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Introduction

Prior study of water use by the pine vole, *Microtus pinetorum*, has indicated that these voles require large volumes of water on a daily basis and exhibit rapid turnover of body water relative to other mammals of similar body size (Rhodes and Richmond, 1981). However, the extent to which these animals are tolerant of water deprivation and hence the importance of available water to the members of this species remains unexplored. Similarly, data on rates of body water turnover in free-ranging pine voles are presently unavailable. Thus, this study examines rates of body water turnover and urine concentrations of pine voles during exposure to 3 ambient temperatures, during a restricted water regime, and under field conditions. We present evidence indicating that pine voles exhibit rapid turnover of body water under both laboratory and field conditions and that these animals are very intolerant of water restriction.

Methods

Water metabolism of laboratory reared pine voles was assessed during exposure to 15, 22, or 30°C. Adult voles were weighed and then housed singly in plastic cages equipped with hardware cloth bottoms. Water supplied in inverted graduated cylinders and food (Charles River-Rat Mouse formula) were provided. After the voles were exposed to an ambient temperature for 24 hr, they were placed over pans of mineral oil and urine samples were collected for measurement of urine concentration. Subsequently, the voles were injected intraperitoneally with 50 ul ^3H_2O (15 uCi). Urine samples were collected once or twice daily for 4 d and analyzed for ^3H_2O concentration. An expression for loss of tritiated water over time was developed with standard regression techniques for each vole and the biological halflife of ^3H_2O was calculated in ln2/k, where k is the slope of the regression line (Richmond et al. 1960).

Ad lib water consumption was determined over a 3 d period for an additional 13 voles maintained at 22°C. The volume of drinking water was then reduced to 75% of the daily *ad lib* water consumption for each animal. All voles exhibited loss of body weight in response to water restriction and did not reach a stable level of body weight over a 5 d period. To counter continued weight loss, an amount of water equal to the previous day's weight loss was added to the vole's daily water ration. This was continued until body weight stabilized. Urine concentrations and tritiated water turnover were then determined as previously described.

Water metabolism of free-ranging voles was assessed in a population of animals located in New Paltz, N.Y. In November 1981, voles were livetrapped, weighed, toe-clipped, and injected with 50 ul ^3H_2O. Prior to injection, an initial urine sample was collected from 22 voles for urine concentration measurement. Collection of urine under field conditions was accomplished by placing the voles in metabolism cages and suspending the entire cage over a layer of mineral oil contained in a plastic pan. Collection of samples usually required 0.5-1 hr. The animals were then released at their original capture site. Traps were checked at 1-1.5 hr intervals during daylight hours for 5-6 d and additional urine samples collected from injected voles as described above. Because of the rapid loss of radioactivity from the animals and regression analysis constraints, injected pine voles had to be recaptured at least twice within 4 d to be included in this analysis.

Results

Comparison of the mean biological halflife of water in *M. pinetorum* exposed to 15°, 22, or 30°C indicates that water turnover by these animals is unaffected by this range of ambient temperature (Table 1). Similarly, urine concentrations of voles exposed to these temperatures did not differ significantly between temperature treatments.

Table 1. Biological halflife of tritiated water and urine concentrations of *Microtus pinetorum* under field conditions, water restriction, or with *ad lib* water maintained at an ambient temperature of 15°C, 22°C, or 30°C. Values represent means ± 1SE, sample sizes are in parenthesis. Means denoted by different letter superscripts differ at $p<.01$ as determined by Duncan's multiple range test.

	Free ranging	15°	22°	30°	Water restricted
Body wt. (g)	23.9 ±0.9^a	22.3 ±0.6^a	24.6 ±1.0^a	21.4 ±0.7^a	18.0 ± .7^b
Halflife of tritiated water (hr)	13.1 ±0.9^a (7)	13.7 ±0.6^a (16)	14.2 ±0.5^a (10)	15.8 ±1.2^a (16)	20.7 ±0.7^b (13)
Urine concentration (mOsmol/kg)	83 ±5^a (22)	420 ±42^b (16)	395 ±60^b (10)	343 ±25^b (16)	1508 ±69 ^{c} (13)

In contrast to the rate of water turnover observed in animals maintained under an *ad libitum* water regime, pine voles exhibited a substantial increase in the biological halflife of ^3H_2O in response to a reduction in the volume of water received on a daily basis. In this instance, a 46% increase in the biological halflife of tritiated water was observed in water-restricted voles relative to animals maintained at the same temperature with *ad lib* water rations. These voles also responded to a reduction in drinking water with nearly a 4 fold increase in urine concentration relative to similarly treated voles with free access to water.

Lastly, the halflife of ^3H_2O in free-ranging voles was similar to that observed in all groups of animals receiving ad lib water. However, the mean urine concentrations in these voles was 4-5 times more dilute than was the average urine concentration of voles in any treatment receiving ad libitum water.

Discussion

Acute exposure of pine voles to three ambient temperatures ranging from 15 to 20°C failed to elicit pronounced changes in their water turnover rates or urine concentrations in this study. This finding is consistent with the results reported in our previous investigation of water metabolism in pine voles, but differs from results presented by Deaver's and Hudson (1977) for the red-backed vole, *Clethrionomys gapperi*. In their study, cold exposed (5°C) *C. gapperi* exhibited a 76% increase in the rate of body water turnover relative to similarly treated voles maintained at 20°C. The fact that their lowest temperature was 10° lower than that employed in this study may account for the apparent differing physiological responses of the two species.

Assessing water consumption and water turnover rates when water is provided ad libitum provides little information about the ability of a species to respond a varying water availability. Specifically, we can compare the biological halflife of body water in pine voles supplied with water ad libitum with the halflife observed under water restricted conditions to obtain an index of the water conservation abilities of the pine vole. The results from this study indicate that pine voles cannot reduce the body water turnover rate to low levels, nor can they produce a highly concentrated urine relative to related species. Deavers and Hudson (1977) have shown that the biological halflife of body water in the related *C. gapperi* supplied with ad libitum water is only slightly shorter than that exhibited by water-restricted pine voles (19.9 vs. 20.7 hr, respectively). Further when presented with limited water, *C. gapperi* have body water halflives 47% longer than those of water-restricted pine voles. Maximum urine concentrations of *C. gapperi* (Deavers and Hudson 1979) also exceed those of pine voles as do those of both *Microtus pennsylvanicus* and *Microtus ochrogaster* (Heisinger et al. 1973). Ostensibly, the pine vole's high energy requirements (Bradley 1976) coupled with a diet low in calorie value but high in water content results in the intake of amounts of water exceeding this species' needs. Thus, no apparent selective pressure exists for elaborate water conservation mechanisms by the pine voles.

Further evidence that these laboratory data accurately portray the water dynamics of pine voles is found in the measurements of water turnover derived from free-ranging voles. In this study, we found concordance between the halflife of body water in laboratory-maintained animals and that exhibited by voles under field conditions. However, in contrast to urine concentrations of approximately 350 mOsm observed in pine voles in the laboratory, animals in the field produced urine at concentrations averaging only 83 mOsm. Thus, in order for free ranging voles to maintain the same water turnover rate as laboratory animals, while simultaneously producing a more dilute urine, an alternate route of water loss must be reduced. We suggest that it is evaporative water loss which is significantly reduced by voles living in natural conditions. Because these animals lead a predominantly subterranean existence, they continually encounter an atmosphere of high moisture content (Dubost 1968), thus potentially reducing their rate of evaporative water loss (Schmidt-Nielson et al. 1970).

In summary, pine voles exhibit rapid turnover of body water and an inability to slow rates of water exchange relative to other related species. We suggest that this physiological characteristic of pine voles is potentially amenable to manipulation, chemical or physical, to control the numbers of pine voles inhabiting orchard situations.

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