

The Ecology of the White-throated Woodrat: Reviewing Theories and Exploring
Possible Adaptive Strategies

By

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ABSTRACT

The white-throated woodrat, *Neotoma albigula*, is a desert rodent, common in the southwestern United States. This species relies on behavioral and physiological adaptations in order to cope with a desert environment. The physiological adaptations of the white-throated woodrat prevent the animal from overheating but do not promote water conservation. The woodrat's ability to survive in an environment with little water is attributed to behavioral modification, primarily food choice and nocturnality. However, it is possible that the white-throated woodrat may use other survival strategies that are not currently known. Although much of the literature regarding the white-throated woodrat promotes the idea that the species is dependant on cactus as a source of food that provides water, I observed a population of white-throated woodrats that survived in the absence of cactus. After making observations on this population, I reviewed the literature that pertained to the white-throated woodrat and similar species and used my own observations to explore means by which the white-throated woodrat may be surviving in desert environments. Review of the literature of *N. albigula* and the genus *Neotoma* suggests that there is tremendous variation among woodrat populations. I propose that woodrat populations are highly individualized and are very responsive to their environment.

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INTRODUCTION

Plants and animals have specialized ways to deal with their environment. Adaptations expressed in animals are either physiological or behavioral and their effectiveness can determine the success or extinction of a species (Brown 1968). Many animals have effectively adapted to life in a desert environment. For instance, kangaroo rats, *Dipodomys* spp., survive in the desert with the help of physiological adaptations, such as a specialized kidney, which allows the animal to produce highly concentrated urine, thereby increasing water conservation (Koontz et al. 2001, McNab 1979). This is an effective physiological adaptation, though the kangaroo rat still has a very tight water budget, exactly balancing water use/loss and water intake (Schmidt-Nielsen 1997).

The white-throated woodrat, *Neotoma albigula*, is unique in that it, while it does have physiological means of dealing with extreme heat (Brown 1968), it does not have a known physiological means of conserving water (Dial 1988; Macêdo and Mares 1988) and is highly susceptible to dehydration, yet it survives in desert environments (Macêdo and Mares 1988). While there has been some investigation into the white-throated woodrat's homeothermic mechanisms (Brown 1968), water balance has been attributed to food choice. Much of the literature suggests that *N. albigula* uses cactus (*Opuntia* spp.) as a food source and a source of water (Vorhies and Taylor 1940; Macêdo and Mares 1988; Hoffmeister 1986; Olsen 1976; Brown et al. 1972). Because of this, woodrats are usually expected to be found in association with cactus in desert regions. While

Brown et al. (1972) state that this relationship is not strictly obligate; the relationship is often presented as the standard rather than an optional habitat requirement. Indeed, Vorhies and Taylor (1940) stated that it was difficult to find woodrat nests in the absence of cactus.

SPECIES BIOLOGY AND ECOLOGY

Vorhies and Taylor (1940) conducted the initial research on the white-throated woodrat in a study extending from 1920 to 1940, which focused on rodents in the southwestern United States. Their study on the woodrat focused on the *N. albigula albigula* subspecies in the Lower Sonoran zone of Arizona. The purpose of their survey was not strictly to advance scientific knowledge of the species but rather; their goal was to assess the possible nuisance factor or economic impact of certain species. Vorhies and Taylor (1940) concluded that the woodrat did not need to be exterminated due to the fact that the species' presence was neither advantageous nor detrimental to humans. They also determined that the presence of woodrats did not cause overgrazing on rangelands, rather their presence was a result of overgrazing, and finally that it might be considered as a 'novel pet'.

The genus *Neotoma*, family Muridae, was originally described created in 1825 (Edwards and Bradley 2002). The systematics of the genus have been subject to some controversy and have a history of reevaluation and reclassification. Currently, there are 22 species in the genus (Edwards et al. 2001). *Neotoma*

albigula is a medium-sized (181-217 g) rodent (Vorhies and Taylor 1940), which resembles a common rat (*Rattus*) but is grayish, has soft, chinchilla-like fur, and a hairy tail (Hoffmeister 1986). This solitary species (Macêdo and Mares 1988) thrives in a wide variety of habitats (Vorhies and Taylor 1940, Macêdo and Mares 1988) including desert environments.

The white-throated woodrat survives temperatures that closely approach its lethal limits by relying on behavioral and physiological adaptation (Koontz et al. 2001). Heat is dealt with through reduced pelage (Brown 1968) and physiologically through a modified vascular system (Nelson and Yousef 1979). Water conservation is dealt with through behavioral adaptations, such as nocturnality and food choice (Vorhies and Taylor 1940; Dial 1988). Most populations of *N. albigula* in desert regions depend heavily on cactus as a food source that provides water (Brown et al. 1972). Cactus (cholla, *Opuntia* spp.) density has been found to determine woodrat abundance in southern Arizona (Vorhies and Taylor 1940). Young woodrats are able to extract cactus spines from their flesh by the time they are 2 months old and adult woodrats are skilled at handling, climbing, and transporting cactus without injury (Vorhies and Taylor 1940). Cactus, which may be up to 90% water, constitutes 43.8% of the woodrat's annual diet (Table 1). Other common foods eaten by *N. albigula* include mesquite (*Prosopis* spp.), grasses (*Gramineae* spp.), and other miscellaneous plants (Vorhies and Taylor 1940). The white-throated woodrat also relies on other plants, such as juniper (*Juniperus* spp.), and soapweed (*Yucca glauca*) in

other parts of its range, outside of southeastern Arizona (Macêdo and Mares 1988). *N. albigula* is an excellent climber, which allows it to access the bark and leaves of trees for food (Brown and Zeng 1989).

Woodrat dwellings consist of a large nest above ground and a series of burrows beneath (Macêdo and Mares 1988). In some areas, rock crevices are utilized. The nest is commonly placed at the base of a tree or cactus (often prickly pear, *Opuntia* sp.), which is called the shelter tree. Usually, the woodrat's nest is made of a base material of something very common, such as sticks, and is decorated with more interesting items found in the woodrat's environment, including human possessions (Vorhies and Taylor 1940). The species' habit of 'stealing' items of interest and stashing them around in the nest is what has earned it the nickname of 'packrat' or 'trade rat'.

The burrows are 10-30 cm below ground (Koontz et al. 2001) and provide a fairly stable microclimate (Brown 1968), which enables the woodrat to avoid the lethal heat of the day by spending daylight hours underground. One population of white-throated woodrats that Brown (1968) studied in extreme southwestern Arizona had average temperatures between 33° C and 36° C in their burrows in the summer. In this study, two populations of *N. albigula* suffered heavy mortality when exposed to a temperature of 40° C (a temperature commonly reached in the summer) but were able to tolerate a hyperthermic state at an ambient temperature that was between 34° and 36° C.

The age of sexual maturity for *N. albigula* is not specifically known but is most likely between 150 and 300 days (Hoffmeister 1986). There is some disagreement as to the exact breeding season of the woodrat. For the state of Arizona, Hoffmeister (1986) found that breeding occurs year round and slows down in midsummer, but also states that it may stop for a few months at the end of late summer. In contrast, Vorhies and Taylor (1940) found that breeding occurs eight months out of the year. The number of litters produced per year is not specifically known except that there is at least one and most likely two per year (Hoffmeister 1986, Vorhies and Taylor 1940). Females average two young per litter (Hoffmeister 1986). Little is known about the woodrats' home range size (Conditt and Ribble 1997).

STUDY AREA

In 2001 I found a population of woodrats in Cochise County, Arizona occupying habitat that contained virtually no cactus (Figure 1). I made general observations about this population of *Neotoma albigula* and then reviewed the literature to compare this population to others that have been studied.

This study was conducted in extreme southeastern Arizona, near the border of New Mexico, and approximately 60 miles north of the U.S.-Mexico border in the Chihuahuan Desert, Cochise County, Arizona, from June 27 to July 23, 2001. In general, this region contains a wide array of habitats. The site was in high desert flats (elevation 762 meters) where summer temperatures can reach 40° C. This

desert has strong seasonal rain cycles that can create ephemeral pools during part of the year. The vegetation of the immediate study area included genera such as *Acacia* spp., *Ephedra* spp., and *Prosopis* spp. The vegetation outside of the direct study area contained the previously mentioned genera but also included *Yucca* spp. and *Agave* spp.

Most of the woodrat nests were grouped in two areas. While these two areas had no statistically significant differences in vegetation measurements, they were qualitatively different habitat types. Therefore, in order to easily refer to a particular nest grouping, the study site is labeled with two main areas, 1 and 2 (Figure 2). Vegetation in area 1 consisted primarily of mesquite trees (spaced approximately four meters apart) and there was little other vegetation than the trees that were present and it was very sandy. Area 2 was dominated by acacia (*Acacia* spp.) and catclaw (*Acacia* spp.) and contained short grasses in some areas (Figure 3). This area changed on a daily basis due to the dramatic response of the vegetation to the seasonal rains. At the beginning of the observation period, there was ample room to walk amongst the acacia and catclaw. After a few rains, branches started to grow together and ultimately overlapped one another, making passage difficult, if not impossible. These dense, thorny bushes likely afford great protection to woodrats from a variety of predators, other than reptiles.

METHODS

Researchers who study woodrats have different names for both the underground and aboveground portions of woodrat dwellings. I will refer to the underground portion as either den or burrow and the conspicuous stick mound aboveground as nest or house. My research began by locating woodrat nests; I found 22 nests, 11 in each of the two areas (Figure 2). After locating the nests, I recorded information about their contents, presence of latrines, and any other significant observations (Appendix 1). I recorded the species, height, and greatest width of the shelter trees. As a part of the general observations on this population of woodrats, I surveyed the vegetation around the nests. I accomplished this by randomly spinning the azimuth adjustment dial on a compass and noted the degree at which dial stopped. I then performed a 10-meter transect at that angle and three subsequent angles, each 90 degrees apart. I recorded all woody vegetation along these transects, measuring the height of trees and bushes and the amount (width) of bush/tree crown on the transect line. I chose to measure the crown of the tree because this is what offers shade to the woodrat and so may offer a benefit to the woodrat. Diameter at breast height (DBH) was not measured because the trees were often very shrub like and branched several times only a few feet from the ground.

After a week of surveying the two areas and recording woodrat nests, I began trapping woodrats, rotating six live traps among the nests. There were one or two locations that looked abandoned that were only trapped once. After having found

no sign of occupancy at these nests, I did not trap them again. Traps were set in the early evening, baited with peanut butter, placed near the nest, and were checked at about 04:30 PST. When woodrats were captured, they were sexed, weighed, marked by clipping their fur with a specific pattern using a small pair of scissors, and dusted with a fine-pigmented fluorescent powder. The following night, trails left by the pigment dropping off the animal were followed using a blacklight, which illuminated the powder (Mullican and Streubel 1989; Mullican 1988). This was done to gain insight about woodrat behavior and determine the distance traveled by individuals.

RESULTS AND DISCUSSION

Habitat

Average transect tree width and height for area 1 was 175.32 cm (SD 37.23) and 131.62 cm (SD 24.69), respectively (Table 2). Area 2 trees had a width of 152.48 cm (SD 77.89) and an average height of 174.23 cm (SD 58.29) (Table 2). Qualitative observation revealed that the trees in area 1 had more space to spread out than those in area 2, which were very crowded. The average number of trees at each nest site for area 1 was 5.18 (SD 4.17) and 15.45 (SD 6.26) for area 2. The species composition for the transect survey is listed in Table 3. The average length, width, and height for the nests were 166.26 cm (SD 41.29), 121.14 cm (SD 39.14), and 34.09 cm (SD 22.39), respectively (Table 4). The average width for the shelter trees was 429.32 cm (SD 159.87) and the average

height was 198.86 cm (*SD* 59.06) (Table 5). Most of the shelter trees were mesquites (16) followed by acacia (5), and finally Mormon tea (*Ephedra*) (1).

When I surveyed the vegetation for my study, I chose not to include the grasses in area 2 because I did not think that grass was a major determining factor in site selection due to the fact that the grasses were ephemeral in nature. Also, while this type of vegetation may have been of some value to the animals in area 2, the animals in area 1 did not benefit from the presence of grasses or even much vegetation beyond mesquite and acacia. Relying on grasses and weedy vegetation may be of some use, but the woodrats surely have other, additional means of obtaining food. As to the value of grasses as a food source, Monson and Kessler (1940) suggested that woodrats benefited from the grasses that are created from grazing. However, Vorhies and Taylor (1940) noted that grass is not a preferred food of the woodrat, which obviously conflicts with the ideas of Monson and Kessler (1940).

The woodrats in area 1 had little cover available to them, yet they were present in the same quantities as the woodrats with more cover in area 2. Vorhies and Taylor (1940) suggested that the amount of suitable shelter bushes was a determining factor in woodrat abundance. Olsen (1973) hypothesized that cover was advantageous to woodrats and that shelter sites with more cover were preferred to those with less cover because they afford more protection from heat, especially during house construction. Since area 1 was lacking ground cover, it

leads me to believe that woodrats, perhaps, are not as dependant on ground cover as previously suggested. Admittedly, shelter site choices of area 1 cannot be used to determine a true site selection preference by the woodrats, as there is no alternative choice in a distance reasonable for a woodrat to travel easily. However, my study included a nest that was not built directly around a shelter tree; this nest was built within a meter of an acacia tree, which I counted as the shelter tree. In this case, the animal had an option to maximize cover but chose not to.

Olsen (1973) promoted the idea that shade and cover would be advantageous to a woodrat constructing a house, due to the heat extremes of the desert, but also stated in the same article that houses, "often are maintained by successive generations of woodrats" (Olsen 1973:595). So, some maintenance is performed but major construction is no longer necessary and even abandoned and collapsed nests are fairly complete. At the very least, excessive resource gathering would be unnecessary because most of the materials would be on-site, ready to be reassembled. Also, *N. albigula*'s account in Hoffmeister's (1986) *Mammals of Arizona* included Olsen's hypothesis regarding the advantage of shade for the purposes of house building but adds, "...construction of it (the house) takes place at night" (Hoffmeister 1986:406). This could be interpreted as casting doubt on Olsen's theory by implying that the advantage conveyed by the presence of shade would be negated by the nocturnality of *N. albigula*. As Olsen (1973) suggested, cover is most likely a site-selection factor for the woodrat, but

it is important to consider that there are most likely many variables weighing into the selection of a nest site.

Nests

The nests in my study areas were made mostly of sticks, primarily mesquite and also acacia (Figure 4). A favorite decorative item for the nest was cow dung followed by rocks and pinecones. While most nests were elliptical or circular, some were very odd shapes and some were architectural marvels. One woodrat had a porch adjacent to her nest made from an arching mesquite branch thatched with grasses for a roof. This structure could have been accidental, with no real use, but it looked far too purposeful not to be recorded. Another woodrat had a well-used sleeping depression a few meters away from her nest. The structure was a well-shaped bowl made in the grass. There was a path leading from her nest to this location and this woodrat was once tracked to this location using pigment, where it was apparent she spent at least a short amount of time there.

Latrines were found around 32% of the nests (Table 6). Vorhies and Taylor (1940) made a special note of the fact that the woodrats in their study had no designated latrines anywhere inside or outside of the house. In my survey, 32% of the houses had distinct latrines outside of their houses. Since I did not tear apart any houses, I do not know if there were any latrines inside, as well.

Crickets were present in 77% of the nests (Table 6).

Movement

For the tracking exercise, the maximum distance any woodrat was tracked was 77.15 meters. This trail started at nest 19 and traveled through an open area. In other instances, the trail of powder ran out or was lost before the trail backtracked or circled around toward the nest. Tracking in area 2 was limited due to the dense foliage, which created a physical barrier to the tracker and sometimes made finding pigment difficult because of the dense leaves.

Diet

For the course of one year, Vorhies and Taylor (1940) recorded the contents of 360 stomachs in order to determine the woodrat's diet. These observations revealed the presence of both fur and gravel in *N. albigula*'s stomach. Vorhies and Taylor (1940) could not come up with a perfect explanation but suggested that the gravel, the size of which was not mentioned, in *N. albigula*'s stomach was present due to searching for mineral matter or from grooming, ingesting gravel which was in the fur. They graphed the gravel and fur for the course of a year in order to determine if there was a trend (Figure 5). Vorhies and Taylor (1940) seemed confident in the similarity of the presence of fur and gravel across months that this graph showed. In general, gravel and fur increases throughout the year from February/March to December/January but the two items do not follow one another closely. Therefore, one factor may not be causing the other as this trend could be attributed to other factors, such as seasonal activity levels of the woodrat. Suggesting that the presence of fur and gravel in the stomach is

correlated when the information has not been quantified does not help define the ecology of the species. I initially considered the possibility of gravel being accidentally consumed while eating certain foods. However, after adding some of the monthly consumption rates of *N. albigula*'s food choices to this graph, I was unable to find a better trend. Finding the significance of the varying presence of these two items could potentially illuminate some aspect of woodrat ecology if it was explored further.

While the literature (Brown 1968) mentions that *N. albigula*'s relationship with cactus is not obligate, it strongly suggests that cactus does play some factor in the success of woodrats. Many researchers have presented this relationship for both the white-throated woodrat and the genus *Neotoma* (Vorhies and Taylor 1940; Macêdo and Mares 1988; Hoffmeister 1986; Olsen 1976; Brown et al. 1972). Regarding the food preference studies by Vorhies and Taylor, Hoffmeister wrote (1986:407), "...one rat ate between 30 and 39 grams per day and others ate even more." Hoffmeister did not mention what was written later in that section about one of the subjects in that trial, "Following this period of nearly a month on the unvaried diet, this individual ate less and less, and after 8 more days died at a weight of 112 grams. Apparently prickly pear, much as it is liked and used in the open, is not satisfactory as an exclusive diet" (Vorhies and Taylor 1940:504). It seems as though the close relationship of many woodrat populations with cactus is highly accepted and promoted by some, even though it is obviously not a panacea for the woodrat's food and water requirements.

Adaptive Strategies

Due to the popular theory that *N. albigula* utilizes cactus to survive in desert environments and statements such as the one made by Vorhies and Taylor (1940:465), that in, "Cochise County, Arizona, in 1933, where cactus was absent only one den was found in 2 days' work." I concluded that the woodrats in my study area were not just present, but successful in an area functionally devoid of cactus (Figure 1). This leads me to believe that the white-throated woodrat has underestimated adaptations that enable it to survive in its desert habitat. Here I will explore ideas resulting from my own observations and some survival strategies currently known in similar species.

It is possible that the white-throated woodrat is able to decrease water loss by creating a favorable microclimate. Brown (1968) has already confirmed the fact that the temperature within the den is fairly constant and below the high, outside temperatures of the day. I would also suggest that it is possible that the humidity level within the den is different than at ground level, outside the den. With a higher relative humidity, mammals are less subject to respiratory water loss (Palgi and Haim 2003). Therefore, if a woodrat were able to create a favorable microclimate in the den then this loss would be reduced. Perhaps, water needs may be partially met by storing seeds in this favorable microclimate, as they would regain some moisture (Palgi and Haim 2003). The woodrats studied by Vorhies and Taylor (1940) had access to plenty of cactus and they found an unspecified species of crickets in 55% of the houses that were surveyed. The

woodrats in my study area did not have free access to cactus and crickets were present in 77% of the total number of houses found in my survey.

Due to the conspicuous presence of crickets at certain nests, I believe that the microclimate of woodrat nests must be different from both the climate outside the nest and any other entity that only offers shade. Of all the nests from which woodrats were trapped, there was only one occasion where a woodrat was trapped from a nest that did not contain crickets (nest 7). In this case, I suspect that the nest was recently reoccupied. If this nest was recently reoccupied by a woodrat, it may not have been repaired enough to have created a microclimate favorable to attracting crickets or may not have had favorable conditions in existence for a long enough period of time in order for crickets to have colonized the nest.

The colonization of nests by crickets does not correspond to proximity of nests to one another. If colonization of a nest by crickets depended merely on shade or presence of burrows, then crickets would colonize a nest that was directly adjacent to another with crickets. It is logical that nests 14 and 15 would be colonized and nests like 11 and 12 would be less likely to be colonized, but such is not the case. It is apparent that active nests offer crickets something that is favorable to them. Four of the five nests that did not contain crickets looked abandoned and the fifth looked very new. These observations point to the fact that established, active nests attract crickets. The characteristics of a desirable

nest are most likely something other than nest size. A study of the houses of *Neotoma micropus* found no correlation between nest size and temperature (Thies et al. 1996).

It is possible that the presence of crickets in woodrat nests is beneficial to the cricket and neutral to the woodrat. It is also possible that the relationship is symbiotic. Vorhies and Taylor (1940) reported that woodrats did have insects in their diet. After a year-long survey, analyzing the stomachs of 360 white-throated woodrats, Vorhies and Taylor (1940) found that only 0.82% of the stomach contents was 'animal in nature'. Yet, they note that animal matter (insects) is found consistently and introduce the topic by describing it as, "...this small but possibly important animal portion of the wood rat's menu..." (Vorhies and Taylor 1940:500). Though, beyond this, Vorhies and Taylor offer little speculation regarding the role of insects in the woodrat's diet. Another member of the genus, *Neotoma floridana*, considered a diet generalist, is thought to consume animal matter (Williams, et al. 1999). Anecdotal evidence suggests that this species consumes carcasses of northern bobwhite quail, *Colinus virginianus*, when preferred food sources are scarce. Laboratory trials showed that this species of woodrat consumed quail even when suitable food was offered.

In the absence of cactus, *N. albigula* may have found a way to utilize other plants in its environment. One candidate for utilization is mesquite because even in areas where cactus is commonly found, the woodrat relies on mesquite during

certain months as an alternate food source when cactus is less abundant (Vorhies and Taylor 1940). Also, Brown (1968) found most of the nests for his low desert *N. albigula* study, in Arizona, underneath mesquites. In the study conducted by Vorhies and Taylor (1940), mesquite is the woodrats' second most important food source. The woodrat utilizes the bark (Hoffmeister 1986), leaves, and pods of the mesquite and the carbohydrates of the pod offer metabolic water (Brown 1968).

Mesquite is a shrubby tree that has been invading the grasslands in the Chihuahuan Desert for over one hundred years (Gibbens et al. 1992; Kerley and Whitford 2000) and now occupies many areas that used to be grasslands (Tiedmann and Klemmedson 1977). Mesquite alters the soil beneath its canopy by increasing the amount of nitrogen, potassium, sulfur, soluble salts, and organic matter (Tiedmann and Klemmedson 1977) and is quite proficient at extracting water from a great amount of soil (Heitschmidt et al. 1988). These characteristics and others may affect the woodrat, but the relationship between the white-throated woodrat and mesquite has never been explicitly explored, though it is worth consideration.

Since the white-throated woodrat in Arizona has on average two young per litter and most likely has no more than two breeding seasons per year, it is not a prolific reproducer. The kangaroo rat is also similar to the woodrat in that it is very successful and that it does not have the high reproductive rates of some

rodents (Zeng and Brown 1987). According to Zeng and Brown (1987:1328), “...the extremely flexible life history and other facultative behaviors of the kangaroo rat, *Dipodomys merriami*, facilitate adult survival and enable this small mammal to maintain remarkably stable populations despite wide, unpredictable fluctuations in its desert environment.” In the case of the kangaroo rat, responding flexibly according to its environment is necessary for its success in a desert environment. One of these adaptations is only reproducing during optimal periods. This variation is not limited to the existence of a reproductive season but also extends to variation according to climatic variables. Such flexibility could exist in the white-throated woodrat. Indeed, Smith and Charnov (2001) recently proposed that one population of a species in the genus *Neotoma* (*N. lepida*) has changed its reproductive strategy from iteroparity (multiple reproductive events) to semelparity (a single reproductive event). They suggest that the body size of *N. lepida* in Death Valley, California, is such that a single reproductive event is reasoned to be more advantageous than repeated events. The researchers believe that these large adult woodrats (135-175 g) cannot survive the intense heat of Death Valley and die in the summer. Thus, making one great reproductive effort is advantageous. Their survey showed that there are no large woodrats in the population past late spring. Such an adaptation is dramatic, yet is most likely a successful strategy for this particular population of *N. lepida*.

It seems that other members of the genus *Neotoma* display highly individualized adaptation, as well. Recently, Smith et al. (2000) investigated a relict population

of the dusky-footed woodrat, *Neotoma fuscipes* Baird. In this study, the relict population was compared to another species of woodrat and three other *N. fuscipes* populations. In the morphological analysis, there were differences among the three populations of *N. fuscipes*. In their discussion, the authors contemplate the amount of 'discontinuities' that will be found among discrete woodrat populations, especially due to habitat fragmentation. This statement speaks to change due to isolation but is also relevant to the fact that woodrats persist despite changes around them.

Brown (1968) studied adaptation to temperature in five populations of two species of woodrat, *Neotoma cinerea* and *N. albigula*. He tested three populations of *N. cinerea*; one that lived in intense heat and two that lived in more moderate environments. The two populations that lived in a moderate climate reacted differently to temperature than the population of the same species that lived in the heat. This is significant because the desert *N. cinerea* population reacted similarly to the two desert-dwelling *N. albigula* populations, which is another example of the adaptability of individual populations of the woodrat. According to Smith et al. (1998:141), "The genus *Neotoma* is extremely sensitive to temperature." Accordingly, it has been proven that *N. cinerea* follows Bergmann's Rule (Brown and Lee 1969; Smith and Betancourt 2003). As it pertains to *Neotoma cinerea*, Bergmann's Rule dictates that populations in hotter environments will be smaller, allowing the species to more effectively dissipate heat (Macêdo and Mares 1988).

Living in a desert climate leaves little room for error, so considering the diet of an animal in such a circumstance may help evaluate its means of survival. Some woodrat species are considered diet specialists and are able to process plant compounds that would otherwise be toxic. One study has compared the ability of *Neotoma stephensi*, considered a juniper (*Juniperus monosperma*) specialist and *N. albigula*, considered a generalist, to tolerate high levels of a plant toxin found in juniper (Sorensen and Dearing 2003). *Neotoma stephensi* is able to tolerate much higher rates of alpha-pinene than *N. albigula*. The study attributes this to reduction of the absorption of this compound in the gut. Another study also found that *N. stephensi* can process this compound much more effectively than *N. albigula* but offers different explanations for their success (Dearing et al. 2000).

Neotoma albigula is considered a generalist (Sorensen and Dearing 2003), so it would seem logical that the species has not invested in developing a tolerance to any plant compounds. However, white-throated woodrats are able to tolerate a high intake of oxalic acid, a toxin found in cactus (Macêdo and Mares 1988) and can skillfully manipulate and transport spiny cactus parts at a young age (Vorhies and Taylor 1940). However this adaptation is habitat related and would therefore require exposure to cactus in order to be developed. Specializing in cactus is not a habit that can be generalized for all populations of *N. albigula* because not all populations are exposed to cactus. Many habitats require *N. albigula* to be a generalist, but this strategy has its costs, too. A recent study by Dearing et al.

(2002) has shown that woodrats with less experience consuming certain plants, such as juniper, are more susceptible to the diuretic effects that their secondary compounds have. Another study, which compared the effects of plant secondary compounds on *N. albigula* and specialist *Neotoma stephensi*, found that *N. albigula*'s water intake and water output increased when put on a juniper diet (Dearing et al. 2001). This effect would be very costly to a small mammal in a desert environment.

SYNTHESIS

It is clear that not all white-throated woodrat populations follow the predictions suggested by the literature. The white-throated woodrat is generally considered to depend on cactus as a means of hydration in a desert environment; however, the population of white-throated woodrats that I observed lived in a desert environment without the benefit of cactus. This means that the white-throated woodrat may survive by some other means; perhaps by using an unknown or underestimated adaptation, by relying on another plant, or perhaps it was never as dependant on cactus as was previously thought. Other findings that were recorded have not held true for all populations of woodrats. The amount of cover necessary for suitable woodrat habitat is disputable and Vorhies and Taylor (1940), whose study of the white-throated woodrat was extensive, found no sign of latrine use around woodrat nests, however, I found conspicuous latrines. Also, the literature seems to conflict as to the benefit and preference of grass to the woodrat. This may be because some populations of woodrats utilize grass more

than others, which supports the idea that woodrat populations are highly individualized.

Olsen (1973) suggests that cover is a site selection factor for woodrats however I offer that there may be more factors involved in determining suitable nest sites.

In the beginning of my study, an extreme downpour of rain created a flashflood. I was in area 1 at the time, the water was ankle deep everywhere and washes that were bone dry just a few minutes earlier were now raging rivers. It is intuitive that the high mounds of sticks, which made the woodrat nests, would remain above the water, but the land that their nests were built upon was staying above water, too. It was something that would be extremely difficult to recognize on any other day, but the fact was quite obvious when there was water everywhere. I began looking for the other nests that I had already found, to see if they shared this characteristic. I located several nests and they were all well protected from being washed out. Of these nests, it can be said that they were all in areas that offered safety from flooding. Chosen areas included the banks created by the sides of washes and roads, on top of abandoned kangaroo rat mounds, and often times the base of mesquite trees created an elevated area. It is certain that the woodrats fared well in this flood because they were available to be trapped in the weeks following this event. While this observation was not quantified, it suggests that many factors may help determine nest site selection.

There is strong evidence to suggest that woodrats have some type of relationship with crickets. The fact that crickets were only present in those nests that were active supports the idea that woodrats alter their microclimates within their dens and/or burrows in some way. Since the white-throated woodrats can survive without cactus and without a physiological means of conserving water (Dial 1988) they must be relying on some other survival mechanism, such as creating a favorable microclimate. Exploring this relationship could offer a great amount of insight into the ecology of the white-throated woodrat.

Another potential key to discovering how white-throated woodrat survives in the absence of cactus is to better define the species relationships with various plant communities. In particular, the relationship that the white-throated woodrat has with mesquite may not be completely understood. Brown (1968) noted that one population of woodrats he studied used mostly mesquite as shelter trees and I also found that mesquite trees were heavily used. Since much of the founding literature on the white-throated woodrat has emphasized the importance of cactus (Vorhies and Taylor 1940; Macêdo and Mares 1988; Hoffmeister 1986; Olsen 1976; Brown et al. 1972) the role of mesquite or other plants may have been overlooked. The diet strategy of the white-throated woodrat needs to be more clearly defined. The species is considered a generalist (Sorensen and Dearing 2002) yet it can tolerate oxalic acid and handle spiny cactus parts with ease (Macêdo and Mares 1988). However, this is a habitat related adaptation; similar to the tolerance and skill that is acquired when a woodrat is exposed to a

plant, such as juniper, at an early age. A diet generalist is more susceptible to plant secondary compounds so, unless there are a great variety of plants in the area, this is a difficult strategy because only so much of any one plant can be consumed without experiencing negative side effects (Dearing et al. 2002).

There was great individuality expressed within the population I studied. The best example of this is the woodrat who used a sleeping depression in the grass near her nest. What was the purpose of this and how did she remain safe from predators while she was there? The variety of behavior expressed in this population leads me to believe there is much to be learned about the white-throated woodrat, as well as other species of woodrat. Other members of the genus *Neotoma* show a wide variety of adaptations among individual populations. This is significant because it demonstrates that woodrat populations can effectively, and in some cases dramatically, respond to their environments. It also offers insight into the possible adaptations that *N. albigula* may utilize for survival.

Recommendations for Future Study

The following is a list of future research possibilities that may shed more light on the ecology of the white-throated woodrat.

- Investigate the presence of crickets in woodrat nests. Document and compare burrow and nest conditions in those nests occupied by crickets and those nests without crickets. Measurements should include humidity, burrow

depth, direction/orientation of nest, relationship of burrow and shelter tree root system, etc.

- Survey the crickets in woodrat nests. What species of cricket lives with the woodrat? What are the species' preferred living conditions and lethal limits?
- Determine if crickets are less prevalent in areas with a greater abundance of cactus.
- Compare interior microclimates of white-throated woodrats houses in areas of extreme heat with those living in more moderate conditions.
- Determine the mineral needs of woodrats and how they meet these needs in the wild. Find out if these patterns correlate with the presence of gravel determined by Vorhies and Taylor (1940). If this yields no results, investigate what is causing the presence of gravel in *N. albigula*'s gut.
- Find out if presence of fur in stomach correlates to pelage density or insulation. Do the woodrats thin their own pelage through grooming or is this a physiological characteristic?

CONCLUSION

The white-throated woodrat is a species that is highly adaptive to its environment. Traditionally, the species' relationship with cactus has been emphasized; however, this should be reevaluated in light of my observations. Cactus may not be the only plant that offers *N. albigula* a source of water. Also, *N. albigula*'s adaptations may be underestimated. Woodrats, in general, display a wide array of environment specific adaptations, so this possibility is not

unlikely. Further research on the biology and ecology of *Neotoma albigula* appears to be warranted and generalizations about this species should be used cautiously.

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Table 1—Average white-throated woodrat diet. Recorded over the course of a year by Vorhies and Taylor (1940).

Diet Item	Percent Present in Stomach Contents
Cactaceae (cacti)	43.80
<i>Prosopis</i> spp (mesquite)	30.20
Gramineae (grasses)	4.18
<i>Mullogo verticillata</i> (carpetweed)	2 (estimated from graph)
Mimosaceae (mimosas)	1.5 (estimated from graph)
Unidentified Vegetation	10 (estimated from graph)
All Other plant Matter	7.5 (estimated from graph)
All Animal Foods	0.82

Table 2—Measurements of trees from transect survey.

TRANSECT TREES	Width (cm)	Height (cm)
AVERAGE- AREA 1 n=57 (SD)	175.3 (37.2)	131.6 (24.7)
AVERAGE- AREA 2 n=170 (SD)	152.5 (77.9)	174.2 (58.3)
COMBINED AVERAGE (SD)	163.9 (57.6)	152.9 (41.5)

Table 3—Species composition of transect trees.

Transect Trees	MESQUITE	CATCLAW	ACACIA	MORMON TEA	UNKNOWN
AREA 1	32.14%	0%	55.36%	5.36%	7.14%
AREA 2	6.67%	20.61%	57.58%	13.94%	1.21%

Table 4—Dimensions of woodrat houses.

NEST	Length (cm)	Width (cm)	Height (cm)
AREA 1 n=11 (SD)	155.5 (49.2)	110.5 (35.5)	29.6 (15.0)
AREA 2 n=11 (SD)	177.3 (27.4)	131.8 (39.7)	38.6 (27.1)
COMBINED AVERAGE (SD)	166.3 (41.3)	121.1 (39.1)	34.1 (22.4)

Table 5—Measurements of shelter trees used by woodrats.

Shelter Tree	Width (cm)	Height (cm)
AREA 1 n=11 (SD)	495.5 (139.5)	169.6 (48.9)
AREA 2 n=11 (SD)	363.2 (151.4)	228.2 (53.6)
COMBINED AVERAGE (SD)	429.3 (159.9)	198.9 (59.1)

Table 6—Data gathered at woodrat houses.

Nest Number	Shelter Tree	Occupant trapped	Crickets	Latrine
1	Mesquite	Y	Y	Y
2	Acacia	N	Y	Y
3	Acacia	N	Y	N
4	Acacia	N	N	N
5	Acacia	N	Y	Y
6	Mesquite	N	Y	N
7	Mesquite	Y	N	N
8	Mesquite	Y	Y	N
9	Mesquite	Y	Y	N
10	Mormon tea	Y	Y	Y
11	Acacia (nearest)	Y	Y	N
12	Mesquite	Y	Y	N
13	Mesquite	Y	Y	Y
14	Mesquite	N	Y	N
15	Mesquite	N	N	N
16	Mesquite	N	Y	Y
17	Mesquite	N	N	N
18	Mesquite	Y	Y	N
19	Mesquite	Y	Y	Y
20	Mesquite	N	Y	N
21	Mesquite	Y	Y	N
22	Mesquite	N	N	N



Figure 1—Photograph of vegetation outside of area 2 location. This picture represents the scarcity of cactus in the area. It is one small, lone cactus; clearly not sufficient to support a woodrat population.

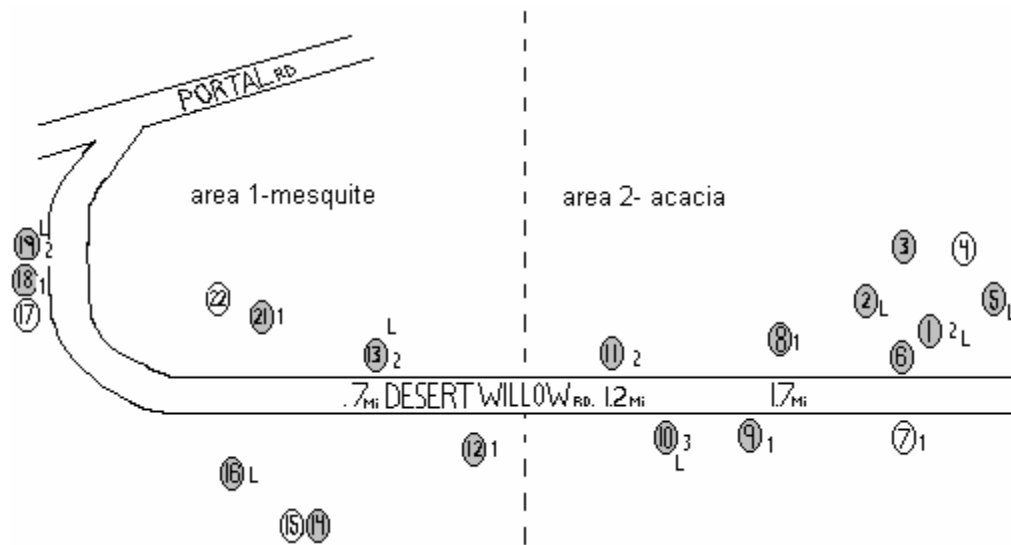


Figure 2—Map of nest locations in relation to one another. Shaded circles represent those nests with crickets present, numbers to the right of the nest represent the number of captures at that nest, and an 'L' represents the presence of a latrine.



Figure 3—Photograph of area 2, which is dominated by *Acacia* spp.



Figure 4—Photograph of a woodrat nest.

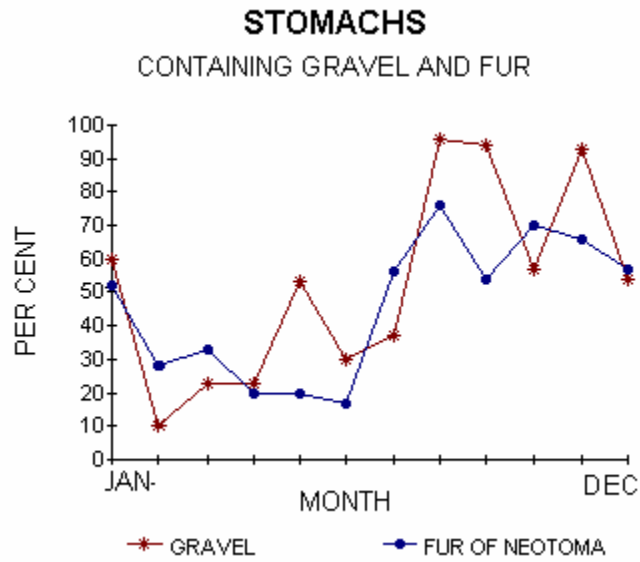


Figure 5—Graph of stomachs containing gravel and fur. Tracking the occurrence of gravel and fur in the stomach of *N. albigula* throughout the course of a year (Reproduced from Vorhies and Taylor 1940).

Appendix I

Nest contents, listed in order of prevalence in each nest.

Nest 1: sticks, grasses (loose, placed together), cow dung, reddish-brown rocks, pinecones, coyote feces, rabbit feces, unidentified feces, cholla, insect carcass.
Comments:

Nest 2: sticks, gray stones, cow dung, pinecones, red piece of plastic (5cmx4cm).

Comments: next to large mesquite, approximately 50 cm from edge of nest is pile of eaten mesquite pods.

Nest 3: sticks, cow dung, pinecones, beer can.

Comments: nest looks a bit collapsed, snakeskin found leading into a burrow opening, signs of clipping on shelter tree.

Nest 4: sticks, rocks.

Comments: looks collapsed, abandoned in/among leafless tree.

Nest 5: sticks, cow dung, rocks, tin can.

Comments: grass growing near an opening, of all collapsed houses this is the worst yet it seems to be active, the shape is almost non-existent and scattered in two, shelter tree bark gnawed, nest to rock wall possible sighting of resident 07:00.



Nest 6: sticks, cow dung, rocks.

Comments: this nest is right next to a large mesquite (410x380 cm).

Nest 7: sticks, rocks, aluminum cans.

Comments: Looks collapsed/abandoned.

Nest 8: sticks, grass.

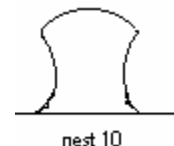
Comments: in mesquite stand (an island of sorts) approximately 10 meters long.

Nest 9: sticks, rocks.

Comments: freshly dug burrow hole approximately 10 cm diameter, shelter tree bark very gnawed.

Nest 10: sticks, cow dung, pinecones, aluminum can, cactus (possibly prickly pear, approx. 10 cm x 10 cm).

Comments: latrine in crevice of a nearby rock, nest looks carved out on both sides, possible small 'shed' across stream, next to dry creek.



Nest 11: sticks, dung, stones, cholla, piece of bone (5 cm x 5 cm).
Comments: Nest on mound with large stones, shelter tree gnawed, nearby trees gnawed, this nest was not built into a tree.

Nest 12: sticks, dung, stones.
Comments: next to dry creek, bark of shelter tree gnawed, shelter tree branches gnawed.

Nest 13: sticks, rocks.
Comments: small branches of shelter tree has very gnawed bark, next to dry creek, nearby acacia gnawed, two latrines.

Nest 14: sticks, dung, small bones, piece of plastic (green and black, flat approx. 6 cm x 7 cm).
Comments:

Nest 15: sticks, rocks.
Comments:

Nest 16: sticks, rocks, grasses, dung, bark.
Comments:

Nest 17: sticks, grasses, beer can.
Comments: looks washed out.

Nest 18: sticks, grasses, rocks, beer can, Styrofoam, tire scrap.
Comments: bark stripped of neighboring mesquite.

Nest 19: sticks, grasses, dung, rabbit skull, thorny sticks, flying insect carcass, coyote feces, paper.
Comments: ephedra also incorporated into nest as shelter.

Nest 20: sticks, grasses, dung, rocks, paper dollars.
Comments: built on old kangaroo rat mound (openings collapsed/unkept).

Nest 21: sticks, rocks, dung, grasses, thorny sticks, packing peanut.
Comments: grass sun porch (130 cm high).



Nest 22: sticks, rocks.
Comments: looks new, very small, on old kangaroo rat mound.

VITA

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Michelle Carlisle received an Associate of Science in Biology, with academic honors, from the College of DuPage in 1996. She received an Associate of Arts in English, from the College of DuPage in 1997. Finally, she earned a Bachelor of Science in Wildlife from the University of Wisconsin- Stevens Point in 2001.

While at the college of DuPage, Michelle held full time jobs, including work as an animal keeper. At the University of Wisconsin-Stevens Point, she held work-study positions. One such position included fulfilling work on raptor research. Since spring of 2002, she has worked for Virginia's Department of Conservation and Recreation at Mason Neck State Park.