PHYSIOLOGICAL CORRELATES OF DEMOGRAPHIC PATTERNS IN THREE SYMPATRIC NAMIB DESERT RODENTS[1]

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G. paeba
Desmo
Rhabdomys
Lab study
Animals caught 1973, 1975

Water metabolism in three sympatric Namib Desert rodents (*Gerbillurus paeba*, *Desmodillus auricularis*, and *Rhabdomys pumilio*) was measured using a complete water-balance methodology, with the objective of relating physiological characteristics to population-level properties in these species. *Desmodillus auricularis* was found to be capable of maintaining water balance on a diet of considerably lower water content than that needed by the other two species. Physiological differences among these species are correlated with differences in (*a*) their reproductive response to the provision of drinking water in an earlier field experiment; (*b*) the seasonality of their demographic patterns; and (*c*) particular features of their life histories. An argument is presented that the water-conserving abilities of these species are intimately related to population processes: *G. paeba* and *R. pumilio*, with relatively high water needs, are restricted to breeding during brief periods of high water availability, and their life-history traits reflect that high degree of seasonality; conversely, the lower free water needs of *D. auricularis* permit a relatively aseasonal demographic pattern, and its life-history attributes differ accordingly from those of *G. paeba* and *R. pumilio*.

The physiological mechanisms of water conservation in small desert rodents have received extensive attention (see reviews by Chew 1961; Schmidt-Nielsen 1964; MacMillen 1972), but relatively few authors (e.g., MacMillen 1964; MacMillen and Christopher 1975) have examined ecological correlates of interspecific variation in these attributes within a community of sympatric desert rodents. Most workers have restricted their inferences about the ecological significance of such physiological traits to phenomena relating only to individual animals and not to populations. An apparent implicit assumption in many studies has been that the capacity to conserve water bears primarily on the ability of individuals to survive physical extremes, which in turn has been related in a general way to whether or not a particular species inhabits a desert environment.

Considerable evidence suggests that water availability—and, by implication, the physiological ability to reduce water loss—may play a broader role in the life histories of desert rodents. For example, reproduction and ensuing population growth in many desert rodents appear

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closely related to rainfall and plant growth (Reynolds 1958, 1960; Beatley 1969, 1976; French et al. 1974), and several authors have proposed that increased water availability is a major factor in this relationship (Beatley 1969, 1976; Bradley and Mauer 1971). Christian (1977, 1979) presented the results of a field experiment which support that hypothesis. Furthermore, several studies have demonstrated increased water demands for reproductive functions in small rodents and deleterious effects of water deprivation (Baverstock and Watts 1975; Breed 1975; Yahr and Kessler 1975; Soholt 1978). There is thus a strong physiological basis for a hypothesis that water supplies exceeding maintenance requirements may be critical for successful reproduction in these animals.

Given (1) this apparent relationship between water availability and reproduction and (2) the fact that water supplies in most desert environments are strongly seasonal and, within a rainy season, highly unpredictable, we might expect a relationship between water availability, water-conserving abilities, and the temporal nature of desert rodent demographic patterns. That is, species that are relatively inefficient at reducing water loss (and which thus have high water requirements) would be expected to reproduce and exhibit population growth only during restricted portions of the year when water availability is near maximal. Conversely, those that are more efficient at conserving water should be capable of meeting the water costs of maintenance and reproduction over a wider range of environmental conditions and should thus exhibit demographic patterns that are temporally less restricted.

This idea was generated by the results of field studies on three sympatric Namib Desert rodents, two nocturnal gerbilline rodents, *Gerbillurus paeba* and *Desmodillus auricularis*, and a diurnal murine rodent, *Rhabdomys pumilio* (Christian 1977, 1979). Populations of these three species during a 14-mo field study showed different seasonal patterns of reproduction, population growth, and response to the experimental provision of drinking water. *Desmodillus auricularis* was relatively aseasonal in its reproduction and population growth and showed no consistent response to the experimental treatment. Both *G. paeba* and *R. pumilio* exhibited seasonal demographic patterns and reproductive responses to the provision of water; their responses indicated that water shortage was a major factor in the highly seasonal nature of their reproductive patterns. Differences among these species suggested, according to the argument presented above, that they may also differ in water-conserving abilities. The present study examined water metabolism in these species with the objective of seeking a physiological explanation for observed demographic differences.

METHODS AND MATERIAL

Water metabolism was examined by estimating daily metabolic water production (MWP) and minimal daily water loss via urine (UWL), feces (FWL), and pulmocutaneous evaporation (EWL), in a modification of the format used by Schmidt-Nielsen and Schmidt-Nielsen (1951). The UWL, FWL, and EWL were summed to estimate the minimal total daily water loss (TWL) in each species. The difference between TWL and MWP provided an estimate of the preformed water (PFW) intake per day that individuals of each species would need to remain in water balance.

EXPERIMENTAL ANIMALS

Gerbillurus paeba and *D. auricularis* were captured in 1975 at Gorrasis (25°18′S, 15°55′E) in the Namib Desert in southwestern Africa. *Rhabdomys pumilio* were the descendants of animals caught in 1973 at Gorab (25°09′S, 16°31′E), in the same general area as Gorrasis. Animals were housed in plastic cages, and water and food (Wayne Lab-Blox, used in all tests described below) were provided ad libitum. Temperatures in the animal room were 22–27 C, relative humidities (rh) were generally above 50%, and the photoperiod was constant at 14L:10D.

DIETARY PARAMETERS

Daily fecal production and ad libitum food consumption were measured to obtain data for computing several water-balance parameters (MWP; dietary solute loads, urea and chloride, that would require obligatory UWL; and dry fecal production for calculating daily FWL). Measurements were made when all species were fed the same diet and ate sufficient food to maintain body weight. Water was provided in excess at all times, and no attempt was made to measure absorption of water by food. Three days prior to each test, animals were weighed to the nearest 0.1 g and placed individually in cages equipped with wire mesh floors. Food, previously oven dried to a constant weight at 80 C, was available in excess. Following this period, animals were weighed and returned to the cages with a weighed amount of oven-dried food. At the same time (±0.25 h) on each of the following 3 days a new batch of weighed, oven-dried food was introduced, and feces and unconsumed food were removed, segregated, and oven dried to constant weight. Daily food consumption was determined by subtracting the dry weight of remaining food from that introduced each day. Three-day average values of food consumption and fecal production were calculated for each animal. The mean of the final body weight and that at the end of the 3-day adjustment period were used in weight-specific expressions.

Pertinent composition of the food used is (in g/g dry food): protein (0.245), fat (0.041), carbohydrate (0.602), and chloride (0.005). In metabolizing 1 g of this diet, an animal produces 0.476 g metabolic water (calculated from composition data and values for MWP from basic foodstuffs, from Schmidt-Nielsen [1964]) and incurs solute loads of 0.14 mmole chloride and 1.4 mmole urea. Computations of these measures were based on weight-specific food consumption minus weight-specific fecal production (net food consumption). It was assumed that there were no marked differences in assimilation of various dietary components among species.

EVAPORATIVE WATER LOSS

The EWL was measured at three rh's (about 12%, 30%, and 40% relative humidity at 23 C) using a modified open-flow system and procedures described in Christian (1978). The lowest hourly loss rate observed for each animal in any one sampling interval (1.2–3.0 h) over an approximately 24-h test period was multiplied by 24 to estimate minimal daily EWL; these were used to compute mean values for the species. Weight-specific expressions were based on an average of initial and final body weights.

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

EWL (low rh). Animals were weighed and placed individually, with excess food, in cages with wire mesh floors over a layer of mineral oil. Cages were placed in a chamber at temperatures of 22–23 C and rh of about 25% (maintained with trays of Drierite and a 4-liter/min input of dry air). Animals were removed and weighed each morning and afternoon of the test, and urine was drawn from under the mineral oil into plastic syringes and frozen until analyzed. In general, separate morning and afternoon urine samples were collected, but when volumes were small, they were combined to provide a volume adequate for analysis.

Feces were collected from animals during handling and sealed in oven-dried preweighed glass vials within 30 sec of deposition. Fresh feces were tare weighed to the nearest 0.1 mg, oven dried at 80 C to a constant weight, and the dry weight and g water/g dry feces determined. Tests were terminated at the end of 4 days or when the animal's cumulative loss of body weight exceeded 20%, whichever occurred earlier.

Urine osmotic concentration was measured on a Wescor Model 5100A vapor pressure osmometer using samples diluted 1:1 with distilled water. Urea concentrations were determined using a modified urease-Berthelot reaction (Sigma Chemical Co., Tech. Bull. 640) and samples diluted 1:500. Further dilution of some samples and reagent was required. Percent transmission was read at 580 nm on a Bausch and Lomb Spectronic 20. Urine chloride concentrations were determined on a Buchler 4-2500 Digital Chloridometer. Additional tests showed no discernible effects of dilution on measurements of osmotic concentration, and preformed ammonia levels in urine were negligible. The highest values of osmotic, chloride, and urea concentration observed in each animal were used in calculating mean maximum values for each species.

CALCULATION OF MINIMAL DAILY FECAL AND URINARY WATER LOSSES

Mean FWL was calculated as the product of mean daily fecal production (g dry feces/g body weight/24 h) and mean minimum fecal water content (g water/g dry feces). An approximate variance was calculated as the variance of the product of two means following Bowker and Lieberman (1972). Mean obligatory UWL (g water/g body weight/24 h) was calculated by dividing the mean daily dietary load of urea or chloride (mmole/g body weight/24 h) by the mean maximum urine concentration (mmole/g water) of urea or chloride, respectively. Confidence intervals and variances of mean UWL were calculated following Bliss (1967). Other confidence intervals, except in one case noted below, were computed using *t*-statistics and standard errors (Sokal and Rohlf 1969).

RESULTS

FECAL PRODUCTION AND AD LIBITUM FOOD CONSUMPTION

Results of this experiment and values derived from data are shown in table 1. Most animals tested under these conditions experienced slight loss in body weight during the 3-day adjustment period. Mean overall digestive efficiency (calculated as net food consumption divided by gross food consumption) was similar among the species (0.79 in *D. auricularis* and *G. paeba* and 0.80 in *R. pumilio*). As mentioned above, data on differential assimilation of specific dietary components were not obtained.

PULMOCUTANEOUS EVAPORATIVE LOSS

The effects of ambient rh and inter- and intraspecific differences in body size on EWL in these species are discussed

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FECAL PRODUCTION AND AD LIBITUM FOOD AND WATER CONSUMPTION IN "DESMODILLUS AURICULARIS," "GERBILLURUS PAEBA," AND "RHABDOMYS PUMILIO"

	D. auricularis	*G. paeba*	*R. pumilio*
Observed values:			
Sample size	10	5	10
Mean body weight (g)	64.8	29.7	46.8
Body weight change (%)	1.6	2.9	0.1
Food consumption	.079 (.069–.089)	.116 (.109–.123)	.086 (.069–.103)
Fecal production	.016 (.014–.018)	.024 (.021–.027)	.019 (.016–.022)
Net food consumption	.062 (.053–.071)	.092 (.087–.097)	.069 (.057–.081)
Derived values:			
Metabolic water yield	.030 (.025–.035)	.044 (.042–.046)	.033 (.025–.041)
Urea load (mmole/g/24 h)	.088 (.074–.092)	.130 (.121–.139)	.098 (.078–.117)
Chloride load (mmole/g/24 h)	.0087 (.0075–.0099)	.0130 (.0124–.0136)	.0096 (.0079–.0113)

NOTE.—Unless otherwise noted, values are in g/g body weight; data shown are means and 95% confidence intervals.

TABLE 2

ESTIMATES OF MINIMUM DAILY EVAPORATIVE WATER LOSS (g/g body weight/24 h) IN "DESMODILLUS AURICULARIS," "GERBILLURUS PAEBA," AND "RHABDOMYS PUMILIO"

	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	...

in Christian (1978). In the present study, only estimates of minimal EWL per day are presented (table 2). In *G. paeba* and *D. auricularis*, EWL is inversely correlated with rh (Christian 1978). The EWL for *R. pumilio* at the two lower rh's showed a similar pattern, but four of the six *R. pumilio* tested at 40% rh had minimal hourly EWL rates about 50% higher than expected (corresponding to daily loss rates of 0.024, 0.029, 0.034, and 0.034 g/g/24 h), based on linear extrapolation of results at the lower rh's (Christian 1978). In the absence of theoretical reasons for expecting increasing EWL with increasing rh, the most likely explanation for the observed increases in *R. pumilio* EWL at the highest rh is that they were more active than at lower rh's. In the interest of consistent comparisons among species, it was decided to discard data for these four *R. pumilio* at 40% rh and use data only for the two animals which fit the pattern shown by the other two species and by *R. pumilio* at the lower rh's. Given the directionality of predicted differences, this seemed an appropriately conservative procedure. Body weights of test animals were similar to those shown in table 1 and, within a species, differed only slightly among the three test rh's.

The EWL rates of all species are significantly different at the low rh; at the two higher rh's *D. auricularis* and *R. pumilio* do not differ significantly from each other but both have lower loss rates than *G. paeba*. These differences were tested separately at each rh using a one-way analysis of variance on data at the two higher rh's and an approximate test of equality of means (Sokal and Rohlf 1969) at the low rh, where variances are heterogeneous. These analyses showed that differences among species described above are highly significant ($P < .001$).

URINE CONCENTRATIONS AND CALCULATIONS OF DAILY UWL

Data on maximum urine concentrations and calculated daily minimum obligatory UWL are shown in table 3. One-way analysis of variance on each urine parameter showed significant variation among species ($P < .001$ in all three cases). Urine osmotic and urea concentrations are clearly different for all species. Urine chloride concentrations of *G. paeba* and *R. pumilio* are not significantly different; both of these species concentrated this solute to a lesser degree than did *D. auricularis*.

The mean minimum daily obligatory UWL values shown in table 3 were computed using data on mean urine concentrations and on mean dietary solute loads, since data on both urine parameters and dietary solutes were not available for all individuals. The close agreement between estimates of daily UWL calculated on the basis of urea and on the basis of chloride indicates that, for each species, data on urea and chloride concentrations are consistent, and also suggests no marked differences among species in assimilation of protein or chloride. *Desmodillus auricularis* loses significantly less water in urine (on the basis of either solute) than the other two species. Differences in UWL between *R. pumilio* and *G. paeba* are not significant, as evidenced by overlapping 95% confidence intervals. In computing daily TWL, the larger of the two UWL values was used, with the assumption that, under this particular regimen of dietary solutes, the higher value would be more indicative of a limiting factor. Mean UWL for *R. pumilio* calculated on the basis of chloride was the same as that for urea; the variance obtained from the chloride calculation was used in estimating variance of TWL.

FECAL WATER CONTENT AND CALCULATION OF DAILY FECAL WATER LOSS

One-way analysis of variance on the fecal water content data (table 4) showed that the probability of a significant species effect is $.05 < P < .10$. Mean daily FWL (table 4) was calculated using data on mean minimum fecal water content and those shown in table 1 on mean daily fecal production. Computed mean daily FWL was identical in *D. auricularis* and *R. pumilio*; daily FWL in *G. paeba* was about 40% higher than in the other two species, but 95% confidence intervals for all three species are overlapping.

INTEGRATION OF RESULTS: DAILY WATER BALANCE COMPUTATIONS

By subtracting the MWP (table 1) from the estimated TWL, an estimate

TABLE 3

MAXIMUM URINE CONCENTRATIONS AND DAILY MINIMUM OBLIGATORY WATER LOSS VIA URINE (UWL)

	Desmodillus auricularis ($N = 8$)	*Gerbillurus paeba* ($N = 4$)	*Rhabdomys pumilio* ($N = 8$)
Urine concentration:			
Osmotic concentration (mOs/kg)...	6,102 (5,816–6,388)	5,029 (4,339–5,719)	3,294 (3,054–3,534)
Urea concentration (mole/kg).....	3.453 (3.186–3.720)	2.473 (2.222–2.724)	2.139 (1.924–2.354)
Chloride concentration (mole/kg)..	.397 (.333–.461)	.232 (.161–.303)	.208 (.154–.262)
Water loss:			
UWL on urea basis (g/g/day).....	.026 (.022–.030)	.053 (.047–.059)	.046 (.036–.056)
UWL on chloride basis (g/g/day)..	.022 (.012–.032)	.056 (.043–.077)	.046 (.035–.063)

NOTE.—Values are means and 95% confidence intervals.

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MWP (table 1)
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Rhabdomys pumilio ($N = 8$)
3,294 (3,054–3,534)
2.139 (1.924–2.354)
.208 (.154–.262)
.046 (.036–.056)
.046 (.035–.063)

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of the preformed water (PFW) required to maintain water balance was obtained (fig. 1). The variance of mean TWL was computed as the sum of the variances of means of each of the three water-loss routes. For mean UWL and FWL these are as previously described; variance of mean EWL was calculated as s^2_{EWL}/n. Variance of mean PFW was calculated as the variance of the difference between two means with heterogeneous variances (Bliss 1967). Confidence intervals (95%) on estimates of mean TWL and mean PFW were computed as ±2 SEs, where 1 SE = $\sqrt{(s^2_{\bar{x}}/x)}$. Since TWL and PFW are an integration of mean values, the 95% confidence intervals are the only statistical means available for assessing significance of differences among species and are clearly a conservative way of doing so. As the sample size for *R. pumilio* EWL at 40% rh was only two, no variance or confidence intervals were computed on mean EWL or TWL at that rh.

Plotted in the upper portion of figure 1 are daily MWP and minimum daily TWL partitioned into UWL, FWL, and EWL. The TWL of all species are significantly different at the two lower rh's. If variation in water loss of *R. pumilio* were constant across rh, its TWL at 40% rh would be significantly less than that of *G. paeba* but would not differ from *D. auricularis* TWL. In general, differences in water loss among species become less marked with increasing rh.

Mean PFW requirements of *G. paeba*

TABLE 4

FECAL WATER CONTENT AND DAILY FECAL WATER LOSS

	Desmodillus auricularis	*Gerbillurus paeba*	*Rhabdomys pumilio*
Minimum fecal water content (g/g dry feces)	.960 (.792–1.128)	.895 (.863–.927)	.773 (.720–.826)
Minimum daily fecal water loss (g/g/24 h) . .	.015 (.011–.019)	.021 (.018–.024)	.015 (.006–.024)

NOTE.—Values are means and 95% confidence intervals.

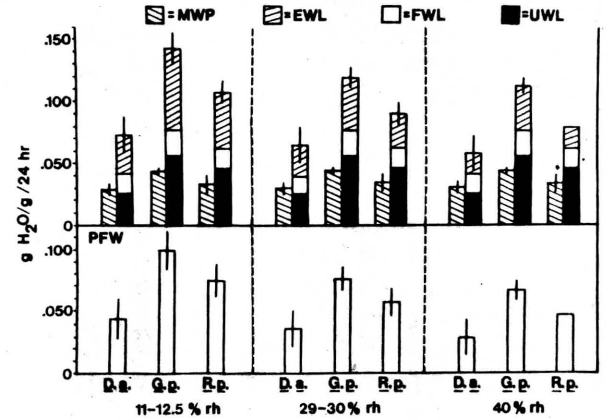

FIG. 1.—Water balance data in three Namib Desert rodents. The upper portion shows daily metabolic water production (MWP) and total daily water loss partitioned into evaporative (EWL), urinary (UWL), and fecal (FWL) water losses. The lower portion of the figure shows daily requirements of preformed water (PFW). Vertical bars are 95% confidence intervals.

(fig. 1, lower portion) are significantly higher than those of *D. auricularis* but not of *R. pumilio* at the two lower rh's. *Desmodillus auricularis* requires significantly less PFW than *R. pumilio* at the low rh; it is unlikely that these species differ at the other two rh's. At high rh, PFW needs of *R. pumilio* appear less than those of *G. paeba*, but there is no significant difference at intermediate rh.

Since most of the free water consumed by desert rodents is obtained in the diet, it seemed appropriate to express PFW requirements in terms of proportions of free water in food. This was done using food consumption data (table 1) and PFW requirements (fig. 1). These results are shown in table 5. No direct numerical method was available for calculating confidence intervals on these estimates, so only mean values are presented. Although these data must be viewed tentatively, they illustrate differences among species in the "ease" of obtaining calculated PFW needs. At each rh, *G. paeba* and *R. pumilio* could maintain water balance on diets of nearly identical water content. *Desmodillus auricularis*, however, would require a diet (of similar composition) with considerably lower water content than that needed by the other two species. All of these data have been expressed weight specifically. Although a number of the measured water balance parameters are influenced by body size, this expression of PFW needs is independent of size. Thus, 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 conclusion remains that water needs of *G. paeba* and *R. pumilio* are similar and both require more free water than does *D. auricularis*.

DISCUSSION

The present study is, to my knowledge, the first report of water conservation in rodents from the Namib Desert, except for Louw's (1972) description of urine concentrations in *G. paeba*. The three species exhibit, to a greater or lesser extent, physiological abilities of a similar nature to those reported for rodents from other deserts.

The urine concentrations observed in the present study occurred when animals were fed a fixed diet of relatively

TABLE 5

CALCULATED DIETARY PREFORMED WATER REQUIREMENTS IN "DESMODILLUS AURICULARIS," "GERBILLURUS PAEBA," AND "RHABDOMYS PUMILIO"

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% relative humidity:				
D. auricularis	.043	.079	.54	.35
G. paeba	.098	.116	.84	.46
R. pumilio	.074	.086	.86	.46
29%–30% relative humidity:				
D. auricularis	.035	.079	.44	.31
G. paeba	.075	.116	.65	.39
R. pumilio	.057	.086	.66	.40
40% relative humidity:				
D. auricularis	.028	.079	.35	.26
G. paeba	.067	.116	.58	.37
R. pumilio	.046	.086	.53	.35

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high protein content and very low chloride content. No attempt was made to measure urine concentrations under dietary conditions that would impose extreme loads of particular solutes. All three species were given the same diet, and data obviously do not account for possible differences among species in selection of diets of varying composition under natural conditions. Since data on the composition of diets of these species in nature are not available, I used 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 excrete those solutes with minimal water loss, are factors in determining dietary selection in desert rodent species.

The major objective of this research was to relate differences in the ability of these rodents to conserve water to demographic differences described briefly above and in detail elsewhere (Christian 1977, 1979). The physiological differences among these species indicate that *D. auricularis* needs less water to maintain water balance than both *G. paeba* and *R. pumilio*; presumably the directionality of differences among the three in water needs for reproduction would be similar. The reproductive response to the provision of drinking water in the field by *G. paeba* and *R. pumilio*, and the lack of response by *D. auricularis*, support that contention.

During the field studies, reproduction in *G. paeba* and *R. pumilio* occurred primarily during times of high water availability (during and following the rainy season and during the winter months when condensation occurred regularly, temperatures were cool, and potential evaporation was quite low). These species responded to the provision of drinking water in part by extending the breeding season into the hot, dry months of the year, suggesting that water shortage is a major factor in their demographic seasonality (Christian 1977, 1979). It would appear that these species may be incapable of conserving sufficient water to meet reproductive demands during potentially water-stressful times of the year, and are restricted to breeding during periods of high water availability. Conversely, *D. auricularis* reproduced during portions of the year when the other two species were relatively inactive reproductively. To meet the increased water demands of reproduction during these periods of low water availability would presumably require particularly well-developed abilities to conserve water. The correspondence between the free water needs of these species and (1) seasonality of demographic patterns and (2) responses to increased water availability suggests that the physiological ability to conserve water may indeed be closely related to seasonal patterns of reproduction and population growth in at least some desert rodents. A critical assumption of this argument is that small rodents in nature actually utilize water-conserving mechanisms to the same degree as in laboratory water-stress experiments. Although supportive data are not available for these Namib rodents, information from other studies (MacMillen 1972; Bradford 1974; MacMillen and Christopher 1975) suggests that assumption is not unreasonable.

A correspondence is also apparent between physiological attributes and particular life-history features. To demonstrate this point, I ranked each species relative to the other two using four life-history traits: rate of increase in population size, mean litter size, life span, and body size (table 6; data from Christian [1977]). The species with the highest or lowest value for a particular character

TABLE 6

LIFE-HISTORY PARAMETERS IN THREE NAMIB DESERT RODENTS

	Rhabdomys pumilio		*Gerbillurus paeba*		*Desmodillus auricularis*	
CHARACTER	Trait	Value	Trait	Value	Trait	Value
Rate of increase	Intermediate	2	Highest	1	Lowest	3
Mean litter size	Largest	1	Intermediate	2	Smallest	3
Life span	Shortest	1	Intermediate	2	Longest	3
Body size	Intermediate	2	Smallest	1	Largest	3
Total ranking score		6		6		12

NOTE.—See text for description of ranking procedure.

was assigned a numerical value of 1 if that ranking correlated with a high degree of demographic opportunism, or 3 if that ranking correlated with less immediate demographic response; a numerical value of 2 was assigned for the intermediate value of a character. The lowest sum of these individual values indicated life-history traits emphasizing rapid population response and high seasonality; the highest total indicated attributes associated with relative aseasonality and slower population response. I recognize the limitations of such a classification and the danger of oversimplifying complex life-history patterns (see Nichols et al. 1976; Stearns 1976, 1977; Conley, Nichols, and Tipton 1977), but these data provide a general idea of differences in life-history correlates among these species.

Gerbillurus paeba and *R. pumilio* occupy similar positions in this ranking, whereas *D. auricularis* possesses a quantitatively different set of life-history traits. There is thus an inverse relationship in these species between the ability to conserve water and the possession of attributes which favor rapid demographic response. The water-conserving abilities of *G. paeba* and *R. pumilio*, according to the above interpretation, restrict their temporal latitude in carrying out important demographic functions. These species do, however, possess life-history traits which allow them to capitalize on brief periods of favorable conditions. On the other hand, *D. auricularis*, by virtue of its high degree of physiological efficiency, experiences greater temporal flexibility and its life-history characteristics reflect little premium (relative to the other two species) on immediately exploiting seasonal events. This interpretation suggests that these species have used different "tactics" for solving the demographic problems presented by the highly seasonal and unpredictable water availability of a desert environment. Further, the data indicate that we might properly view demographic properties and physiological attributes in each of these species as coadapted traits.

In much of the research on desert rodent water metabolism it has been implied that differences in these physiological abilities reflect differing "degrees of adaptedness" to desert life. Certainly the continued presence of all three of these species in the same desert connotes some similarity in the overall effectiveness of their adaptations to living in a desert environment. Similarly, while *D. auricularis* appears better suited than the other two species for dealing with water shortage, the water-conserving abilities of all three are at least adequate for existence in this region (*R. pumilio*

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may be a colonizing species in some habitats, but it is unknown whether water availability bears on this problem). Thus the physiological differences among these species appear irrelevant to their continuance in this environment (i.e., to their "degree of adaptedness"). They do, as described above, have important bearing on the manner in which each species has contended with certain problems presented by that environment.

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