

A Review of the Literature Concerning the Need
for Metabolic Water of the Genus *Peromyscus*

A paper presented for completion
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Lya Swaner

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To the Honors Committee:

I am submitting this paper written by Lya Swaner entitled “A Review of the Literature Concerning the Need for Metabolic Water of the Genus *Peromyscus*”. I have read the final form and content of this manuscript and recommend that it be accepted in partial fulfillment of the requirements for my Honors Project with a major in Biology.

Troy A. Ladine, Ph.D.
Honors Committee Chair
Professor of Biology

J. Catherine Cone, Ph.D.
Professor of Biology

Dave Collins
Assistant Professor in Kinesiology and Exercise Science

A REVIEW OF THE LITERATURE CONCERNING THE NEED FOR METABOLIC WATER OF THE GENUS *PEROMYSCUS*

ABSTRACT:

Energy is oxidized from food and used as fuel for metabolic processes in organisms. Water is a waste product of this oxidation in aerobic organisms and can be used to supplement a dietary intake of water. *Peromyscus leucopus* (white-footed mouse) inhabits a variety of environments and although primarily found in mesic environments, some of the environments inhabited by *P. leucopus* have a limited supply of freshwater that can be assessed in their diet. The genus *Peromyscus* has several adaptations for conservation of metabolic water. These include both physiological adaptations (e.g., reducing the volume of urine production) and behavioral modifications (e.g., reducing heat loss, consumption of foods higher in carbohydrates and proteins, and consumption of foods higher in water content). While not known if concentration of urine occurs in *Peromyscus*, this physiological adaptation occurs in closely related species (kangaroo rats; *Dipodomys spp.*). This paper summarizes the literature pertaining to specie of *Peromyscus*, particularly *P. leucopus*, in relation to water conservation and the need for water in their environment.

METABOLIC PROCESSES:

Metabolism is the sum of biochemical processes in an organism that provides energy and metabolic water. Metabolic water refers to water produced as a result of these metabolic processes. Processes occur when a living organism oxidizes energy-containing substances in their food or environment. When an animal is under water stress, grains and nuts that are high in carbohydrates and low in proteins are specifically chosen for maximum metabolic water

production and minimum nitrogenous waste production (which requires the elimination of water; Frank 1988).

Metabolic water is produced by the oxidation of hydrogen ions in the food consumed by an animal. This occurs at the end of the electron transport chain which drives oxidative phosphorylation and maximizes ATP production for the eukaryotic cell. Metabolic water is lost in urine and a variety of regulating organs of osmosis; e.g. skin, kidneys, and lungs. The need for water is determined by the amount an animal is able to retain through the organs of osmosis.

Food products that have been absorbed but cannot be metabolized or eliminated through urinary system must be eliminated through cellular respiration (Randall et. al. 1990). Cellular respiration allows organisms to utilize energy to make ATP for cellular processes to take place. Sugars that are consumed are catabolized to provide energy for the organism (Figure 3).

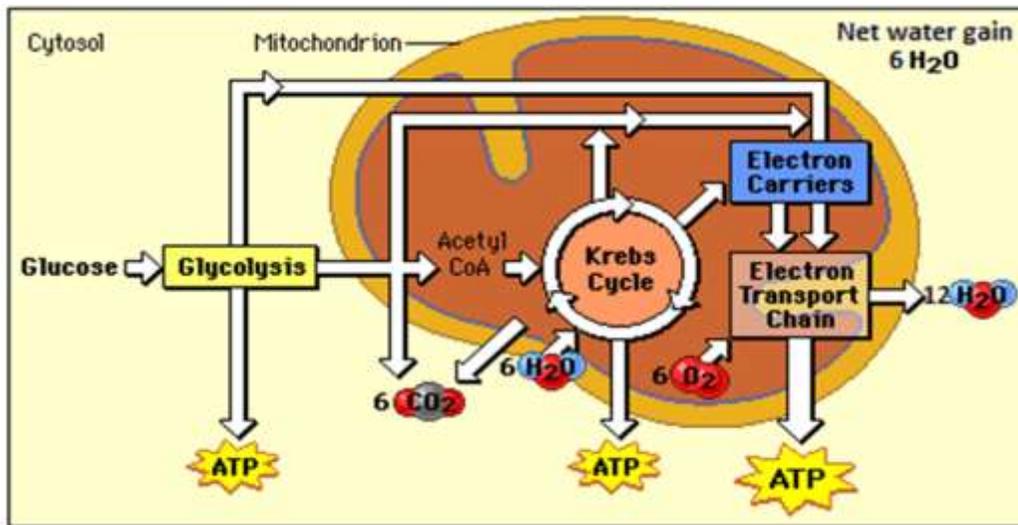


Figure 3: The net gain of water in cellular respiration. Adapted from Pearson Education, Inc.

Accessed on 6 September 2012.

Cellular respiration includes glycolysis, the Krebs cycle, and the electron transport chain. For every one molecule of glucose, six water molecules are used in the Krebs cycle and 12 water molecules are produced in the electron transport chain to make during ATP synthesis (Stryer 1995). The net gain of water is six molecules of metabolic water. This water is important to continue the cellular respiration process for the next glucose molecule. However, for most animals, this net gain is not enough to supply nourishment for the body without some consumption of water.

Water is important for the body not only for cellular respiration but also in the temperature control, excretion, humidity regulation, and reduction of external surface evaporation (Schmidt-Nielsen & Schmidt-Nielsen 1950). However, some species, like the kangaroo rat (*Dipodomys ordii*, a rodent relative of *Peromyscus*), have the ability to conserve water, rely almost always on metabolic water. Thus have little need for water consumption. Most of their requirement for water is obtained through metabolism and consumption of food. They are able to control their body temperature, modify excretion, and regulation of humidity and evaporation to better accommodate the lack of water available in their desert environment (Walker 1975). However, *Peromyscus* conserves water primarily through urine volume reduction and about 66% of its metabolic water is lost each day through respiratory evaporation, urine, and feces (Lackey et. al. 1985). Therefore, constant need for the replenishment of water is necessary for the survival of the white-footed mouse.

Due to water's high heat of vaporization, the greatest benefit of water elimination is through the epithelial cells. Water molecules with the highest energy take thermal energy as they evaporate. The methods of increasing evaporative heat loss in mice are saliva spreading and panting (Robertshaw 2006). Water is important in temperature regulation which leads to

compromises and conflicts between osmotic stresses, physiological adaptation, and environmental temperatures (Randall et. al. 1990). To reduce osmotic stress, animals that rely on metabolic water will rest during the day during the warmer temperatures and come out at night when it's cooler and more humid, thus, reducing water loss (Schmidt-Nielsen & Schmidt-Nielsen 1950).

Temperature regulation is controlled in part by water evaporation and heat dissipation. This occurs by the elimination of water through the skin or evaporative cooling over the respiratory surfaces such as the lungs, tongue, and air passages. Most heat exchange takes place at the nasal epithelial lining where venous drainage can be directed to a network of arteries at the base of the brain where heat transfer and selective brain cooling occurs (Robertshaw 2006). During exercise at higher temperatures in some mammals, water is lost through the respiratory surfaces and through the skin, increasing the necessity to cool the body (Randall et. al. 1990). In more active mammals, such as mice, body temperature rises during exercise but the brain temperature remains normal due to heat exchange in the nasal region that cools the blood supply to the brain. Even during basal conditions where no exercise other than breathing is taking place, the respiratory mechanisms lead to the loss of water through respiratory surfaces (Randall et. al. 1990)

Cellular osmoregulation includes the regulation of cell volume, ion transport, cell turnover, protein structure, and other cellular parameters (Kültz 2001). Osmoregulatory capabilities in organs depend on the transport properties of epithelial cells which are located in the kidneys, skin, and intestines. The epithelial cells are highly specialized anatomically, and functionally polarized (Randall et. al. 1990). The apical surface (the mucosal or luminal surface) of an epithelial cell is continuous with the lumen of the gastrointestinal tract and the lumen of the

kidney tubule. The basal surface (the serosal surface) has deep basal clefts and meets the internal compartment containing extracellular fluid. Epithelial cells are highly hypertonically stress-resistant and have non-specific pathways for adaptations to protect against the hypertonicity for more productive use in the body (Kültz 2001). Hypertonic stress causes apoptosis of cells which affects osmoregulation, and ultimately, excretion of metabolic wastes.

Respiratory surfaces are primary exits for water in air-breathing mammals. Water loss associated with respiration is dependent on the relationship between body temperature and the inhaled air temperature. As unsaturated air is warmed in the lungs, it will take up moisture until the air is saturated (Randall et. al. 1990). The air is cooled in the nasal passages during exhalation and most of the water is recovered. Internalization of the respiratory surfaces reduces evaporative loss; however, ventilation of the respiratory epithelium by unsaturated air will cause evaporation in moist epithelial surfaces (Randall et. al. 1990) and add to water loss.

The excretion of nitrogenous wastes varies among water availability and species. The kidneys are the main organ involved in the excretion of ammonia, urea, and/or uric acid. In most mammals, urea is the primary end product and most is excreted in the kidneys. Because the nitrogenous end products vary, excretion is not organ specific (Randall et. al. 1990). Not all urea is excreted by the mammalian kidneys. The urea that is not excreted is retained by the kidneys. It acts as an alternative source of energy and is used in osmoregulation by maintaining the osmolarity gradient functions for water reabsorption (Sakami and Harrington 1963).

Desert animals are faced with limited water supply and high temperatures. These animals must avoid overheating while avoiding large quantities of body water loss. The survival strategies of the kangaroo rat demonstrate a variety of osmoregulatory adaptations that are

characteristic of many small desert mammals which are faced with excessive heat and the absence of freshwater. These adaptations include the avoidance of high temperatures and heat-generating exercise during the day, living in cool burrows, and modified kidneys (Figure 4) that excrete highly concentrated urine, all of which conserve energy. Because the habitat of the kangaroo rat is in drier areas with little freshwater for consumption, there is heavy reliance on metabolic water and available food to provide the water necessary for life.

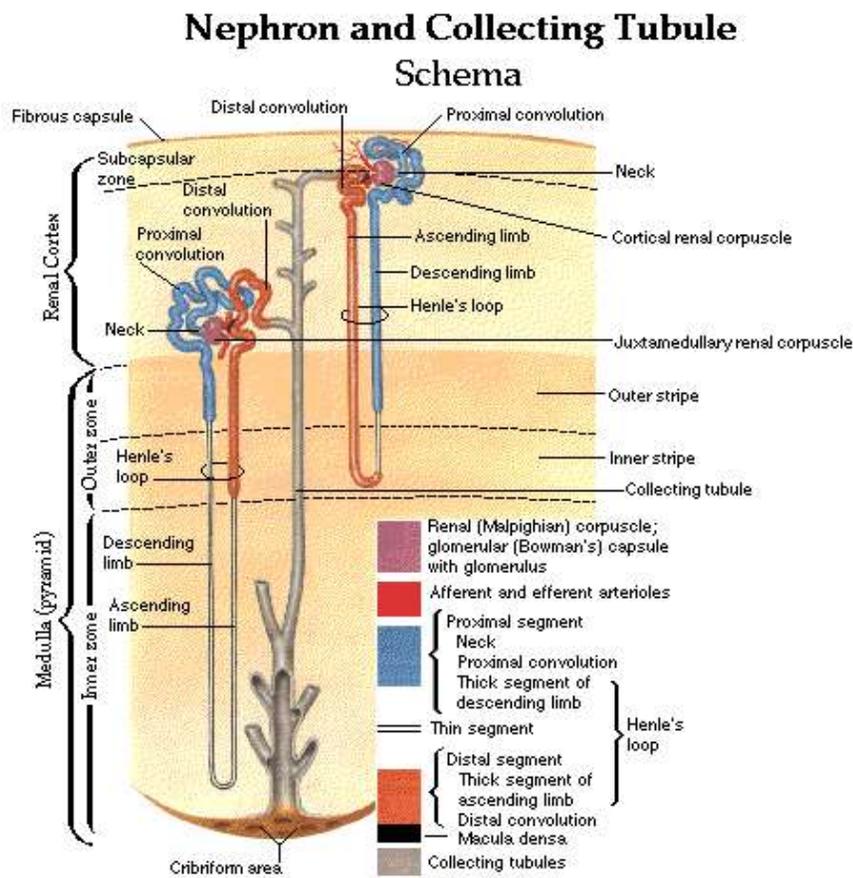


Figure 4. General structure of a nephron in a mammalian kidney.

From <http://www.irvingcrowely.com>. Assessed on 22 October 2012.

Kangaroo rats obtain about 90% of their body water from metabolic water. The remaining 10% is obtained from the free water in dry food (Schmidt-Nielsen 1972). The

kangaroo rat loses 70% of its bodily water through evaporation and perspiration and the remaining 30% is lost as urine or feces (Schmidt-Nielsen 1972). The kangaroo rat avoids the daytime heat by remaining in burrows during the daylight hours (Randall et. al. 1990). They can survive temperatures of 42.5° C for up to an hour and any exposure to temperatures of 35° C or higher, water loss increases rapidly (Tracy and Walsberg 2000). The cool burrow reduces the temperature load on the rat and reduces the loss of respiratory water. If the small desert rodent leaves the cool burrow into air temperatures similar to its own body temperature, the respiratory water loss will rise. When water is scarce during the warmer seasons in the semi-desert habitat of *Peromyscus*, the mouse must use these energy conserving techniques. However, during the cooler months that exist in the habitat of *Peromyscus*, they do not have to conserve energy as much as the kangaroo rat.

Desert mammals, like the kangaroo rat, avoid heat-generating exercise during the day at higher temperatures. At increased temperatures, removal of excess heat from the body is slowed due to the reduced cooling properties of the nasal epithelium in specific respiratory systems. This system has a nasal countercurrent that warms and hydrates inhaled air as it passes through the nasal passages, then cools and dehydrates the exhaled air, minimizing water loss. *Peromyscus* species must use the same cooling techniques to conserve water during in the warmer climates in their habitat. However, during decreasing temperatures with seasonal changes, *Peromyscus* species will lose less water and will not need to conserve as much water.

The kangaroo rat has efficient kidneys that excrete a high uric acid concentration which allows them to use much less water to excrete wastes (Figure 4). When reported on a dry diet, the genus *Dipodomys* had higher concentrations of urea in their urine than any other mammal

(Howell and Gersh 1935). The rat also has the ability to absorb water from its feces resulting in dry fecal pellets (Randall et. al. 1990).

The major organs for reabsorption of water are the kidneys. Ions and water begin to be reabsorbed in the lumen of the proximal convoluted tubule and completed in the distal convoluted tubules and nephric ducts leading to the bladder and urethra, but the major location of reabsorption is in the Loop of Henle. Most of the ions and water require active transport which causes a greater need for energy by the organism (Howell and Gersh 1935). The results were found that white-footed mice consumed more daily energy, (2.38 Kcal·g/live wt/day) than the golden mouse (1.48 Kcal·g/live wt/day; Knuth and Barrett 1984; O'Malley et al. 2003; Peles and Barrett 2008) which indicated *Peromyscus leucopus* had greater energy requirements, thus consuming more food. Because the energy requirements are higher in *Peromyscus* than *Ochrotomys*, *Peromyscus* also has higher energy costs in daily life. Alternatively, this could simply be an artifact of a more sedentary lifestyle of the golden mouse (Komarek 1939, Paerson 1953, and Linzey 1968).

Anatomical modification of the kidney will aid in the retention of water. Research shows that the nephrons of the kangaroo rat have been modified over time in order to increase water reabsorption in the kidneys, specifically, longer Loops of Henle than other rodents (Howell and Gersh 1935). Measurements of the medulla thickness and medulla-to-cortical ratios are much greater in the kangaroo rat than other mammals another modification to increase water retention (Abdalla 1979). The size of kidneys is determined by an organisms need for water reabsorption. Nothing is known of the kidney structure of *Peromyscus* species. However, the genus may have longer loop of Henle and modified nephrons than most mammals. However, because the habitat is less heat-generating and less harsh on the organism, *Peromyscus* should not have as great of a

modification of the Loop of Henle and nephrons as the Kangaroo rat. *Peromyscus* does not require as much water to be reabsorbed as the kangaroo rat because there is more available for consumption in the wooded and semi-desert habitat.

P. eremius (cactus mice) have two main adaptations for their semi-desert habitat, a lowered metabolism and an ability to enter torpor, temporary hibernation, when deprived of food and water. The lowered metabolism is a result of low thyroid gland activity as indicated by the low amount of measured plasma thyroxin level (Hulbert et al. 1985). The slowed activity of the thyroid gland and low thyroxin levels appeared in animals in desert habitats and not animals in coastal habitats, providing support for environmental adaptations (Hulbert et. al. 1985). Low thyroid levels decrease the amount of oxygen used by cells, therefore, conserving energy. In extreme conditions, such as the absence of food or water, the cactus mouse can enter torpor within 12 hours, and once the environment's temperature drops below 30°C, the oxygen consumption and body temperature decreases (Veal & Claire 1979). Torpor allows the rodent to conserve energy, and ultimately conserving its metabolic water.

While a slowed metabolism and torpor is beneficial in the maintenance of metabolic water and survival in the harsh conditions of the cactus mouse, it causes stress on the metabolism of the females during gestation and lactation (Glazier 1985). In order for the female cactus mouse to carry and provide nourishment for both the unborn and born offspring, there is greater need for a higher basal rate of metabolism, which requires more water. During this period, the female mice are at greater risk for not surviving during extreme conditions of high or low temperature or the absence of food and water. They cannot slow their metabolism or go into torpor at risk of harming the offspring, thus, in a drier habitat, they are limited to a small litter size to provide maximum survival opportunity for both the mother and offspring (Parker 1990).

Most small mammals drink water regularly in captivity; however, less water is consumed in the natural habitat. Instead, they rely on adequate combinations of preformed and oxidative water yielded from their food (MacMillen 1983). The restricted availability of drinking water does not dehydrate the tissues as body fats are metabolized for energy. Even with a decrease of 39% in normal drinking water uptake, body mass of the mice remains at normal level (Chew 1951). Water requirements are low in *P. maniculatus* (deer mouse) because they rely on free water in succulent foods and water formed in the oxidation of those foods to provide water required for their body functions (French 1956).

Energy demands change in the natural habitats of mice. *Peromyscus maniculatus* live at both high and low altitudes in western North America (Chappell and Snyder 1984; Chappell et. al. 1988; Hayes 1989a, 1989b; Hayes and Chappel 1990). At higher altitudes, oxygen availability and temperature are lower than those in lower altitudes, causing high-altitude mice to have greater physiological demands than those at low altitudes. Research shows the energy expenditure at high altitudes is closer to their short-term aerobic limits than the deer mice at low altitudes (Hayes 1989a, 1989b; Hayes and Chappell 1990).

Deer mice at high altitudes also acquire hemoglobin polymorphisms for blood-oxygen affinity that correlate with native altitudes, helping them adapt to low oxygen availability at higher altitudes (Chappell and Snyder 1984; Chappell et. al. 1988). Hemoglobin is expressed differently at these altitudes to allow for more oxygen uptake. Oxygen is required by mice to produce ATP for cellular processes. With poor oxygen affinity, the need for metabolic water increases for cellular processes. Therefore, hemoglobin polymorphisms to increase blood-oxygen affinity may lessen the need for metabolic water, or allow the water to be used more efficiently for other processes.

At higher altitudes, there are significantly larger cardiopulmonary and digestive organs found in the bodies of mice due to the lower temperature and the lower oxygen particle pressures. The mass of central processing organs (kidney, intestines, and liver) increases at high altitudes, where decreased temperatures cause an increase in energy demands due to low oxygen availability. The mass of cardiopulmonary organs (heart and lungs) increases at high altitudes where oxygen is at lower pressures. A decrease in oxygen tension with respect to altitude decreases the oxygen availability for respiration at higher altitudes and the larger organ mass then aids the mice in accommodating lower oxygen tensions.

Oxygen uptake is aided by increasing the surface area of the respiratory exchange surface, or decreasing blood tissue membrane thickness. Increasing bulk transport of fluid over respiratory membranes assists in obtaining more oxygen by either increasing the blood flow of alveoli air surfaces or increasing ventilation, thus, helping animals adapt to the higher altitudes (Lenfant 1973). With these adaptations, animals do not need as much oxygen for metabolic functions and, therefore, do not lose as much oxygen through diffusion in the lungs. Because the need for oxygen has decreased, they can better utilize the low levels of oxygen present to maintain more metabolic water for their metabolic functions on reserve when water sources and food are not available.

In the northern temperate zones, small animals are exposed to severe seasonal changes in the environment, affecting energy expenditure and survival. Mice in the genus *Peromyscus* utilize behavioral and physiological mechanisms that reduce heat loss and increase heat production during the winter (Hill 1983). However, heat production is metabolically expensive because large surface-area-to-volume ratios of small animals make weight-specific heat loss noticeable (Pierce & Vogt 1993). Therefore, the small body size allows for fat reserves that may

limit the amount of heat produced. (Cossins & Bowler 1987). The fat reserves serve as a source for energy when food and water are scarce, producing body heat, which limits the amount of heat utilized by metabolic water.

Fat reserves act as a calorie reserve for meeting dietary and climatic challenges (Bronson, 1987). They serve cellular maintenance, thermoregulation, and movement/activity of organisms. At a smaller size, such as in the genus *Peromyscus*, less heat is lost. However, the genus is often found in colder climates that require excessive heat regulation for survival. The fat reserves are not used up because of the small surface area of the mice, and thus help regulate body temperature (Bronson 1987).

It cannot be shown from the results of Hammond et al. (1999) that higher energy demands and larger organ size are a result of increased maintenance metabolism, although it may provide evidence for an increased need for food. Deer mice have additional energy demands when native to higher altitudes (Hayes 1989a, 1989b). This results from a colder environment and/or increased social/territorial or reproductive activity (Fairbairn 1977). Animals living in harsh environments have greater energy needs than those living in mild environments. Organ mass increases are necessary to aid the higher energy demands and metabolic costs. These costs represent the adaptations needed before other demands such as migration, reproduction, and terrestrial defenses can be met (Hammond et al. 1999).

Based on the energy requirements and osmoregulatory adaptations, it can be determined that white-footed mice rely on metabolic water for survival. They are able to produce metabolic water similar to their relatives the golden mouse, deer mouse, cactus mouse, and kangaroo rat, but modify body adaptations for their specific environmental conditions. These adaptations

include living in cool dwellings and having fat reserves in the body to regulate temperature and modifying their kidney function to excrete higher concentrations of urine to conserve energy.

ECOLOGY:

Peromyscus leucopus is a medium-sized, short-tailed, nocturnal, white-footed mouse with thinly scattered hair covering its body and average sized ears (Lackey et. al. 1985) The species differs from the others in the genus, being in smaller size, brighter colors, lighter weight, lacking tufts at base of ears, and having less hair (Figure 1).



Figure 1. *Peromyscus leucopus*. Photo taken by Troy A. Ladine.

The white-footed mouse is native to the Nearctic region of the world, found throughout most of the eastern United States (Figure 2). The geographic range eastward is Nova Scotia in

the north to Virginia in the south and westward in Saskatchewan, throughout the plains states, Mexico, and the Yucatan Peninsula (Wilson & Ruff 1999). There is no record of the species from the Gulf Coast Plain of North Carolina, South Carolina, Georgia, Alabama, and some parts of Florida.

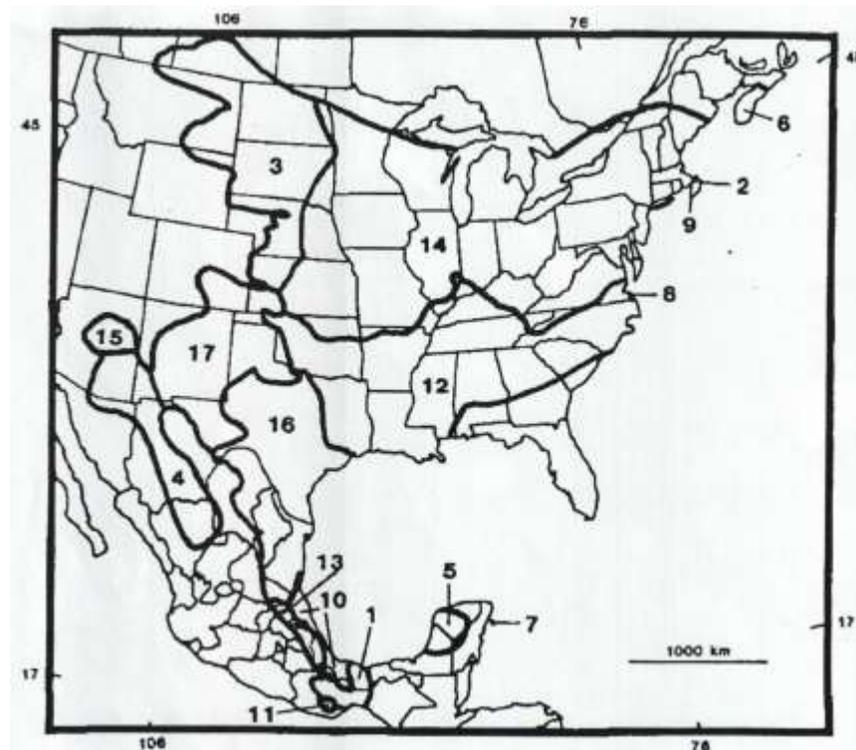


Figure 2. Distribution of *Peromyscus leucopus*. Subspecies are: 1, *P. l. affinis*; 2, *P. l. ammodytes*; 3, *P. l. aridulus*; 4, *P. l. arizonae*; 5, *P. l. castaneus*; 6, *P. l. caudatus*; 7, *P. l. cozumelae*; 8, *P. l. easti*; 9, *P. l. fusus*; 10, *P. l. incensus*, 11. *P. l. lachinguiensis*, 12. *P. l. leucopus*, 13. *P. l. mesamelas*, 14. *P. l. novebaracensis*, 15. *P. l. achraceus*, 16. *P. l. texanus*. (Hall 1981). Map from Lackey 1985.

The habitat of *P. leucopus* consists of chaparrals, warm-dry forests, and scrub forests. The most common habitat is in the brush lands at middle elevation (500-1500 meters) bordering agricultural lands (Van Deusen & Kaufman 1997, Barry & Frang 1980). In southern and western areas of their geographical range they are limited in distribution and are found mainly in semi-desert scrub near waterways or wooded areas (Blair 1954, Wilson 1968, Kaufman & Fleharty 1974). They build nests in warm, dry places such as hollow trees, stumps, brush piles, burrows, buildings, woody debris, or under logs (Mumford & Whitaker 1982). In these areas near waterways there is more available freshwater than in the dry forests, however, the habitat is still classified as a semi-desert scrub where other conservation methods, such as temperature regulation, are necessary to conserve metabolic water. Because water is more available in dry forests, the need for water decreases, but it is still important for *Peromyscus leucopus* to regulate body temperature to conserve metabolic water to further reduce the amount of water needed for survival.

The cactus mouse resides in a semi-arid desert environment that is considered an intermediate position for water availability (Veal & Caire 1979). This species consumes both dry and moist food. The weight response and survival is more efficient in granivores than herbivores, because on a consistent diet and water availability, water regulation is most efficient (MacMillen 1983). The efficiency of water regulation is demonstrated by weight response to rodents when controlled to have the same dry diet and deprivation of water. If weight and size remain consistent, the rodent is regulating water efficiently, getting the most water from food, and not becoming dehydrated, thus they are able to utilize metabolic water obtained from food. Granivores are exposed to more dry foods and less water causing more efficient water regulation. Herbivores consume moist foods which subject them to inconsistent water availability for less

consistent and efficient water regulation. This intermediate position in food habitats and water availability is most likely reinforced through interactions among the granivorous and herbivorous organisms (MacMillen 1983).

Peromyscus species are primarily omnivorous consuming a variety of moist foods such as insects, leaves, fruits, flowers, and fungus (MacMillen 1983). However, due to food availability, they can also be granivorous, consuming dry foods such as wood, bark, grains, seeds, and nuts. The maximum water obtainable by percent mass in free water is 100%. If free water is unavailable, dry food proteins can provide 41.3% and carbohydrates can provide 55.4% of the necessary water (Howell and Gersh 1935).

Gibbes and Barrett (2011) compared nutritional caloric values, including fats and carbohydrates, and protein values of *Cornus florida* (flowering dogwood) fruits, *Ligistrum sinense* (Chinese privet) fruits, *Rhus typhina* (staghorn sumac) fruits, *Quercus nigra* (water oak) acorns, and *Quercus alba* (white oak) acorns (Table 1). In this study, the energy requirements of white-footed mouse and the golden mouse (*Orchomtomys nuttalli*) were compared based on their energetic costs and caloric consumption.

The white footed mouse primarily consumed the most of *Q. alba* and *C. florida*, followed by *Q. nigra*, *L. sinense*, and lastly, a much smaller amount of *R. typhina* (Gibbes and Barrett 2011). The golden mouse primarily consumed the most of *C. florida*, followed by *Q. nigra*, *Q. alba*, and lastly a very small, equal amount of *L. sinense* and *R. tympkina* (Gibbes and Barrett 2011). Based on the caloric values, there was no direct correlation between protein percentage and amount consumed. The white-footed mouse preferred seeds to flowers but the golden mouse showed no preference. Both the white-footed mouse and the golden mouse consumed the *R.*

typhina fruit the least even though its caloric value was in the midrange of values compared. Because carbohydrates provide more water for the body than proteins, this could explain the insignificance of protein percentages and the choice of what type of food to consume.

Table 1: Summary of caloric and protein values (Kcal· g dry wt-1 Kcal N g dry wt⁻¹ ± SD) for each food item based on five sample diets. From Gibbes and Barrett 2011.

Diet	Caloric Value	Percent protein
<i>Quercus nigra</i>	5.2 ± 0.17	3.99 ± 0.10
<i>Quercus alba</i>	3.6 ± 0.03	4.68 ± 0.07
<i>Cornus florida</i>	5.2 ± 0.12	7.90 ± 0.03
<i>Ligistrum sinese</i>	4.8 ± 0.13	10.46 ± 0.03
<i>Rhus typhina</i>	4.6 ± 0.18	5.93 ± 0.23

Conclusion:

Based on the energy requirements and osmoregulatory adaptations, it can be determined that white-footed mice rely on metabolic water for survival. They are able to produce metabolic water similar to their relatives the golden mouse, deer mouse, cactus mouse, and kangaroo rat, but modify body adaptations for their specific environmental conditions. These adaptations include living in cool dwellings and having fat reserves in the body to regulate temperature and modifying their kidney function to excrete higher concentrations of urine to conserve energy. Even though the environment is not as harsh as that of the kangaroo rat, when moist foods and

freshwater are scarce, *Peromyscus* may be limited to some degree by the presence of water in mesic environments. During the long-term drought in East Texas (2001-2012), *Peromyscus leucopus* have only been captured within 15 meters of a permanent water source (T. A. Ladine unpublished data). *Peromyscus leucopus* is a habitat generalist (see Lackey et al. 1985). And vegetation analysis (Pressley and Ladine, in press) has found the habitat in the area to be similar to other reported sites (see Lackey et al. 1985). Therefore, there may be some unknown mechanism or a mechanism lacking in *P. leucopus* limiting them to areas near water during periods of drought. Further studies are needed to confirm the limitations during periods of water restriction in the habitat. Additionally, anatomical data are lacking to fully understand the use and conservation of metabolic water in *P. leucopus*.

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