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EFFECTS OF HUMIDITY AND BODY SIZE ON EVAPORATIVE WATER LOSS IN THREE DESERT RODENTS

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1978

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G. paeba - } 1975
Desmo,
Rhabdomys - 1973

lab study

Abstract—1. Pulmocutaneous evaporative water loss (EWL) was studied in 3 Namib Desert rodents at three relative humidities (RH).

2. Mean EWL at each RH in these species was inversely correlated with RH, and the dependence of EWL on RH was described relatively well by a linear model.

3. In 2 species, EWL sample variances tended to decrease with increasing RH.

4. Interspecific differences in body size were inversely correlated with mean EWL, EWL sample variances, the slopes of the regressions of EWL on RH, and the intraspecific correlations between body size and EWL.

5. Body size effects on EWL appeared to interact with RH effects.

INTRODUCTION

Pulmocutaneous evaporative water loss (EWL) constitutes a major portion of the total water loss experienced by a number of small desert rodents (Schmidt-Nielsen & Schmidt-Nielsen, 1951; Schmidt-Nielsen, 1975). Several authors have reported on the abilities of some desert rodents to limit EWL (Schmidt-Nielsen & Schmidt-Nielsen, 1950; Chew & Dammon, 1961), often to the extent that its magnitude, under certain environmental conditions, is exceeded by the production of metabolic water (MacMillen, 1972). One of the primary environmental factors influencing EWL is ambient vapor pressure. Several studies have observed a general inverse relationship between EWL and absolute humidity in rodents, bats and birds (Baudinette, 1972; Chew & Dammon, 1961; Lasiewski *et al.*, 1966; Proctor & Studier, 1970; Studier, 1970), but our understanding of the effects on EWL of this important physical parameter, and its interaction with other factors affecting EWL, is meager.

Bartholomew & Dawson (1953) demonstrated an indirect relationship between body size and EWL in birds. MacMillen (1972) suggested that such a relationship may exist in desert rodents at thermal neutrality, but few attempts have been made to analyze the effects of body size on EWL in desert rodents. The present study describes a method for controlling humidity in EWL studies and examines the effects of ambient humidity and body size differences (both within and among species) on EWL in 3 species of small desert rodents.

METHODS AND MATERIALS

EWL was measured in 3 coexisting Namib Desert rodents, 2 nocturnal gerbilline rodents, *Gerbillurus paeba* and *Desmodillus auricularis*, and a diurnal murine rodent, *Rhabdomys pumilio*. The *G. paeba* and *D. auricularis* 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), in the same general area as Gorrasis. Animals were housed individually or in small groups in 47 × 24 × 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 (lights on 07:00–21:00 EST). Animals were maintained on Wayne Lab–Blox (Allied Mills, Inc.), and this food was provided in the tests described below.

All measurements were made at an ambient temperature of 23°C. Pulmocutaneous EWL was measured gravimetrically at 3 relative humidities (RH) using a modified open-flow system (Schmidt-Nielsen & Schmidt-Nielsen, 1950; Lasiewski *et al.*, 1966). This method consisted of establishing various humidities by mixing, in different proportions, regulated streams of moist air and air dried by passage through a train of tubes containing Drierite (W. J. Hammond Co.). Air for the moist stream was bubbled through dispersing stones in a series of three sequentially interconnected 400 ml bottles partially filled with water. The bottles were immersed in a water bath which was maintained at a constant temperature with an aquarium heater, thus counteracting a tendency for decreases in the minimum temperature at which the moist air stream became saturated (due to evaporative cooling in the bubbler jars). A high flow rate was required to maintain stable flows through the bubbler stream; a portion of this flow was bled off downstream from the bubbler jars. All flows (moist, dry, and mixed) were regulated with Gilmont (size no. 2) flowmeters, previously calibrated volumetrically with a spirometer.

Moist and dry streams were mixed to achieve the desired RH, and mixed air was metered into the animal chamber at a flow rate of 1000 cm^3/min. The metal animal chamber (approx. vol. 12 l.) 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 provided for introduction of 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 161 cm^2 window was

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cup of food, previously equilibrated to the approximate chamber humidity, was suspended by a stiff wire from the side of the chamber. The bubbler system, flowmeters, and animal chamber 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 leaving 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/hr) was then subtracted from the total g water/hr collected in the presence of an animal to obtain pulmocutaneous loss. Tests were made at chamber RH's that averaged 11–12.5%, 29–30% and 40% (chamber RH's were elevated above RH's of the influent air stream by animal EWL). The amount of moisture (g/hr) contributed by the moist air stream at each of these humidities was, respectively (mean, range of 10 measurements), 0, 0.234 (0.229–0.239) and 0.439 (0.435–0.445).

Relatively high flow rates were used to minimize the effects on chamber humidity of changes in EWL of animals during the test (see equation of Lasiewski *et al.*, 1966, for calculating chamber humidity). In spite of this precaution, there was some variation in the specific humidity at which minimal EWL rates were obtained. For *D. auricularis* at the low RH, these values ranged between 10 and 13% (mean 11%); at medium RH, between 28 and 31% (mean 30); and at the high RH, from 38 to 41% (mean 40). The RH's 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).

An animal to be studied was weighed and placed in the test chamber, with excess food, during the light part of the cycle, and the apparatus was checked for airtightness by verifying that influent and effluent air flow rates were equal. After an equilibration period of about 2 hr (well in excess of the 55 min time needed to reach 99% equilibrium, calculated by the formula of Lasiewski *et al.*, 1966), downstream air was directed through pre-weighed tubes containing Drierite. During the day sampling was carried out over successive 1.2–3.0 hr intervals, but the entire working night (generally 19:00–07:00 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 RH of this air was determined, so as to have a direct measure of RH 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 0.001 g. Each test continued for a total of 21–24 hr of measurement time, thereby allowing examination of temporal changes in EWL. After each test, the animal was removed and weighed to the nearest 0.1 g, and the animal chamber was thoroughly washed. Weight-specific expressions were based on an average of initial and final body weights. The lowest observed hourly loss rate for each test animal was used in calculating mean minimal rates for each species. Hereafter, EWL will refer to minimal weight-specific evaporative water loss, unless stated otherwise. The RH during the interval in which each minimal rate occurred was calculated as the average of the RH's at the start and end of the interval.

RESULTS

Minimal hourly weight-specific EWL for the 3 species is shown in Fig. 1, plotted at the mean RH's at which minimal loss rates were obtained for each species. Due to losses of some animals and the unavailability of replacement animals, it was necessary in some cases to obtain EWL measurements on the same animals at more than one RH. This was not, however, a strict repeated-measures design, and it was decided to treat tests at the various RH's as independent from one another. Sample sizes used were, for low, medium, and high RH, respectively, 10, 7 and 6 *R. pumilio*; 7, 9 and 6 *D. auricularis*; and 8, 5 and 5 *G. paeba*. Body weights of test animals were about 64 g for *D. auricularis*, 27 g for *G. paeba* and 49 g for *R. pumilio*. Within each species, body weights of test animals differed only slightly among the 3 test RH's.

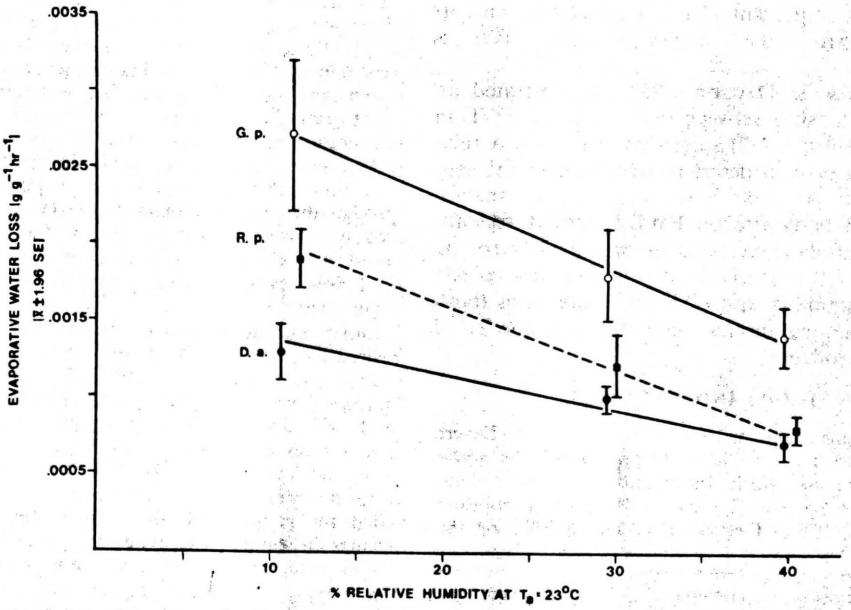

Fig. 1. Minimal hourly EWL in *G. paeba* (G. p.), *R. pumilio* (R. p) and *D. auricularis* (D. a.).

The regression lines in Fig. 1 were computed by a least-squares method (Sokal & Rohlf, 1969), disregarding problems due to heterogeneous variances (resulting from the high variance of *G. paeba* EWL at low RH). The problem of the significance of this variation will be addressed below. In *G. paeba* and *D. auricularis*, linear regression of EWL on RH explains at least 93% of the variation among groups (i.e. humidities), and 59–62% of the total variation in EWL. The probabilities of these regressions being significant (that is, that linear regression on RH explains a significant portion of the variation in EWL) are $0.05 < P < 0.10$. None of the deviations from linearity is significant ($P > 0.10$).

Four of the six *R. pumilio* tested at the highest RH had minimal EWL rates averaging about 50% higher (mean EWL for these four = 0.0012 g/g per hr, S.E. = 0.00001) than those expected (0.008 g/g per hr), based on linear extrapolation of results for this species at lower RH's; the results for these 4 animals indicated an increase in EWL with RH between the middle and high RH's. In the absence of any theoretical reason for expecting an increase in EWL at higher RH, there remain three major potential reasons for the observed increases: (1) problems with the apparatus; (2) seasonal changes in the animals and (3) an increased level of activity at the higher RH, which is known to have marked effects on EWL (Chew & Dammon, 1961; Wunder, 1970). After experimentally rejecting alternatives (1) and (2), it was concluded that the most likely explanation for the elevated EWL in these 4 *R. pumilio* at the high RH is that they were more active than at the lower humidities. As described above, the dependence of EWL on RH in the other two species is described relatively well by a linear model. A similar relationship has been reported by other authors (Baudinette, 1972; Chew & Dammon, 1961). Therefore, in the interests of obtaining consistent comparisons among the 3 species, it was decided to discard data for these 4 *R. pumilio* at 40% RH and use data only for the 2 *R. pumilio* (mean EWL = 0.008) which fit the pattern shown by the other 2 species and by *R. pumilio* at the lower RH's.

Given this selection of data for *R. pumilio* EWL, it was found that linear regression on RH explained over 99% of the variation in EWL among RH's and 80% of the total variation in EWL. The probability of this regression being significant is $0.01 < P < 0.025$.

EWL rates of the 3 species clearly differ at the lowest test RH; at 29 and 40% RH, *D. auricularis* and *R. pumilio* do not differ from each other but both have lower EWL 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 at the low RH, where variances were heterogeneous (Sokal & Rohlf, 1969). These analyses showed that the differences among species described above are highly significant ($P < 0.001$).

Mean EWL in each of these species is highly inversely correlated with relative humidity, with correlation coefficients, r, for *G. paeba*, *D. auricularis* and *R. pumilio*, respectively, of −0.999, −0.984, and −1.000. Of course, at a single temperature, other humidity measures such as ambient vapor pressure and saturation deficit vary proportionally with changes in RH. Likewise, a theoretical value for the vapor pressure difference between the animal's evaporative surfaces and the environment (assuming a constant surface temperature) changes in a similar fashion with RH. It is not possible to state which of the various humidity measures is most functionally significant, although there are theoretical reasons for placing the greatest reliance on the vapor pressure difference between the animal's evaporative surfaces and the environment (Lowry, 1969). Because this vapor pressure difference cannot be calculated precisely due to a lack of knowledge of evaporative surface temperatures and because the relationship between EWL and humidity will be approximately the same regardless of the expression of humidity used, humidity is herein expressed simply as RH.

Differences among these species in weight-specific EWL at given RH are generally, as expected, inversely related to body size, with *D. auricularis*, the species of largest body size, having the lowest weight-specific EWL's and *G. paeba*, the smallest, having the highest rates. Correlation coefficients between mean EWL of the species and mean body weight at low, medium, and high RH, respectively, were −0.987, −0.987 and −0.947.

Differences in body size among species appeared to have other, perhaps more subtle, effects on EWL. Although differences in the slopes of the regression lines shown in Fig. 1 were slight, those slopes were highly correlated with body size ($r = -0.842$). The variability of EWL measurements, in general, decreased with increasing humidity, an effect most marked in *G. paeba* (Table 1). Sample variances at given RH were highly correlated with interspecific differences in body weight (at low RH, $r = -0.971$; at medium RH, $r = -0.967$; no calculation was made for the high RH due to the small sample size of *R. pumilio*). This pattern of variability, to be discussed further below, did not parallel the degree of variation in body weight within each species.

If the observed differences in mean EWL at given RH among these species are due solely to disparate body sizes, a logarithmic plot of body weight vs whole-body EWL at given RH for the species is expected to be linear. EWL is expected to be related to (1) body surface area, which increases as the 0.67 power of weight for similarly-shaped objects and (2) respiratory ventilation, which, in general, increases with metabolic rate as the 0.73–0.75 power of body weight. Thus, in theory, the above-described plot

Table 1. Sample variances (s^2) × 10^6 of minimal EWL and within-species correlations between body weight and minimal EWL at each of the 3 test humidities

		RH		
		Low	Medium	High
D. auricularis	$s^2 \times 10^6$	0.0528	0.0294	0.0296
	r	−0.489	−0.470	−0.493
R. pumilio	$s^2 \times 10^6$	0.0684	0.0414	—
	r	−0.516	+0.014	—
G. paeba	$s^2 \times 10^6$	0.4212	0.1079	0.0579
	r	−0.740	−0.717	−0.578

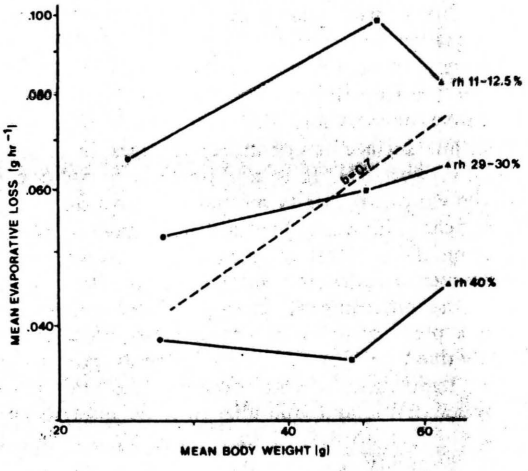

Fig. 2. Relationship between mean hourly whole-body EWL and mean body weight in *G. paeba* (●), *R. pumilio* (■) and *D. auricularis* (▲) at the 3 test RH's. Dashed line indicates expected slope.

should have a slope of approximately 0.7. The relationships between whole-body hourly EWL and mean body weight for *G. paeba*, *D. auricularis* and *R. pumilio* at each of the three test RH's are shown in Fig. 2, along with a line having the expected 0.7 slope. Only at 29–30% RH does the body weight vs whole-body EWL plot approach linearity. However, the slope of that line, as well as those of the lines at the other RH's, does not approximate the theoretical expectation. At all RH's, logarithmic differences between *G. paeba*, the smallest species, and *D. auricularis*, the largest species, are similar; the slopes of the lines drawn between points for these 2 species, however, are more on the order of 0.16–0.33, rather than the expected 0.7. *Rhabdomys pumilio* at the low RH experience higher losses than expected on the basis of the line for *G. paeba* and *D. auricularis*. Conversely, at 40% RH, EWL of this species is relatively lower than expected on the basis of body size. Thus, these data indicate that, while body size appears to have important effects on EWL in these species, interspecific differences are clearly not due solely to differences in body size. Furthermore, the data suggest that the effects of body size on EWL may be a complex function of ambient humidity.

Intraspecific differences in body size appeared to influence EWL, and the magnitude of those effects is related to each species' relative body size. As described above, differences among species in EWL sample variances at given RH were inversely related to body size. That effect is likely due, at least in part, to the degree of correlation (within each species) between body size and EWL (Table 1). Differences in those correlations were themselves highly correlated with interspecific differences in body size ($r = -0.983$) at low RH; $r = -0.907$ at medium RH), and showed no relationship to interspecific differences in the variation of body weights of test animals of each species. These results indicate that variations in body size within a species can affect EWL and that those effects are more marked in smaller-bodied species.

In *D. auricularis*, the correlation between body weight and EWL was relatively constant across humidities (Table 1). In the other 2 species, these correlation coefficients were largest at the lower humidities, and tended to decrease with increasing RH. This pattern suggests, again, that there is an interaction between ambient humidity effects on EWL and body size effects.

There were marked temporal changes in EWL (Fig. 3). The data presented are means (in g/hr) of all measurements made at low and high RH's during the hours of the day shown along the abscissa. It should be recalled that the data at the earliest times shown are from animals which had been in the chamber for at least 2 hr. In all 3 species at the low RH, consistently low mean EWL rates were not observed until the second day. Sample variances showed similar changes over time. Several tests conducted for an additional 12 hr at that RH did not produce consistently lower EWL, suggesting that the data obtained on the second day of the test are reasonably representative of minimal rates. At 40% RH, mean EWL between 13:00 and 17:00 hr on the first day was similar to that at comparable times on the second day.

DISCUSSION

Pulmocutaneous EWL in each of these 3 species is highly correlated with ambient humidity at an ambient temperature of 23°C. As noted above, it is not possible, with the available data, to determine what measure of humidity (e.g. relative humidity, saturation vapor pressure deficit, or the difference in vapor pressure between the environment and the animal's evaporative surfaces) is functionally most significant in determining this relationship.

The dependence of EWL on RH across the ranges of test humidities is described relatively well by a linear model for *G. paeba* and *D. auricularis* and, given the selection of data at 40% RH, for *R. pumilio*. It should be noted, however, that if the regression lines shown in Fig. 1 were extrapolated beyond 40% RH, they would intersect the abscissa at humidities well below 100% RH. Thus, there appears to be some curvilinearity in the dependence of EWL on RH in these species at the higher humidities. It is conceivable that the unsystematically high EWL rates observed in 4 of the 6 *R. pumilio* tested at high RH are not due to increased activity but are indicative of the start of such a curvilinear pattern. However, the sample variance of EWL data for all 6 *R. pumilio* tested at that RH is over twice that at the intermediate RH, and is thus contrary to the general pattern of decreasing variation in EWL with increasing RH. This suggests that viewing the high EWL rates exhibited by these four *R. pumilio* at the high RH as unrepresentative may be the most appropriate procedure at this time.

In addition to affecting mean EWL, humidity had an effect on the variance of EWL, with variability tending to increase under presumably more stressful conditions (i.e. low RH), especially in *G. paeba*. That is, animals tended to function more similarly to each other under conditions of high RH than under low RH. Few attempts have been made to explain the biological relevance of variation of this sort. This pat-

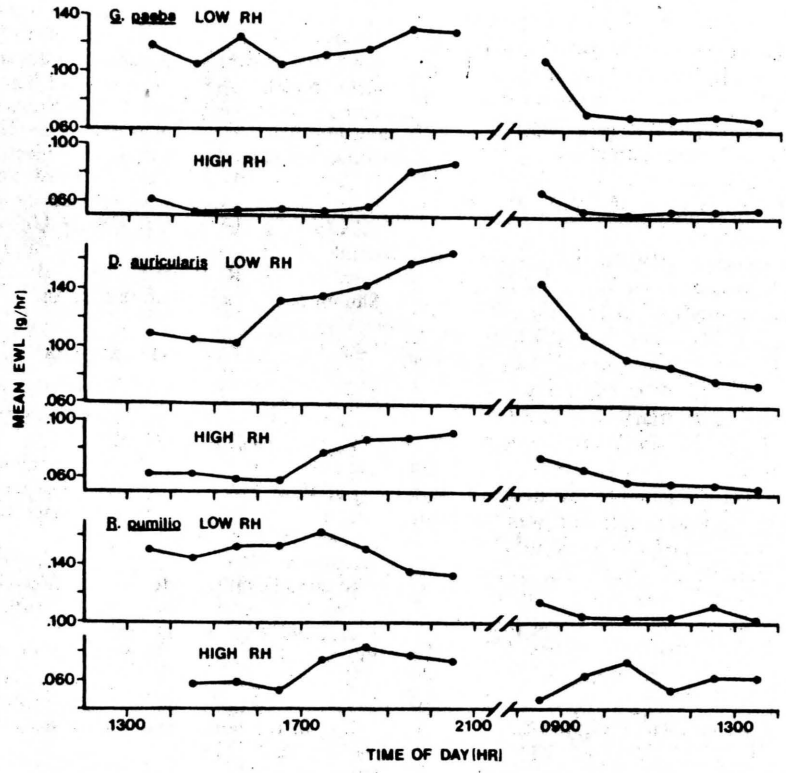

Fig. 3. Temporal changes in mean hourly whole-body EWL in the 3 species at low and high RH's.

tern of changes in the variability of a physiological characteristic across changing environmental conditions may, however, have important implications. For example, breeding intensities and the prevalence of pregnancy in at least some desert rodent populations are higher during years of high rainfall and plant production than during less favorable years (French *et al.*, 1974). Under certain conditions, all or nearly all animals may reproduce, while under less favorable conditions, some animals may breed and a relatively high proportion not. Several studies suggest that reproduction in desert rodents is related to water availability and the ability to conserve water (Beatley, 1969; Baverstock & Watts, 1975; Breed, 1975; Christian, 1977). This type of variation in reproductive performance with changing environmental conditions might be explicable in terms of variations among individuals in EWL or other water conservation parameters that are evident under relatively stressful conditions but not under more favorable ones.

Interspecific differences in body weight appeared to have several effects on EWL. Obviously, these species differ in a number of characteristics other than body size, but the latter difference is one that is both immediately obvious and theoretically justifiable as potentially influencing EWL. The extensive use of correlations between body weight and EWL parameters in this study certainly does not establish cause-and-effect relationships; these analyses do, however, illustrate some obvious trends in the data. Body weight was highly (inversely) correlated with a number of EWL parameters: mean EWL at given RH, the variance of EWL, the slopes of the regression lines of EWL on humidity, and the intraspecific correlations between body weight and EWL.

The inverse relationship between mean body weight and mean EWL was generally expected. A critical question in evaluating the effects of this relationship on interspecific differences in the attainment of water balance is whether or not size-related differences in EWL are accompanied by compensating differences in metabolic water production (MWP). MacMillen (1972) used ratios of MWP/EWL in examining this question. Although data on metabolic rates of the three species examined in the present study are not available, their MWP at an ambient temperature of about 23°C has been estimated by measuring the daily utilization of a diet of known protein, lipid, and carbohydrate composition, from which MWP was calculated (Christian, 1977), using MWP values for basic foodstuffs given by Schmidt-Nielsen (1964). These data, when expressed as ratios of daily MWP over daily minimal EWL (calculated as hourly EWL × 24) show that, at the low RH, *D. auricularis* (MWP/EWL = 0.94) would be in a much more favorable state of water balance than either *R. pumilio* or *G. paeba* (MWP/EWL = 0.68–0.72). This same trend is evident at the medium RH, whereas at the high RH, *D. auricularis* and *R. pumilio* would have similar ratios of MWP/EWL (1.76–1.83), considerably higher than that for *G. paeba* (1.29). These data thus indicate that the size-related differences in EWL may not be offset by similar differences in MWP.

As described previously, the differences in mean EWL among these 3 species are not as large as would be predicted on the basis of body weight differences.

Moreover, the nature of the relationship between body size and EWL appears to be influenced by RH, being linear only at the intermediate humidity. The marked nonlinearity at low and high humidities is due to *R. pumilio*'s unsystematically high and low EWL, respectively, at those humidities. These data indicate that, although body size is clearly important in determining the magnitude of EWL, its effect is not entirely predictable.

The inverse correlation between body weight and the slopes of the regressions of EWL on RH indicate that EWL of smaller-bodied species may be more affected by changes in RH than is that of species of larger body size. This sensitivity is evidenced in other ways. The effects on EWL of intraspecific differences in body weight were more marked in the smaller *G. paeba* than in the larger *R. pumilio* and *D. auricularis*. In the former 2 species, the strength of the correlation between body size and EWL tended to decrease with increasing RH, whereas that correlation was relatively constant across RH in *D. auricularis*. Additionally, the previously-noted pattern of decreasing variance of EWL with increasing RH was most conspicuous in *G. paeba*. Of these species, *D. auricularis* possess the greatest renal concentrating capabilities (Christian, 1977), which might confer on that species a wider latitude for tolerating RH changes. However, *G. paeba* has considerably more efficient kidneys than *R. pumilio*. Thus, these effects of changing RH on EWL appear more closely related to body size differences than to renal efficiency or any other known physiological differences among these species. Data are needed on more desert rodent species of a wide range of body sizes to fully evaluate the effects of body size on both the magnitude of EWL and its sensitivity to changes in RH.

The observed temporal changes in EWL may have serious implications for past and future studies purporting to measure minimal EWL rates in small rodents. Typically, EWL measurements have been made over a period of, at most, a few hours, after the animal has been allowed an adjustment period of perhaps 2 hr. The changes in EWL over time observed in the present study suggest that such procedures may yield highly unsatisfactory results, especially for studies comparing minimal EWL in two or more rodent species, and particularly at the low ambient RH's commonly used in EWL studies. At higher RH's short measurement periods may be sufficient to obtain approximately minimal EWL rates, but this is clearly not the case at the lower RH. The high initial rates of EWL at the low RH may be due to the fact that animals were still hydrated at the start of each test. If this were the case, however, one would expect that dehydration would proceed more rapidly at the low RH than at higher ones, and that animals would achieve minimal rates sooner under the former conditions. Studies cited above (Chew & Dammon, 1961; Wunder, 1970) have found that EWL is extremely sensitive to changes in activity. The high EWL rates at the start of the tests may have been caused by a high level of activity that continued for several hours after introduction into the chamber. Whatever the reasons for these changes in EWL over time, their methodological implications are clear.

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