sep.-Nov.	13.3	10.8	17.6	17.1	14.1	10.5	19.2	15.2
	Nov.-Feb.	----	----	----	----	7.9	8.6	12.0	13.1
G. paeba	March-July	18.3	7.4	18.3	8.3	11.8	5.6	23.0	8.7
	July-Aug.	11.4	13.6	18.0	17.2	10.1	9.0	16.4	15.4
	Aug.-Sep.	16.4	14.8	19.0	20.5	7.5	13.3	12.0	14.3
	Oct.-Nov.	11.8	10.0	17.4	12.2	11.2	9.8	12.6	16.2
		(Pooled sexes)							
D. auricularis	March-Feb.	10.8	9.3	17.1	14.1				
G. paeba	"	11.4	10.6	13.0	13.1				
R. pumilio	"	7.4	6.6	10.7	8.6				

of both sexes and species entering the experimental populations between March and July 1974 was much lower than for the corresponding "cohort" on the control area. This difference is especially pronounced in D. auricularis males. There were only slight differences in e_x for animals entering these populations after July, although there was a tendency for continued lower e_x in experimental D. auricularis females. The e_x values for pooled sexes of all animals captured for the first time between March 1974 and February 1975 show that D. auricularis and G. paeba had similar overall longevity, although the maximum calculated e_x value for D. auricularis (38.7 weeks) is about 1.7 times the maximum G. paeba e_x (23.0 weeks). Rhabdomys pumilio appears to be the shortest-lived of the three species.

The observed differences in life expectancy between the two areas during the early months of the study had varying effects on the subsequent weight structure of the populations. Body weights of G. paeba and D. auricularis were examined first by comparing mean body weights in each trap period, and, second, by dividing the entire weight distribution for each species into 12 weight classes, and comparing the proportions found in the top six weight classes in each trap period. There were no consistent seasonal changes in mean body weight or in body weight distributions in either sex of both G. paeba populations. Likewise, there were no significant differences between these two populations in mean body weights or in the mean proportion of animals in the upper half of the weight distribution, for the entire study or for any shorter time intervals. Overall mean body weights, and mean weight distributions, of both sexes of D. auricularis on the experimental area were significantly lower than in the control population (t-test, all $P<.05$), with the differences being most marked in males. These parameters were then compared separately for trap periods 5 through 16, the time when both *D. auricularis* populations were increasing in parallel, and trap periods 17 through 30, when experimental numbers were lower than those on the control. There were no significant differences in mean body weights or in mean weight distributions during the early part of the study (t-test, all $P > .10$), but differences during the latter trap periods were highly significant (t-test, all $P < .01$), with experimental animals being of lower body weight than those on the control area. An obvious explanation for these weight differences during the latter part of the study is the shorter life expectancy of experimental *D. auricularis* entering the population during the early part of the study. While *G. paeba* first captured early in the study on the experimental area also had shorter life expectancy, there was no apparent effect on subsequent weight structure. These differential effects are in fitting with apparent differences in the life history patterns of these two species, as will be presented in the discussion.

DISCUSSION

The major objective of this research was to examine the effects of the experimental provision of drinking water on reproduction in desert rodents. The three species of rodents studied exhibited different responses to this experimental treatment, and these responses were correlated with differences in their demographic patterns on the control grid. A consideration of these basic demographic patterns will precede discussion of the effects of supplementary water.

Annual rainfall at the study locality is low, highly seasonal, and unpredictable. Substantial rains fall only between December and March or April. The winter months of May to September are cool, condensation occurs regularly, and potential evaporation is low. The months of September through April are hot, characterized by high potential evaporation, and unless precipitation occurs, represent a period of potential water stress for small rodents. This environment is reasonably predictable as to the timing of seasonal events (e.g., rainfall), but the effectiveness of those events for the production of resources is highly unpredictable (see Low, 1976).

The demographic patterns of G. paeba, D. auricularis, and R. pumilio appear, to a greater or lesser extent, keyed to these seasonal climatic variations. Rodent populations at the beginning of the study in March 1974 were very low (0-1 individual of each species per 2.7 ha live-trap grid), following a decline during the preceeding year that presumably resulted from a failure of the 1973 rains. Following rainfall between January and April 1974, rodent populations began to increase, and all three species exhibited good abilities to recover from low numbers.

Gerbillurus paeba and *R. pumilio* on the control grid increased rapidly during the winter months, and showed little or no population growth after September or October. The former species showed especially rapid population growth, and then declined slowly and steadily until the end of the study. The species completed a high proportion of their recruitment by September (*G. paeba*) or December (*R. pumilio*). Reproduction in both of these species appeared to take place 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* were observed on the control area. As described earlier, these declines in breeding activity occurred during the hottest, driest months of the year.

Populations of these two species, especially *G. paeba*, exhibited a type of growth pattern shown by several desert rodents (French *et al.*, 1974), i.e., rapid exploitation of favorable periods following rainfall and plant growth. *Desmodillus auricularis*, while also apparently responding to the rainfall/plant growth that occurred at the start of the study, exhibited a much more aseasonal demographic pattern. Population growth in this species continued throughout most of the study, and, in fact, changes in population size over time were described very well by a linear model. Recruitment occurred over a longer part of the year in *D. auricularis* than in the other species, and peak population sizes were not reached until March or April, 1975. Breeding proportions in this species, at least of females, were relatively constant throughout the study, showing little of the seasonal variation shown by the other two species.

It should be stressed that these populations were studied during a year following exceptional rains, 60 to 70 percent above average. Data on the seasonal demographic patterns of these species may thus be peculiar to this unusual year, but it is clear that during the present field studies *D. auricularis* reproduced and experienced population growth relatively uniformly over most of the year, and showed little of the seasonal restrictions observed in *G. paeba* and *R. pumilio*. These different temporal patterns have important bearing on differences in the responses of these species to increased water availability, as discussed later.

The mortality patterns of these rodents on the control area are difficult to interpret. Given the apparent inverse relationship observed between survival and breeding activity (or perhaps above-ground activity) in at least some desert rodents (French *et al.*, 1966, 1967), and the differences in breeding patterns of *G. paeba* and *D. auricularis*, I expected to find that survival rates would be more variable in *G. paeba* than in *D. auricularis*. The opposite case, however, was observed. Two-week survival rates in *G. paeba* were relatively constant over time. The high variability of *D. auricularis* survival rates is accounted for largely by reduced survival during the early part of the study.

The data on life expectancy on the control area show that, overall, *R. pumilio* have shorter lifespans than the two gerbils. The maximum life expectancy values suggest that *D. auricularis*, especially females, may be longer-lived than G. paeba, although this difference is not entirely clear.

On the experimental area, the three species exhibited different reproductive responses to the increased availability of drinking water. Breeding proportions in D. auricularis were not increased on the experimental area. Proportions of male D. auricularis with scrotal testes on the experimental area were, in fact, significantly lower than on the control area in several trap periods.

Gerbillurus paeba showed an appreciable response to the provision of water. More than twice as many pregnancies were observed on the experimental area as on the control, and there was a tendency for an increased frequency of repeat pregnancies in experimental females of this species. Breeding percentages in the experimental population remained high during the hot, dry months following September, when control breeding percentages showed marked declines. It is striking, however, that this increased breeding did not continue indefinitely, but at least in females, eventually showed declines similar to those observed on the control area. This suggests that the control of reproduction by water availability in this species is not complete, but is perhaps partially complemented by social factors or other climatic changes such as those in temperature or photoperiod. Thus, while greater water availability was sufficient to increase breeding intensity in G. paeba during a portion of the year, it produced no visible effect at other times.

While small sample sizes of R. pumilio prevented time-specific comparisons of breeding intensity between control and experimental populations, several data indicate that this species showed a reproductive response to supplementary water. More than twice as many pregnancies were observed on the experimental area as on the control. As evidenced by the seasonal distribution of these pregnancies and of the occurrence of lactating females, the experimental treatment also had the effect of extending the breeding season longer into the dry months.

Thus, two of these three desert rodent species exhibited a reproductive response to the experimental provision of supplementary water. These results support the contentions of several authors (Beatley, 1969, 1976; Bradley and Mauer, 1971) that increased water availability following rainfall and plant growth is at least one of the stimuli for reproduction in desert rodents. It is important to note that, in the two species which did respond to water, a large portion of that response occurred at a time of the year when there was no condensation, temperatures were high, and potential evaporation was probably near maximum. Thus, the effect of water was most noticeable at times when the potential for water stress was high. However, as described above, there were apparently other factors contributing to the control of reproductive activity, at least in _G_. _paeba_.

The exceptional conditions prevailing during the study may have served to minimize differences in water availability between the control and experimental areas, and may account for the lack of a demonstrable reproductive response in _D_. _auricularis_. The data support an hypothesis that increased water availability is sufficient to increase reproductive output, at least in the two species, but it was impossible to test the hypothesis that increased water availability is a necessary condition for reproduction in these desert rodents. A year during which little or no rain fell would be required to examine the latter idea experimentally.

It is of interest that increased water availability on the experimental area resulted in greater reproductive output in the two species with relatively seasonal demographic patterns, but had no apparent effect on the relatively aseasonal *D. auricularis*. At least two alternative explanations for these differences may be offered. It appears that *G. paeba* and *R. pumilio* may utilize the availability of seasonal resources (such as water) as cues to initiate breeding activity. Such species would be expected to show seasonally-restricted breeding patterns and rapid population responses to favorable conditions. This type of opportunistic breeding response to seasonal events has been documented for a number of vertebrates inhabiting unpredictable arid environments (Low, 1976; Keast, 1959; French *et al.*, 1974). The relatively aseasonal demographic pattern of *D. auricularis*, and the species' lack of response to added water availability, may be evidence that the initiation of breeding activity in this species is not dependent on such seasonal cues as water availability. However, it is difficult to imagine that this type of breeding strategy would be successful in an environment where the effectiveness of rainfall and the ensuing events is unpredictable. The probability of wasted reproductive effort and the potential loss of investment in young with such a strategy seem high. These difficulties, and the fact that *D. auricularis* are not completely aseasonal, suggest that this is likely not a reasonable interpretation of the differences among these species.

A perhaps more tenable explanation for the differences in seasonality and responses to water among these three species is that, while all three may have basically seasonal breeding patterns that may be cued to the same or similar seasonal resources, they differ in the minimal levels of those resources that are needed for reproductive activity. In an environment where resource availability shows strong seasonal variation, a species with high requirements of resource availability would be expected to concentrate its breeding and population growth into a short time of the year when resource abundance is at its peak. Conversely, a species that requires lower levels of resource availability to breed should exhibit a less seasonally-restricted demographic pattern in such an environment.

As described earlier, water becomes available in this Namib Desert environment at the onset of rains in December through April. Green vegetation is available for several weeks after the rains. During the ensuing months of May or June to September, temperatures are cool, and condensation occurs regularly and fog occasionally. Beginning in September, conditions become increasingly more arid until alleviated by the following year's rainfall. The available data indicate that the declining breeding intensities in *G. paeba* and *R. pumilio* during the hot, dry months of the year were at least partly due to decreased water availability. On the other hand, reproduction in *D. auricularis* showed little decline during this period and was not altered by increasing water availability. In the above context of differential resource requirements, it may be argued that the relatively aseasonal breeding pattern shown by *D. auricularis* is due to a constant abundance of water (relative to critical levels). This would imply that *D. auricularis* has lower water requirements then *G. paeba* and *R. pumilio*. Thus, it might be predicted that *D. auricularis* is physiologically more capable of conserving water than the other two species. This hypothesis is tested and discussed in Part II.

There were some interesting differences in mortality patterns between control and experimental populations. Male and female survival rates were more highly correlated with each other on the experimental area than on the control grid in both G. paeba and D. auricularis. Reasons for this difference are not known, but the data indicate that the timing of mortality, and perhaps the causes, were more similar for each sex on the experimental area than on the control. This may have been due to altered behavior associated with visiting the experimental waterers and corresponding changes in relative vulnerability to predation between the two sexes.

Rosenzweig (1974) hypothesized a reproductive "cost" function in desert rodents. Data obtained in the present study suggest that mortality rates in some groups may increase with increased breeding, but differences in survival rates of breeding and nonbreeding animals were not demonstrated. The data suggest that the experimental treatment may have reduced mortality costs associated with being in breeding condition in female G. paeba and D. auricularis, and of lactating in the latter species, but no differences were observed in mortality associated with breeding condition in males. These differences are in accord with the envisioned water costs of reproduction presented in the Introduction, which suggested that water demands may be disproportionately higher in breeding females than in males. The differences in mortality associated with lactation in D. auricularis on the two areas may imply that this is an especially expensive process (in terms of water) in this species.

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This cost may have been one of the selection pressures for the small litter size observed in this species.

On the experimental grid, both _G. paeba_ and _D. auricularis_ had shorter life expectancy than control animals if entering the population early in the study. Only in _D. auricularis_, however, did this shorter life expectancy appear to have an effect on subsequent weight structure, resulting in an experimental population consisting, on the average, of smaller animals than the control population.

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 which showed reproductive responses to supplementary water, _R. pumilio_, did the increased reproduction result in marked numerical differences between the experimental and control populations. In the experimental _G. paeba_ population, reproduction continued over a longer part of the year and 28 percent 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 this increased reproduction were apparently offset by increased mortality or emigration. It would appear from these data that, while reproduction was partly under the control of water availability, other factors, at least during this year of superabundant resources, were ultimately responsible for regulating population size in this species.

There are at least two potential explanations for the relatively smaller experimental _D. auricularis_ population size and lower male breeding percentages during the second half of the study. It is possible that the increased water availability on the experimental area altered competitive regimes and caused R. pumilio, which were twice as abundant on that area as on the control, to have a negative influence on D. auricularis. In years of normal rainfall, these two species are probably segregated into different habitats, at least for most of the year, with R. pumilio being a year-round resident primarily in riverine habitats (Coetzee, 1969). Whether R. pumilio are seasonal inhabitants of the plains habitats where the present study was conducted during such years is not known. Baker (unpubl. data), in his 1973 study, found R. pumilio present in river beds but absent from the plains habitats. It appears that R. pumilio invades the latter habitats as year-round residents only following years of exceptional rainfall and plant production. The greater abundance of this species on the experimental area suggests that water availability is a factor in these changing distributions.

The numerical and reproductive differences between control and experimental D. auricularis may have been a function of the differential mortality between control and experimental populations during the early months of the study. It is not known whether the higher mortality on the experimental area was a consequence of increased competition with R. pumilio. If reproduction in D. auricularis is dependent on a weight distribution skewed towards heavier (and probably older) animals, the weight distribution differences resulting from the differential mortality (i.e., an experimental population composed of, on the average, smaller animals) would account for the lowered male reproduction and smaller population size.

II. LABORATORY EXPERIMENTS

INTRODUCTION

The physiological characteristics of small desert-dwelling rodents that allow them to remain in water balance have received extensive attention in the literature (see reviews by Chew, 1961; Ghobrial and Nour, 1975; Hudson, 1964; MacMillen, 1972; Schmidt-Nielsen, 1964, 1975). Numerous studies elaborating the mechanisms of contending with aridity in a variety of desert rodent species have led to a general classification of species as: 1) "dry" rodents, which conserve water through the production of high urine concentrations, the production of relatively dry feces, and the ability to minimize pulmocutaneous evaporative water loss, and can maintain water balance on a diet of relatively dry seeds (without drinking water); or 2) "wet" rodents, which are less efficient at conserving water and are thereby dependent on a diet of succulent food (Lee, 1963; Hudson, 1965; Schmidt-Nielsen and Schmidt-Nielsen, 1951). Aside from this correlation between food habits (and the associated distributional patterns) and the physiological capacity for conserving water, little consideration has been given the ecological consequences of different degrees of independence from exogenous water supplies among desert rodents.

It is important to note that the majority of studies of water metabolism in desert rodents have restricted their inferences about the significance of these physiological attributes to phenomena relating only to individual animals, and not to populations. Furthermore, there appears to be an implicit assumption in most studies that the ability to conserve water bears only on a very narrow aspect of a species' life history, namely, the ability of individuals to survive physical extremes. However, succeeding in desert environments, as elsewhere, involves not only avoiding mortality but also optimizing reproduction, and there is considerable evidence that water plays an important role in the reproductive biology of small rodents. For example, Breed (1975) found that water deprivation had a variety of deleterious effects on the reproductive physiology of female *Notomys alexis*. Other authors (Dice, 1922; Lindeborg, 1950; Smith and McManus, 1975) have reported increased water consumption in gestating and lactating females of a number of rodent species. Baverstock and Watts (1975) observed that restriction of water intake in nursing *N. alexis* and *Mus musculus* led to decreased growth rates of the young, especially in larger litters. The results of these studies, and the obvious survival value of the ability to minimize water loss, suggest that at least two parameters of crucial demographic importance, survival and reproduction, may be at least partly dependent on the ability of individual animals to conserve water. It thus becomes of interest to examine water metabolism in desert rodents relative to population processes, and, in particular, to question the life-history consequences of differences in water metabolism among coexisting desert rodent species.

Reproduction and population growth in at least some desert rodents exhibit extreme seasonal and year-to-year variation (see especially French *et al.*, 1974), and this variation has been correlated with variability in rainfall and the resulting plant growth (Beatley, 1969; French *et al.*, 1974; McCulloch and Inglis, 1961). These rodents appear to capitalize on good conditions by rapidly producing young; when adequate resources for reproduction are not available, they "pause", in effect, to await the return of good conditions (see Conley *et al.*, 1977 and Nichols *et al.*, 1976 for discussions of this life-history pattern and some of the demographic correlates). A number of factors, including plant estrogens or gonadotrophins (Bodenheimer and Sulman, 1946; Pinter and Negus, 1965), energy availability (French *et al.*, 1974) and dietary water (Beatley, 1969, 1976; Bradley and Mauer, 1971) have been proposed to explain the relationship between rodent reproduction and rainfall/plant growth. The evidence cited above for the increased water demands of reproductive activity in small rodents suggests that water may indeed be a critical resource for reproduction in desert rodents, with breeding occurring only when water availability exceeds threshold levels of water demands for both maintenance and the added reproductive costs. The ability to conserve water should reflect these threshold levels of water availability. We might expect coexisting rodent species that differ in their ability to minimize water loss to also exhibit temporally different patterns of reproduction and population growth in environments with strongly seasonal water supplies.

In Part I, I discussed the results of field studies on three coexisting Namib Desert rodent species, two nocturnal, primarily granivorous gerbilline rodents, *Gerbillurus paeba* and *Desmodillus auricularis*, and a diurnal murine rodent, *Rhabdomys pumilio*. The climate of the area where that study was conducted is strongly seasonal, with low rainfall (less than 100 mm annual average) that falls almost entirely between December and April. The winter months following the rainy season are generally cool, and condensation occurs frequently (see Part I for a detailed description of the area). At the start of that 14-month study in March 1974, rodent populations consisted of only a few widely-scattered individuals. Following exceptional rains in February and March of that year (at least 165 mm), rodent populations began to increase in May and June. From that time until the end of the study, populations of these three species exhibited marked differences in their temporal patterns of population growth, recruitment of new animals, and breeding. Gerbillurus paeba populations increased explosively between June and September or October, and then declined steadily until the end of the study in early May 1975. This species bred intensively until about September, and then exhibited a lull in breeding during the hot dry months of November through February. While sample sizes of R. pumilio were small, there were suggestions of seasonal breeding in this species, and they reached peak numbers in August or September. Both of these two species had completed 80 percent of their total recruitment of new animals during the study by October (G. paeba) or December (R. pumilio). In contrast to these two species, D. auricularis population growth continued until at least February or March, and 80 percent of the total recruitment did not occur until February. While the proportion of male D. auricularis with scrotal testes declined in September 1974, the proportions of females that were lactating or had perforate vaginas was relatively constant throughout the entire study.

In addition to these demographic differences, individuals of these three species exhibited different responses to the experimental provision of drinking water. Both male and female Gerbillurus paeba on an area where drinking water was supplied bred at high intensities longer into the hot, dry months than did animals on a control area. In addition, there was a slightly higher incidence of repeat pregnancies in *G. paeba* females on the experimental area, and more than twice as many total pregnancies observed there as on the control area. More than twice as many pregnant female *R. pumilio* were observed on the experimental area as on the control, and there were indications of an extended breeding season on the area where water was provided. *Desmodillus auricularis* showed no consistent response to the artificial supply of drinking water.

The seasonal patterns of breeding, recruitment, and population growth in these three species, and their differential responses to the provision of drinking water, suggested that they also differ in their ability to conserve water. The present study was designed to examine water metabolism in *G. paeba*, *D. auricularis*, and *R. pumilio*, with the objective of relating physiological differences to observed demographic differences.

METHODS AND MATERIALS

If an animal is to remain in steady-state water balance, its water intake (via preformed water in food or by drinking, and metabolic water production) must equal its losses (via urine, feces, and pulmocutaneous evaporation). Water metabolism in the three species of interest in the present study was examined by obtaining estimates of 1) daily production of metabolic water, when all species were fed the same diet and ate sufficient food to maintain body weight; and 2) minimal daily water loss by each of the three major routes. Minimal daily urinary, fecal, and evaporative water losses were summed to provide an estimate of the minimal total daily water loss in each species. The difference between this value of minimum total water loss per day and the daily metabolic water production provided an estimate of the preformed water intake per day that individuals of each species would need to remain in positive water balance.

A. Experimental Animals

The *Gerbillurus paeba* and *Desmodillus auricularis* used in this study were wild-caught in 1975 at Gorrasis (25°18'S, 15°55'E), on the edge of the Namib Desert in southwestern Africa. *Rhabdomys pumilio* were the laboratory-born descendants of animals caught in 1973 at Gorab (25°09'S, 16°31'E), South West Africa. Animals were housed individually or in small groups in 47 x 24 x 22 cm plastic cages, with either sawdust (*R. pumilio*) or a sand and dust mixture (the gerbils) for bedding. Water and food were provided *ad libitum*. Temperatures in the animal room averaged 22-24°C, and the photoperiod was constant at 14L:10D. Animals were maintained on Wayne Lab-Blox (Allied Mills, Inc.), and this food was used in all tests described below. Pertinent compositional data for this diet are shown in Table 11.

B. Fecal Production and *ad libitum* Food and Water Consumption

Daily fecal production and *ad libitum* food and water consumption were measured simultaneously in 25 x 20.5 x 17.5 cm stainless steel metabolism cages with 1-cm-mesh wire floors and 0.6-cm-mesh wire tops. Water was provided in straight ball-bearing sipper tubes attached to graduated 30 cm^3 plastic syringes; a sipper tube outside of the cages served as a check on evaporation, which proved to be negligible. Food, previously oven-dried to a constant weight at 80°C, was hung from the side of each cage by drilling a small hole through each food block and stringing 3-4 blocks on a wire loop. A cardboard tray was placed underneath each cage to collect feces and scraps of uneaten food. Three days prior to each test, animals were weighed to the nearest 0.1 g and placed individually in metabolism cages with water and excess oven-dried food. Following the three-day adjustment period, the animals were again weighed, and returned (at 1700 ± .25 hr EST) to the metabolism cages with a weighed amount (9-14 g) of oven-dried food. At the same time (± .25 hr) on each of the following three days, water consumption over the preceeding 24 hr was recorded, the sipper tubes were refilled, and feces and remaining food were removed and segregated. A new batch of oven-dried food was introduced. On the final day, animals were removed and weighed, and the entire apparatus was washed. Ambient temperatures during the tests ranged from 22-27°C. Feces and unconsumed

Table 11. Composition of Wayne Lab-Blox. Data provided by Allied Mills, Inc.

Component	g/g dry food
Protein	.245
Fat	.041
Fiber	.036
Ash	.077
Nitrogen-Free Extract	.502
Chlorine	.005

food collected on each day were oven-dried to a constant weight at 80°C, and the daily food consumption was determined by subtracting the dry weight of remaining food from that introduced each day. Three-day average values of food and water consumption and fecal production were calculated for each animal tested. In computations of weight-specific values of each of these parameters, a mean of the final body weight and that at the end of the three-day adjustment period was used.

From the food consumption and fecal production data for each animal tested, I computed values of metabolic water production and of solute loads (urea and chloride) requiring obligatory urinary water losses. Since animals obviously did not assimilate all food ingested, these values were based on "net food consumption", i.e., weight-specific food consumption minus weight-specific fecal production. It was assumed that there were no marked differences in assimilation of various dietary components between the species. In metabolizing 1 g of the diet used, an animal produces 0.476 g of metabolic water (calculated from the data shown in Table 11 and values for metabolic water production from basic foodstuffs, after Schmidt-Nielsen, 1964) and incurs solute loads of .005 g (.14 mmole) chloride and 0.084 g (1.4 mmole) urea.

C. Evaporative Water Loss

Pulmocutaneous evaporative water loss was measured gravimetrically at three humidities using a modified open-flow system (Schmidt-Nielsen and Schmidt-Nielsen, 1950; Lasiewski et al., 1966). This method consisted of establishing various humidities by mixing, in different proportions, regulated streams of moist air (achieved by passing air through a bubbler system) and air dried by passage through a train of tubes containing Drierite (W. J. Hammond Co.). All flows were regulated with Gilmont (size no. 2) flowmeters, previously calibrated volumetrically with a spirometer.

Mixed air was metered into the animal chamber at a flow rate of 1000 cm^3 per minute. The metal animal chamber (approximate volume 12 liters) was equipped with a 0.6-cm-mesh wire floor (surface area about 615 cm^2) suspended over a layer of mineral oil to prevent evaporation from urine and feces. Air entrance and exit ports were baffled to insure mixing of air in the chamber. A third port held a rubber stopper through which was inserted a thermistor probe (Yellow Springs Instrument Co., type 402, connected to a model 43-TD Telethermometer). The chamber had a two-layer top, a bottom layer of Plexiglas and an upper layer of 1.9-cm-thick plywood into which a 12.7-cm-square window was cut. Food, previously equilibrated to the approximate chamber humidity, was suspended by a stiff wire from the side of the chamber. The animal chamber and flowmeters were placed in an environmental chamber (Sherer Model CEL 25-7) which maintained ambient temperature at 23 ± 0.5°C in all tests and allowed regulation of the light cycle (14L:10D) in phase with that in the animal room.

Air exiting the animal chamber was directed through tubes of Drierite to collect water vapor lost pulmocutaneously. The amount of moisture added to the system by the moist air stream was determined by collecting air downstream from the animal chamber when it contained no animal; this amount (in g water per hr) was then subtracted from the total g water per hr collected in the presence of an animal to obtain pulmocutaneous loss. Tests were made at relative humidities that averaged 11 - 12.5 percent, 29 - 30 percent, and 40 percent at 23°C.

The amount of moisture (g/hr) contributed by the moist air stream at each of these humidities was, respectively, (mean, range of ten measurements) 0, 0.234 (0.229 - 0.239), and 0.439 (0.435 - 0.445).

Animals were weighed and placed in the test chamber, with excess food, during the light part of the cycle, and the apparatus was checked for airtightness with a downstream flowmeter. After an equilibration period of about two hours (well in excess of the 55 minute time needed to reach 99 percent equilibrium, calculated by the formula of Lasiewski _et al._, 1966), downstream air was directed through pre-weighed drying tubes. During the day sampling was carried out over successive 1.2 to 3.0 hour intervals, but the entire night (generally 1900 to 0700 EST) was treated as a single sampling interval. At the end of each sampling interval, after disconnecting the drying tubes, downstream air was collected in a large plastic bag, and the humidity of this air was determined, so as to have a direct measure of humidity in the animal chamber, using a Yellow Springs Instrument Co. electronic psychrometer (Model 90) and psychrometer probe (Model 9019). Drying tubes were weighed to the nearest .001 g. Each test continued for a total of 21 to 24 hours of measurement time, after which the animal was removed and weighed to the nearest 0.1 g, and the animal chamber thoroughly washed.

Weight-specific expressions were based on an average of initial and final body weights. The lowest observed hourly loss rate for each animal tested was used in calculating an estimate of mean minimum daily evaporative water loss for the species. The humidity during the interval in which each minimal rate occurred was calculated as the average of the humidities at the start and end of the interval.

D. Urine Concentrations and Fecal Water Content

Urine and feces were collected from rodents placed under conditions designed to minimize water intake (no drinking water, oven-dried food) and maximize evaporative water loss (low relative humidity). It was assumed that under these conditions animals would achieve maximum urine concentrations and minimum fecal water contents.

Animals were weighed and placed individually, with excess food, in 28 x 17 x 12 cm plastic cages with 0.6-cm-mesh wire floors over a layer of mineral oil. Cages were placed in a large plastic chamber with a small fan for circulating air and trays of Drierite to absorb moisture. Air, dried by passage through a Drierite train, was introduced into the chamber at a flow rate of 4 liters per minute. Relative humidities varied with the activity of the animals, and increased when the chamber was opened, but were generally less than about 25 percent at an ambient temperature of 22-23°C.

Animals were removed and weighed each morning and afternoon of the test period. At these times, urine was drawn from under the mineral oil into plastic syringes and frozen until analysis. In general, separate morning and afternoon urine samples were collected, but when volumes were very small, they were combined to provide a volume adequate for sampling.

Animals generally defecated when handled or when placed in the weighing basket; feces were collected within 30 seconds of deposition and sealed in pre-weighed, oven-dried glass vials with screw-on tops. Fresh feces were tare-weighed to the nearest 0.1 mg, then oven-dried at 80°C to a constant weight, and the dry weight and g water/g dry weight determined. Tests were terminated at the end of 4 days or when the anima

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animal's cumulative weight loss exceeded 20 percent, whichever occurred earlier.

Urine osmotic concentrations were measured with a Wescor Model 5100A vapor pressure osmometer. Urine samples were diluted 1:1 with distilled water, using 10 μℓ disposable pipettes (Corning). Tests made with urine samples from both hydrated and dehydrated animals of each of the three species used in this study, and with urine from other mammalian species, showed no discernible effects of dilution on measurements of osmotic concentration. Bradford (1974) reported similar findings.

Urine urea concentrations were determined using a modified urease-Berthelot reaction (Sigma Chemical Co., Technical Bull. 640). Urine samples were diluted 1:500 with 10 μℓ disposable pipettes and Bohr-type measuring pipettes. Percent transmission was read at 580 nm on a Bausch and Lomb Spectronic 20. Separate tests on selected samples of urine from all three species showed preformed urine ammonia levels to be negligible.

Urine chloride concentrations were measured on a Buchler Model 4-2500 Digital Chloridometer, using a serial titration technique. Samples measuring 10 μℓ were delivered with disposable pipettes.

The highest values of osmotic, chloride, and urea concentrations observed for each animal during the water deprivation studies were used in calculating mean maximum values of these measures for each species.

E. Calculation of Minimal Daily Fecal and Urinary Water Losses

Mean minimum daily fecal and obligatory urinary water losses were calculated from data obtained by methods described in sections B and D above.

Mean minimal daily fecal water loss for each species was calculated as the product of mean daily fecal production (g dry feces/g body weight/24 hr), measured under conditions of ad libitum food and water, and mean minimum fecal water content (g water/g dry feces), measured under conditions of water deprivation. An approximate variance on mean minimum daily fecal water loss was calculated following Bowker and Lieberman (1972).

Mean daily obligatory water loss via urine was calculated by dividing the mean daily dietary load of urea or chloride (mmole/g body weight/day) by the mean maximum urine concentrations of urea or chloride, respectively (mmole/g water). Urinary water loss was calculated on the basis of each of the two urine components measured, thus providing a check on the data on dietary composition and on urine concentrations of the two solutes. The variance of mean urinary water loss was calculated as the variance of the ratio of two means (Bliss, 1967).

RESULTS

A. Fecal Production and ad libitum Food and Water Consumption

Results of the experiments under conditions of *ad libitum* food and water, and values derived from these data for use in later computations, are shown in Table 12. Most animals tested under these conditions experienced losses of body weight during the three-day adjustment period. During the three-day test period, body weight changes were slight, averaging + 1.6 percent for *D. auricularis* (mean body weight of test animals 64.8 g), + 2.9 percent for *G. paeba* (mean weight 29.7 g), and + 0.1 percent for *R. pumilio* (mean weight 46.8 g). In general, the observed differences among species in weight-specific food consumption and fecal production are as expected on the basis of body weight differences. Within each species, none of the measured parameters was significantly correlated with body weight. Mean overall assimilation efficiency (calculated as net food consumption divided by food consumption) was similar among the three species (0.785 for *D. auricularis*, 0.793 for *G. paeba*, and 0.802 for *R. pumilio*). However, as mentioned above, data on differential assimilation of specific dietary components were not obtained.

One-way analysis-of-variance, AOV, (Sokal and Rohlf, 1969) on daily weight-specific *ad libitum* water consumption showed the three species to differ significantly ($P < .05$), with *D. auricularis* drinking significantly less than the other two species. One individual *R. pumilio* consumed 0.57 g water/g/day; when this value is excluded, a mean daily

Table 12. Fecal production and ad libitum food and water consumption in *D. auricularis*, *G. paeba*, and *R. pumilio*. Unless otherwise noted, values are in g/g body weight/24 hr. Data shown are means ± 1.96 standard errors.

		D. auricularis	*G. paeba*	*R. pumilio*
	Sample size	10	5	10
Observed values	Water consumption	.08 ± .02	.15 ± .04	.20 ± .09
	Food consumption	.079 ± .009	.116 ± .005	.086 ± .013
	Fecal production	.016 ± .002	.024 ± .002	.019 ± .003
	Net food consumption	.062 ± .008	.092 ± .003	.069 ± .011
Derived values	Metabolic water production	.030 ± .004	.044 ± .002	.033 ± .005
	Urea production (mmole/g/24 hr)	.088 ± .012	.130 ± .006	.098 ± .017
	Chloride production (")	.0087 ± .001	.0130 ± .000	.0096 ± .002

weight-specific water consumption of 0.16 g/g/day is obtained for the species.

B. Pulmocutaneous Evaporative Water Loss

Minimal hourly weight-specific evaporative water losses for the three species are shown in Figure 10. Due to losses of some animals and the unavailability of other experimental animals, it was necessary in some cases to obtain evaporative water loss measurements on the same animals at more than one humidity. This was not, however, a strict repeated measures design, and I have chosen to treat tests at the various humidities as independent from one another. At each of the three general test humidities, there was some variation in the specific humidity at which minimal evaporative losses were obtained. For D. auricularis at the low humidity, these values ranged between 10 and 13 percent (mean 11 percent); at medium humidity, between 28 and 31 percent (mean 30); and at the high humidity, from 38 to 41 percent (mean 40). The humidities at which minimal rates were observed in G. paeba were 10-12 (mean 11.5), 28-30 (mean 29), and 39-41 (mean 40); and in R. pumilio, 10-15 (mean 12.5), 28-33 (mean 29); and 38-42 (mean 40). In Figure 10, evaporative water loss data are plotted at the mean humidites at which minimal loss rates were obtained for each species.

Four of the six R. pumilio tested at the highest humidity had minimal evaporative water loss rates averaging about 75 percent higher than those expected (assuming a linear inverse dependence of evaporative water loss on humidity). In the absence of any theoretical reasons for expecting an increase in evaporative loss at higher humidity, there remain three major potential reasons for the observed increases: 1) problems with the apparatus; 2) seasonal changes in the animals;

Figure 10. Minimum hourly evaporative water loss in *D. auricularis*, *G. paeba*, and *R. pumilio*.

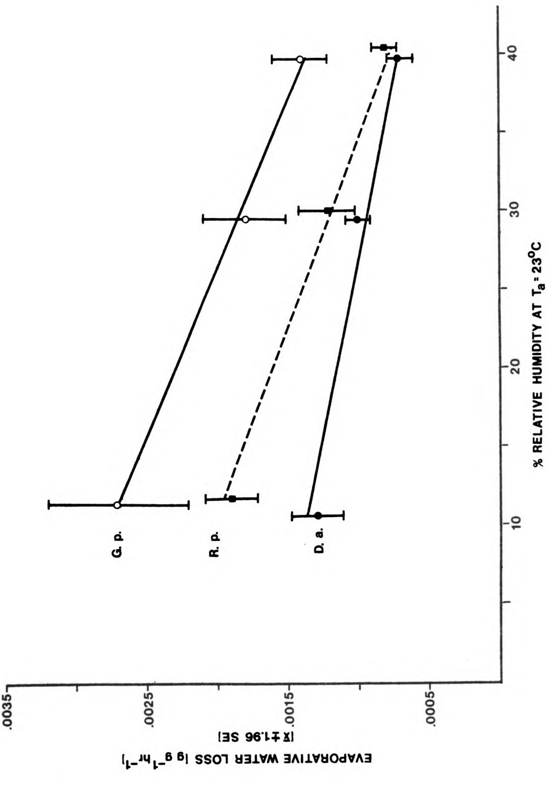
G. p.
R. p.
D. a.
10
20
30
40
% RELATIVE HUMIDITY AT T$_a$ = 23°C
.0035
.0025
.0015
.0005
EVAPORATIVE WATER LOSS (g g^{-1} hr^{-1})
[$\bar{x}$ ± 1.96 SE]

Figure 10

and 3) an increased level of activity at higher humidities. Alternatives 1) and 2) were examined by first repeating tests on the other species at 40 percent relative humidity, and, second, by repeating measurements on two of the aberrant *R. pumilio* individuals at the other two humidities. Both of these procedures yielded results well within the confidence intervals of those previously obtained. The most likely explanation, then, for the elevated evaporative losses in these four *R. pumilio* at 40 percent relative humidity is that they were more active than at the lower humidities. As discussed below, the dependence of evaporative water loss on humidity in the other two species is described relatively well by a linear model. Therefore, in the interests of obtaining reasonable comparisons among the three species, it was decided to discard data for these four *R. pumilio* at 40 percent relative humidity and use data only for the two *R. pumilio* which fit the pattern shown by the other two species. Sample sizes used were, for low, medium, and high humidities, respectively, 10, 7, and 2 *R. pumilio*; 7, 9, and 6 *D. auricularis*; and 8, 5, and 5 *G. paeba*. Body weights of test animals were similar to those found in the *ad libitum* studies described above, and, within a species, differed only slightly among the three test humidities.

Evaporative loss rates of the three species clearly differ at the lower test humidity; at 29 and 40 percent relative humidity, *D. auricularis* and *R. pumilio* do not differ from each other but both have lower evaporative losses than *G. paeba*. These differences were tested, separately at each humidity, using a one-way AOV. This analysis showed that the differences among species are highly significant ($P < .001$) at all three humidities.

The regression lines in Figure 10 were computed by a least-squares method (Sokal and Rohlf, 1969). Linear regression of evaporative water loss on humidity explains a high percentage (at least 93 percent) of the variation among groups (i.e., humidities) in all three species. Linear regression explains 59-62 percent of the total variation in *G. paeba* and *D. auricularis* evaporative water loss, and 80 percent in *R. pumilio*. The probabilities of these regressions being significant (that is, that linear regression on humidity explains a significant portion of the variation in evaporative water loss) are $.01 < P < .025$ in *R. pumilio* and $.05 < P < .10$ in the other two species. None of the deviations from linearity is significant ($P > .50$ in each case).

Weight-specific evaporative losses in these three species are generally, as expected, inversely related to body size. If the observed differences are due solely to disparate body sizes, a logarithmic plot of body weight versus whole-body evaporative water loss for all three species should be linear. Evaporative water loss is related to a) body surface area, which increases as the .67 power of weight for similarly-shaped objects; and b) respiratory ventilation, which, in general, increases with metabolic rate as the .73-.75 power of body weight. Thus, in theory, the above-described plot should have a slope of approximately 0.7. The relationships between mean whole-body hourly evaporative water loss and mean body weight for *G. paeba*, *D. auricularis*, and *R. pumilio* at each of the three test humidities are shown in Figure 11, along with a line having the expected 0.7 slope. Clearly, the differences among these three species are not due exclusively to differences in body size. Only at 29-30 percent relative humidity does the body weight-evaporative water loss plot approach linearity. However,

Figure 11. Relationship between mean evaporative water loss and mean body weight in *G. paeba* (●), *R. pumilio* (■), and *D. auricularis* (▲) at the three test humidities (rh). Dashed line indicates expected slope.

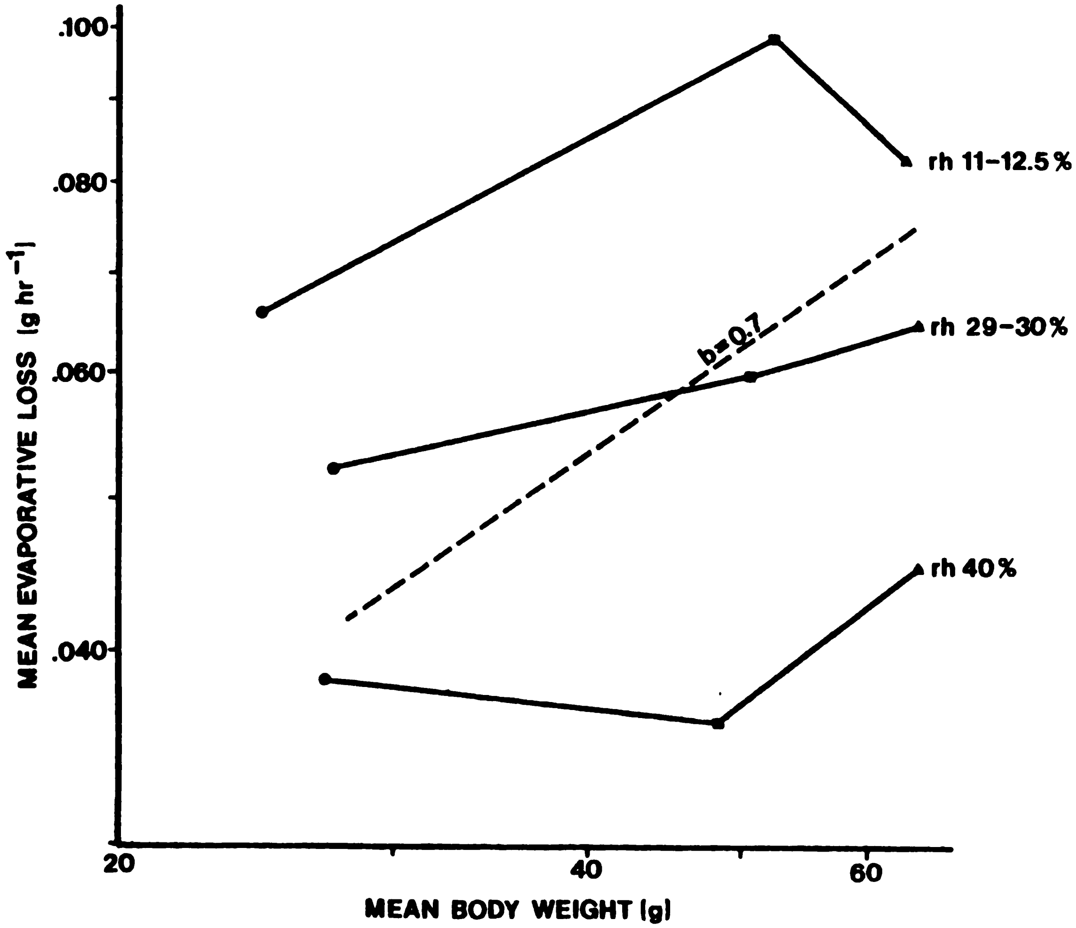
.100
.080
.060
.040
MEAN EVAPORATIVE LOSS (g hr^{-1})
20
40
60
MEAN BODY WEIGHT (g)
rh 11-12.5%
rh 29-30%
rh 40%
b=0.7

Figure 11

the slope of that line, as well as those at the other two humidities, does not approximate the theoretical expectation. At all humidities, differences between G. paeba and D. auricularis evaporative water losses are similar; the slopes of the lines drawn between points for these two species, however, are more on the order of 0.16 - 0.33, rather than the expected 0.7. Rhabdomys pumilio at the low humidity experience higher losses than expected on the basis of body size. Conversely, at 40 percent relative humidity, evaporative losses of this species are lower than expected. (It should be noted that evaporative water loss across humidities in R. pumilio was described well by a linear model, so this low evaporative loss rate at 40 percent relative humidity is certainly not due to the previously-mentioned selection of data at that humidity). Thus, these data suggest that the relationship between body size and evaporative water loss may be a complex function of humidity.

For each species, minimal daily evaporative water loss at each humidity was calculated by multiplying the observed minimum hourly loss rate for each test animal by 24 hours, and computing means from these data. These estimates of minimum daily evaporative water loss, shown in Table 13, were used in computations of minimum total daily water loss described below.

C. Urine Concentrations and Calculation of Daily Urinary Water Loss

The three species showed different patterns of weight loss during the experiments involving water deprivation (Figure 12). Gerbillurus paeba lost weight rapidly, and all individuals were removed from the test chamber after a maximum of three days; no urine or feces could be collected from this species after the second day of exposure to test

Table 13. Estimates of minimum daily evaporative water loss (g/g/24 hr).

		Relative humidity at T_a = 23°C		
		11-12.5%	29-30%	40%
D. auricularis	$\bar{x}$	.032	.024	.017
	s^2	.0000278	.0000174	.0000123
G. paeba	$\bar{x}$	.065	.042	.034
	s^2	.000246	.0000535	.0000283
R. pumilio	$\bar{x}$	.046	.029	.018
	s^2	.0000394	.0000266	--------

Figure 12. Percentage weight loss over time during exposure to water deprivation.

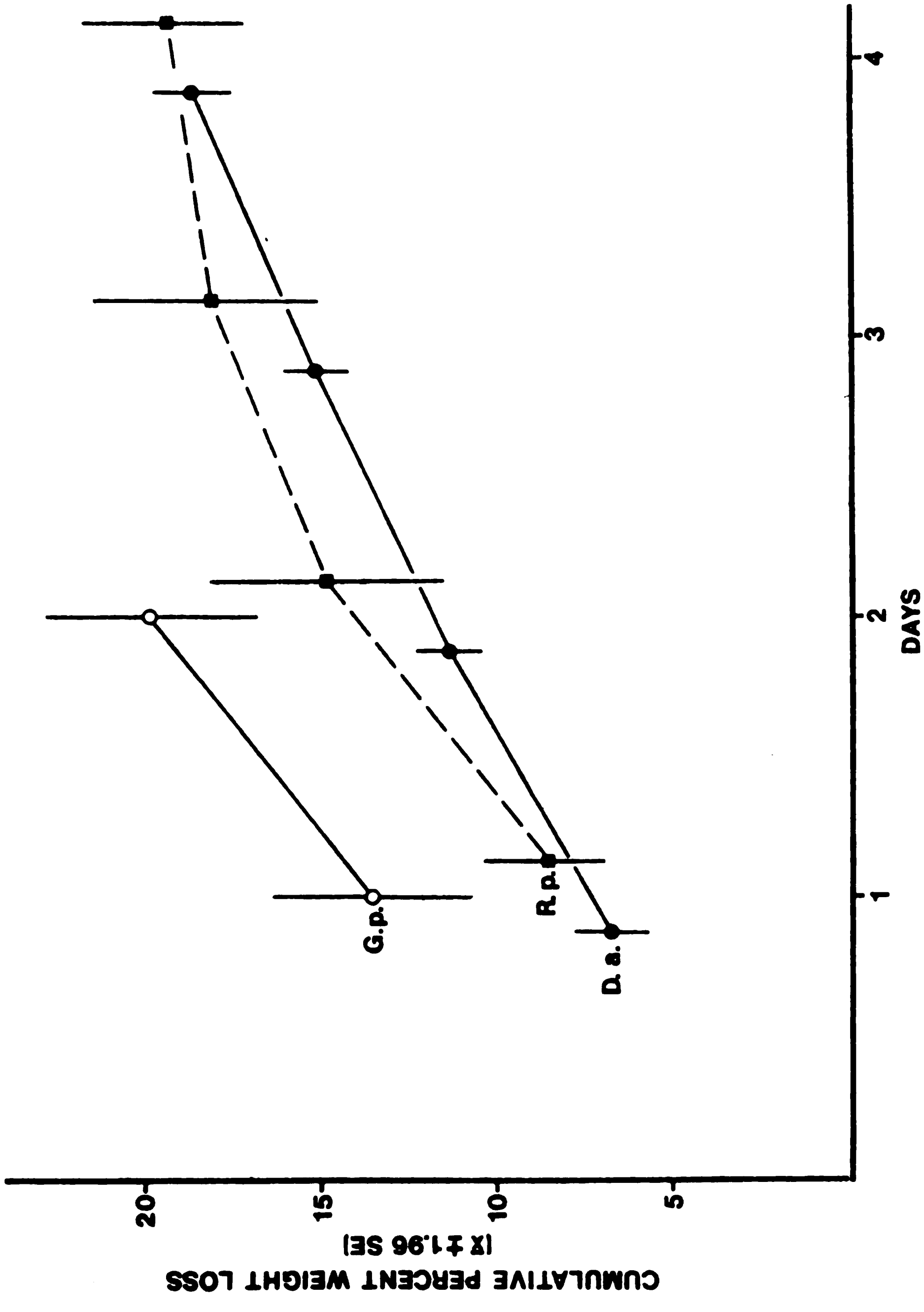
G.p.
R.p.
D.a.
DAYS
1
2
3
4
20
15
10
5
CUMULATIVE PERCENT WEIGHT LOSS
(X̄ ± 1.96 SE)

Figure 12

conditions. One G. paeba died shortly after removal from the apparatus. Desmodillus auricularis and R. pumilio lost weight less rapidly, and all animals of these two species survived the experiment.

Data on maximum urine osmotic, urea, and chloride concentrations observed in this experiment, and calculated daily minimum obligatory urinary water loss, are shown in Table 14. The highest observed urine osmotic concentrations were 6568 mOs/kg in D. auricularis, 5640 in G. paeba, and 3692 in R. pumilio. One D. auricularis achieved a urine urea concentration of 4.073 moles/kg. In general, urine concentrations of G. paeba and D. auricularis tended to increase over succeeding days of water deprivation, whereas R. pumilio mean urine concentrations following one day of water deprivation were nearly as high as those on the last day of the experiment. One-way AOV on each of the three urine parameters measured showed that the three species differed significantly in urine osmotic, urea, and chloride concentrations ($P < .001$ in each case). Urine osmotic and urea concentrations are clearly different for all species. Urine chloride concentrations of G. paeba and R. pumilio are not different; both of these species concentrated this solute to a lesser degree than did D. auricularis.

The mean minimum daily obligatory urinary water loss values shown in Table 14 were computed using observed mean maximum urine urea and chloride concentrations and the data shown in Table 12 on mean dietary urea and chloride loads. Mean maximum urine urea and chloride concentrations were computed using the highest observed value for each test animal, regardless of which day during the test that it occurred. Since data on both urine parameters and dietary solutes were not available for all individual animals, urinary water loss was calculated

Table 14. Maximum urine concentrations and daily minimum obligatory water loss via urine. Measured urine parameters shown are means ± 1.96 standard errors; calculated daily urinary water losses are means and 95 percent confidence intervals.

	D. auricularis	*G. paeba*	*R. pumilio*
Sample size	8	4	8
Osmotic concentration (mOs/kg)	6102 ± 237	5029 ± 425	3294 ± 199
Urea concentration (mole/kg)	3.453 ± .221	2.473 ± .155	2.139 ± .179
Chloride concentration (mole/kg)	.397 ± .053	.232 ± .044	.208 ± .045
Daily water loss, on urea basis (g/g/day)	.026 (.022-.030)	.053 (.047-.059)	.046 (.036-.056)
Daily water loss, on chloride basis (g/g/day)	.022 (.012-.032)	.056 (.043-.077)	.046 (.035-.063)

using mean values of these parameters for each species. The variance of mean urinary water loss (the latter being a ratio of mean solute load, $\bar{x}$, in mmoles/g/day, over mean maximum urine concentration, $\bar{y}$, in mmoles/g water) was computed as

$$s^2_{\bar{x}/\bar{y}} = s^2_{\bar{x}} + (\bar{x}/\bar{y})^2 \cdot s^2_{\bar{y}} \text{ , where } s^2_{\bar{x}} = s^2_x/n \text{ and } s^2_{\bar{y}} = s^2_y/n \text{ .}$$

Confidence intervals on estimates of daily urinary water loss were calculated following Bliss (1967).

The generally close agreement between estimates of daily urinary water loss calculated on the basis of urea and estimates calculated on the basis of chloride indicates that, for each species, the data on urea and chloride concentrations are consistent, and that the data on dietary composition are correct. Furthermore, these data suggest that there were no marked differences in assimilation of protein and chloride among the three species. With the prevailing dietary regimen, _D. auricularis_ experiences significantly lower urinary water losses (calculated on the basis of either solute) than the other two species. Differences between urinary water losses in _R. pumilio_ and _G. paeba_ are not significant, as evidenced by overlapping 95 percent confidence intervals. In the computations of total daily water loss, the larger of the two calculated urinary water loss values was used. It was assumed that, under this particular regimen of dietary solute loads, the higher value would be more indicative of a limiting factor. For _R. pumilio_, mean water loss calculated on the basis of chloride was the same as that for urea; the variance obtained for the chloride calculation was used in estimating the variance of the total water loss.

D. Fecal Water Content and Calculations of Daily Fecal Water Loss

Minimum observed water content of fresh feces and calculated minimum daily fecal water loss are shown in Table 15. One-way AOV on the fecal water content data showed that the probability of these species being different is $.05 < P < .10$. The two lowest observed fecal water contents, .700 and .720 g water per g dry feces (which correspond to 41.2 and 41.9 percent water in fresh feces), were in *D. auricularis*. Two *D. auricularis* tested were unable to dry feces to less than about 1.2 g water per g dry feces, which raised the calculated mean fecal water content for the species and accounts for the large variance. Water content of *D. auricularis* and *G. paeba* feces at the start of the experiment, when animals were still hydrated, was high (averaging 2.052 and 1.431 g water/g dry feces, respectively), while *R. pumilio*, even when hydrated, produced relatively dry feces (mean .863 g water per g dry feces). Mean fecal water content for the two gerbilline species declined fairly consistently over time during the experiment, while the water content of *R. pumilio* feces declined only slightly below that observed at the start.

Mean daily fecal water loss was calculated using the data on mean minimum fecal water content ($\bar{x}$) and those shown in Table 12 on mean daily fecal production ($\bar{y}$). An approximate variance on this estimate of fecal water loss was calculated as

$$s^2(\bar{x}\bar{y}) = \bar{y}^2 \cdot s^2_{\bar{x}} + \bar{x}^2 \cdot s^2_{\bar{y}} + 2\bar{x}\bar{y} \cdot \mathrm{cov}(\bar{x}\bar{y}), \text{ where } s^2_{\bar{x}} = s^2_x/n \text{ and } s^2_{\bar{y}} = s^2_y/n \ .$$

Since data were not available on the covariance between *mean* fecal water content and *mean* daily fecal production, as required by the equation, this was approximated by calculating, for each species, the covariance

Table 15. Fecal water content and daily fecal water loss. Values shown are means ± 1.96 standard error.

	D. auricularis	*G. paeba*	*R. pumilio*
Minimum fecal water content (g/g dry feces)	.960 ± .139	.895 ± .020	.773 ± .041
Minimum daily fecal water loss (g/g/24 hr)	.015 ± .004	.021 ± .002	.015 ± .007

between fecal water content and daily fecal production, using data for those animals where both parameters had been measured. Calculated values of mean daily fecal water loss were identical for *D. auricularis* and *R. pumilio*; the estimate of *G. paeba*'s daily fecal water loss is about 40 percent higher than those for the other two species, but 95 percent confidence intervals on mean daily fecal water loss of the three species are overlapping.

E. Integration of Results: Daily Water Balance Computations

The estimates of daily evaporative, urinary, and fecal water losses described above were summed to provide an estimate of the minimum total daily water loss for each species at each of the three test humidities used in the evaporative water loss experiments. By subtracting from these estimates the values of metabolic water production shown in Table 12, an estimate of the preformed water required by individuals of each species to maintain water balance was obtained. These results are shown in Figure 13, for each species at each humidity. The variance of mean total daily water loss was computed as the sum of the variances of the means of each of the three water loss routes. For mean urinary and fecal water losses, these variances are as previously described; the variance of mean evaporative water loss was calculated as $s^2_{\overline{EWL}} = s^2_{EWL}/n$. Variances on the estimates of mean preformed water required to maintain water balance were calculated using the equation presented by Bliss (1967) for the variance of the difference (d) between two means, $\bar{x}$ and $\bar{y}$, with heterogeneous variances,

$$s^2_d = s^2_x/n_x + s^2_y/n_y = s^2_{\bar{x}} + s^2_{\bar{y}} .$$

Figure 13. Water balance data. The upper portion of the figure shows daily metabolic water production (MWP) and total daily water loss partitioned into evaporative (EWL), urinary (UWL), and fecal (FWL) losses. The lower portion of the figure shows daily requirements of preformed water (PFW). Vertical line at the top of each bar indicates ± 1.96 standard error.

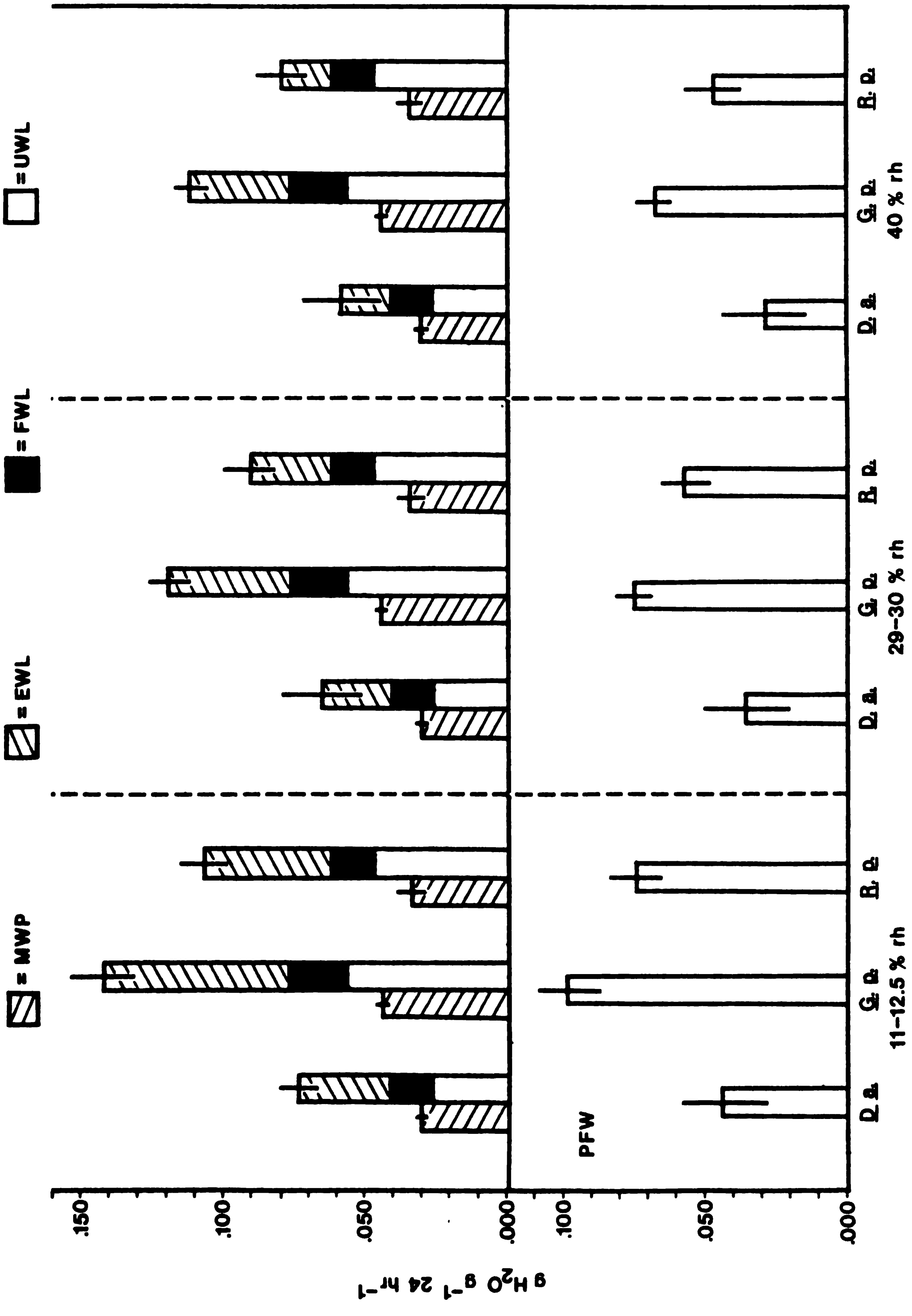
▨ = MWP
▨ = EWL
■ = FWL
☐ = UWL
.150
.100
.050
.000
.100
.050
.000
$g\ H_2O\ g^{-1}\ 24\ hr^{-1}$
PFW
D. a.
G. p.
B. p.
11–12.5 % rh
29–30 % rh
40 % rh

Figure 13

Confidence intervals (95 percent) on the estimates of mean total daily water loss and mean preformed water intake were computed as ± 1.96 standard error, where 1 standard error equals $\sqrt{s_{\bar{x}}^2}$. Since the sample size for *R. pumilio* evaporative water loss data at 40 percent relative humidity was only two, I was hesitant to use the sample variance in estimating the variance on mean evaporative water loss, or total water loss, at that humidity. The standard errors for *R. pumilio* total water loss at 12.5 and 29 percent relative humidity were identical; that standard error, and the standard error of mean preformed water intake at those humidities, were used to approximate confidence intervals on *R. pumilio* total water loss and preformed water intake at 40 percent relative humidity.

Plotted in the upper portion of Figure 13 are daily metabolic water production and minimum total daily water loss, partitioned into losses by evaporative, urinary, and fecal routes. As indicated by the 95 percent confidence intervals, total water losses of each of the three species are significantly different at the two lower test humidities; at 40 percent relative humidity, *D. auricularis* and *R. pumilio* total water losses are not significantly different. At all three humidities, *G. paeba* experiences significantly higher losses than the other two species. In general, differences among species become less marked with increasing humidity.

In the lower portion of Figure 4, mean preformed water requirements for each species at each humidity, and 95 percent confidence intervals, are plotted. At each humidity, *G. paeba* requires significantly more preformed water to maintain water balance than do *D. auricularis* and *R. pumilio*. *Desmodillus auricularis* requires significantly less preformed water than R. pumilio at the low humidity; at the two higher humidities, however, confidence intervals on weight-specific preformed water needs of these two species overlap slightly.

Most desert rodents may only rarely obtain free water by drinking. In most cases, the free water they consume is obtained in the diet. It thus seems appropriate to express the preformed water requirements of these species in terms of different proportions of free water in food. This was done by utilizing the food consumption data of Table 12 and calculated preformed water needs. These results, expressed both in terms of g water/g dry food and as a proportion of water in the diet, are shown in Table 16. Unfortunately, no direct numerical method was available for calculating confidence intervals of these estimates. In addition, any such computation would be confounded by the fact that one of the parameters used in calculating required water content of food, i.e., food consumption, also makes several contributions to the variance of calculated preformed water requirements. Thus, only mean values of the required g water per g dry food and the proportion of water in fresh food have been presented. While these data must be viewed somewhat tentatively, they serve to illustrate the differences among species in the "ease" of obtaining the preformed water requirements shown in Figure 13. At each humidity, G. paeba and R. pumilio could maintain water balance on diets of very similar water content. Desmodillus auricularis, on the other hand, would require a diet (of similar composition) having a water content considerably lower than that needed by the other two species.

Table 16. Calculated dietary preformed water requirements.

Relative Humidity	Species	Preformed water required (g/g/day)	Food consumption (g/g/day)	Water content of food needed to provide preformed water	
				g water/ g dry food	Proportion water in fresh food
11-12.5%	*D. auricularis*	.043	.079	.54	.35
	G. paeba	.098	.116	.84	.46
	R. pumilio	.074	.086	.86	.46
29-30%	*D. auricularis*	.035	.079	.44	.31
	G. paeba	.075	.116	.65	.39
	R. pumilio	.057	.086	.66	.40
40%	*D. auricularis*	.028	.079	.35	.26
	G. paeba	.067	.116	.58	.37
	R. pumilio	.046	.086	.53	.35

DISCUSSION

Water metabolism in these three species was examined by obtaining estimates of daily water intakes and minimal daily water losses by evaporative, urinary, and fecal routes. The three species show marked differences in their abilities to conserve water (i.e., in their minimal total daily water losses) and in their daily preformed water requirements. At the two lowest evaporative water loss test humidities (about 12 and 30 percent relative humidity at an ambient temperature of 23°C), daily water losses of all three species are significantly different, with _D_. _auricularis_ being most capable of minimizing water loss and _G_. _paeba_ the least capable of the three. At the highest test humidity (40 percent), _G_. _paeba_ loses significantly more water than the other two species, which do not differ significantly from each other. At all three test humidities, _G_. _paeba_ requires significantly more preformed water per day to maintain water balance than do the other two species. The preformed water requirements of _D_. _auricularis_ are significantly less than those of _R_. _pumilio_ only at the low test humidity; at the two higher humidities, water requirements of these two species have overlapping confidence intervals. When these preformed water requirements are expressed as proportions of free-water in the food, it is found that _G_. _paeba_ and _R_. _pumilio_ would require diets of very similar water content, while _D_. _auricularis_ could maintain water balance on a diet containing .62 to .67 as much free water (on a g water per g dry food basis) as needed by the other two species. It should be noted that all of these data have been expressed on a weight-specific basis. If values at each step in the entire sequence of calculations used in obtaining the final result are multiplied by the body weights of each species, the overall conclusions about the relative water needs of these three species remain unaltered.

Differences among these species in parameters that are closely related to weight-specific metabolic rate and body surface area (food consumption, fecal production, and parameters derived from those estimates, and evaporative water loss) are roughly as expected on the basis of body weight, with *D. auricularis*, the largest species, having the lowest weight-specific rates for these parameters, and *G. paeba*, the smallest of the three species, having the highest weight-specific rates. Differences in evaporative water loss among the three species are not, however, due to differences in body size alone. Furthermore, the relationship between body size and evaporative water loss appears to be a complex function of ambient humidity.

In all three species, the relationship between evaporative water loss and ambient humidity across the range of test humidities was described reasonably well by a linear model. However, it should be noted that if these regression lines were extrapolated beyond 40 percent relative humidity, they would intersect the abscissa at humidities well below 100 percent. Thus, there appears to be some curvilinearity in the dependence of evaporative water loss on humidity in these species at higher humidities.

While the great variation in procedures used in measuring evaporative water loss in small rodents demands caution in making comparisons among studies, the evaporative water loss rates observed in these three species are, in general, similar to those reported for other small desert rodents of comparable body sizes. Desmodillus auricularis is intermediate in body size between two desert-dwelling members of the heteromyid rodent genus Dipodomys, D. merriami and D. spectabilis, and has, at comparable humidities, evaporative water loss rates intermediate to those reported for these two species (Schmidt-Nielsen and Schmidt-Nielsen, 1950). Evaporative water loss rates in G. paeba are considerably higher than those reported by the same authors for similarly-sized Perognathus sp.; water losses by this route in G. paeba appear comparable to those of arid-dwelling members of the genus Peromyscus (Schmidt-Nielsen and Schmidt-Nielsen, 1950; MacMillen, 1965). Evaporative water loss rates in R. pumilio are similar to those reported for certain desert-dwelling Australian murid rodents of comparable body size (MacMillen and Lee, 1967, 1970).

Mean fecal water content of all three species under conditions of water deprivation was below 50 percent, placing them within the range of values observed for other desert rodent species (MacMillen, 1972; Chew, 1965). Reasons for the relatively low fecal water content in hydrated R. pumilio are unknown.

The ability to minimize water loss by the production of highly concentrated urine is best developed in D. auricularis. Individuals of this species achieved a mean urine osmotic concentration of over 6000 mOs/kg, with a maximum observed value of 6568 mOs/kg, and a mean urine urea concentration of about 3.5 molal. Thus, urine concentrations in this species are similar to those observed in other rodents generally considered to be well-adapted to a desert existence, Jaculus

jaculus (Schmidt-Nielsen and O'Dell, 1961), *Dipodomys spectabilis* (Schmidt-Nielsen and O'Dell, 1961), and *D. merriami* (Schmidt-Nielsen *et al*., 1948), although all of these species produce urine of considerably lower concentrations than those reported for two desert Australian murid rodents, *Notomys alexis* and *Leggadina hermannsburgensis* (MacMillen and Lee, 1967; MacMillen *et al*., 1972).

It should be noted that the urine concentrations observed in the present study were obtained when the animals were fed a fixed diet of relatively high protein content (24.5 percent) and very low chloride content (0.5 percent). No attempt was made to measure urine concentrations under dietary conditions that would produce extreme loads of particular solutes.

Observed urine osmotic concentrations in *G. paeba* (mean of over 5000 mOs/kg) indicate that this species has well-developed renal concentrating mechanisms, although these abilities are considerably less well-developed than in *D. auricularis*. In another study of renal capabilities of *G. paeba*, Louw (1972) found that, when fed a diet of mixed bird seed and deprived of water, these animals achieved mean urine osmotic concentrations of 4035 mOs/l (maximum 4475). The considerably higher urine concentrations observed in the present study may be due to dietary differences or, more likely, to the fact that the animals used in Louw's study were apparently deprived of water only overnight.

Rhabdomys pumilio are largely diurnal in their activity (Christian, 1977). Mean urine osmotic concentrations in this species are similar to those reported for several of the diurnal sciurid rodents that inhabit the desert regions of western North America (Hudson, 1964, 1965;

MacMillen and Lee, 1967). For the most part, these diurnal rodents are less capable of producing concentrated urine than are their nocturnal counterparts. This situation appears enigmatic, as one might expect that being active in the desert during the day would produce more water stress than nocturnal activity, and that selection pressures for the evolution of efficient renal mechanisms would be stronger for diurnal rodents than for those active at night. While few attempts have been made to explain this puzzling relationship between daily activity and renal efficiency (for example, Schmid, 1972), the data presented in this study indicate that this situation prevails with these Namib Desert rodents as well as in the North American deserts; this may be a general pattern for most of the world's deserts.

The method used in this study for calculating daily urinary water loss has considerable appeal because it accounts not only for urine concentrations but also solute loads that require obligatory urinary water loss. This method may provide a more realistic assessment of the effects on water balance of differences in renal efficiency among several species than simply using urinary concentrations as comparative criteria. This may be illustrated using data for _D_. _auricularis_ and _G_. _paeba_. Ratios computed by dividing observed urine concentrations of the former species by corresponding concentrations of _G_. _paeba_ are for osmotic, urea, and chloride concentrations, respectively, 1.21, 1.40, and 1.71. However, calculated daily urinary water losses in these species differed by factors of 2.15 or 2.41, depending on whether urinary water losses calculated on the basis of urea or of chloride were used in the comparison. Thus, comparing these two species only on the basis of observed urine concentrations would have tended to underestimate the effects on water balance of physiological differences.

The data on urinary water losses presented in this study were obtained when all three species were given the same diet, and obviously do not account for possible differences among species in selection of diets of varying composition under natural conditions. Since data on the compositions of diets of these rodents in nature are not available, I attempted to use a rather general diet in these experiments. A question of considerable interest in this regard is whether dietary loads of specific solutes, and the ability to efficiently excrete those solutes with minimal water loss, are factors in determining dietary selection in desert rodent species.

Except for Louw's (1972) description of urine concentrations in *G. paeba*, the present study is, to my knowledge, the first report of water conservation abilities in rodents from the Namib Desert. The three species studied, *Gerbillurus paeba*, *Desmodillus auricularis*, and *Rhabdomys pumilio*, exhibit, to a greater or lesser degree, physiological attributes of a similar nature to those reported for other desert rodents.

The primary objective of this research was to relate differences in the ability of these species to conserve water to the demographic differences observed during the field studies described in Part I. In those studies, *D. auricularis* exhibited a relatively aseasonal pattern of reproduction, recruitment, and population growth, while demographic patterns were more seasonal in *G. paeba* and *R. pumilio*. It is striking that the provision of drinking water in the field had no apparent effect on reproduction in *D. auricularis*, which has the lowest free water requirements of the three species. On the other hand, this experimental treatment increased reproductive output in *G. paeba* and *R. pumilio*, both of which require more preformed water than *D. auricularis*. Two possible alternatives suggested by these different responses to water were discussed in Part I.

First, *D. auricularis* may have foregone "tracking" seasonal cues for the initiation of reproductive activity, adopting instead an aseasonal pattern. The relatively seasonal demographic patterns shown by *G. paeba* and *R. pumilio* suggest that they may use seasonally available resources as cues to initiate reproduction; their responses to supplementary water in the field suggest that water may be one of these resources.

A second possible explanation for these differential responses to the experimental provision of water is that, while all three species may have basically more or less seasonal reproductive patterns, and may track levels of the same critical resource (such as water), they possess different threshold levels of resource availability necessary for reproduction. The physiological differences among these three species would suggest that *D. auricularis* certainly has a lower threshold level of free water availability necessary to maintain water balance than both *G. paeba* and *R. pumilio*; presumably threshold levels of water needed for reproduction in these three species would show similar differences. If this is the case, the lack of apparent increased reproductive output in *D. auricularis* provided with drinking water might be explained by a failure of water availability on the control area to fall below threshold levels for this species. Conversely, the reproductive responses shown by the other two species would indicate differential water availability relative to threshold levels between animals provided with supplementary water and those on the control area. The latter of these two explanations, that is, that differences among these species in critical threshold levels of water availability account for their different responses to water, seems preferable.

Whichever of these explanations, if either, accounts for the differences in responses to drinking water in the field, it is clear that the two species which did show a reproductive response have higher water requirements, especially at low ambient humidities, than D. auricularis, upon which increased water availability had no apparent effect. Furthermore, the two species with the highest preformed water needs, G. paeba and R. pumilio, also exhibited the most highly seasonal demographic patterns. These correlations between the free water needs of these species and 1) the seasonality of their demographic patterns and 2) their responses to increased availability of drinking water suggest that the physiological ability to conserve water may indeed have important demographic effects. A critical assumption of this argument is that small rodents do actually utilize laboratory-measured water conserving mechanisms in nature. While supportive data are not available for these Namib rodents, information from other studies (Bradford, 1974; MacMillen, 1972) indicates that rodents in the field may at times reduce fecal water content and/or concentrate urine to the same degree as animals subjected to severe water stress in the laboratory.

With either of the alternative explanations described above, it is apparent that D. auricularis breed and experience population growth during portions of the year when the other two species are relatively inactive reproductively. To breed during these times would require especially well-developed abilities to conserve water, to insure that the increased water demands of reproduction would be met during periods when availability of water in the environment was low. Reproduction in _G. paeba_ and _R. pumilio_, on the other hand, occurs primarily during and following the rainy season, and during the winter months when condensation occurs with some regularity. One of the consequences of the provision of drinking water in these two species was an apparent extension of the breeding season longer into the hot, dry months of the year. It would appear that these two species may be incapable of conserving sufficient water to meet reproductive demands during unfavorable times of the year, and are thereby restricted to breeding during periods when the availability of water in the environment is relatively high. On the basis of the demographic and physiological data for these three Namib Desert rodents, it may be argued that, among coexisting rodents in environments where water availability varies strongly with season, species that are more capable of conserving water may possess more temporal generality in their demographic patterns than physiologically less efficient species.

The interpretation of physiological differences among these three species as reflections of differences in critical threshold levels of water availability perhaps has broader implications. Conley _et al._ (1977) have argued that predictability of critical resources for a population must be viewed relative to that population's threshold levels for those resources. In that context, the predictability of a resource may be defined as being directly related to its probability of remaining at levels of availability above threshold levels; more predictable resources are more reliably above threshold levels. We might expect that, in environments where resource availability is highly variable over time, species or populations with lower threshold levels of critical resources should experience lower probabilities of resource failure. In other words, such animals should experience greater environmental predictability than coexisting species with higher threshold levels for such resources. In that frame of reference, the relatively low free water needs of D. auricularis may be viewed as providing that species with greater predictability of water availability, relative to that faced by G. paeba and R. pumilio.

If this view is correct, we might expect to find corresponding differences in life-history strategies between D. auricularis and the other two species. Correlations between various demographic parameters and environmental predictability have been stressed in recent discussions of life history strategies, especially the concept of r- and K-selection. It has been argued that in unpredictable environments selection favors attributes such as high maximal rate of increase in population size, large clutch or litter size, rapid development, early reproduction, semelparity, short lifespan, and small body size. These characters have been identified with "r-selected" species. Conversely, in predictable environments, selection favors lower maximal rates of increase, small litters, slower development and delayed reproduction, iteroparity, longer lifespan, and large body size (MacArthur and Wilson, 1967; Pianka, 1970; Gadgil and Bossert, 1970). Species exhibiting characteristics in the latter set have been termed "K-selected". Although these life history patterns may not be predictable in all situations (Stearns, 1976), the applicability of the r- and K-selection concept has been demonstrated in a number of cases, and it serves as a useful conceptual framework for viewing the present problem.

The three species examined in the present study differ in a number of characteristics which suggest that they may occupy different mean or modal positions along an r-K continuum (Table 17). I recognize the limitations of such a classification and the danger of oversimplifying complex life history patterns (see Conley et al., 1977; Nichols et al., 1976), but these data at least provide a basis from which to work in the absence of information on more correlates of r and K strategies or on long-term variability in life history patterns. Obviously, the critical evidence for differences in r and K strategies, i.e., the proportion of an organism's total resources that it devotes to reproduction, is lacking.

The rankings shown in Table 17 were made using demographic data described in Part I. For each of the four characteristics used, each species was ranked relative to the other two. The species with the highest or lowest value for a character was assigned a numerical value of 1, if that ranking correlated with r-selection, or 3, if that ranking correlated with K-selection; the species with an intermediate value for a character was assigned a numerical value of 2. These individual values were then summed; the species with the lowest total would represent the one possessing the greatest number of characters correlating with r-selection, and the highest total would indicate relative K-selection.

The data indicate that, based on the limited number of features utilized, G. paeba and R. pumilio would occupy similar positions along an r-K continuum, while D. auricularis would be relatively more K-selected. These life history differences suggest that the above arguments about differing threshold levels and corresponding differences in

Table 17. Correlates of r- and K-selection in three Namib Desert rodents. See text for description of ranking procedure. Lower rank totals represent relative r-selection; higher totals, relative K-selection.

Character	*R. pumilio*	*G. paeba*	*D. auricularis*
Rate of increase	Intermediate (2)	Highest (1)	Lowest (3)
Mean litter size	Largest (1)	Intermediate (2)	Smallest (3)
Lifespan	Shortest (1)	Intermediate (2)	Longest (3)
Body size	Intermediate (2)	Smallest (1)	Largest (3)
Total ranking score	6	6	12

environmental predictability may represent a reasonable interpretation of some of the ecological consequences of the physiological differences among these three species.

On the basis of available data, I would not argue that D. auricularis is "better adapted" to a desert existence than the other two species. The continued presence of all three species in the same area connotes some measure of similarity in the overall effectiveness of their adaptations to desert life. Similarly, while D. auricularis appears better suited than the other two species for dealing with occasional water shortage, it seems clear that the water conserving abilities of all three species are sufficient for continued existence in this region (R. pumilio may be a colonizing species in some habitats, although it is not known whether water availability bears on this problem). I submit, however, that the physiological differences between, on the one hand, D. auricularis, and on the other, G. paeba and R. pumilio, have been an important factor in the evolution of the demographic patterns of these three species. This argument assumes, as is common, that attributes such as physiological capabilities are less plastic than parameters more closely related to demographic performance, such as litter size, age at first reproduction, and so forth. An alternative argument, perhaps as reasonable as that just presented, is that differences in demographic parameters have provided different selective pressures for the evolution of water conserving abilities in these species. The validity of one or the other of these interpretations is perhaps unanswerable, but the present study suggests that, at the least, demographic and physiological parameters have coevolved in each of these three species.

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