

Pack rats (*Neotoma* spp.): Keystone ecological engineers?

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ABSTRACT

The potential role of two species of pack rats (*Neotoma albigula* and *Neotoma micropus*) as keystone ecological engineers was examined by estimating the species diversity of invertebrates living in the nest middens, and nitrogen mineralization rates in soils associated with the middens. Although pack-rat middens in tarbush (*Flourensia cernua*) shrublands were smaller than those in creostebush (*Larrea tridentata*) shrublands, they housed a higher abundance and diversity of arthropods. The *Neotoma* spp. middens were an important microhabitat for crickets (*Gryllus* sp.), wolf spiders (*Lycosa* spp.), and lycid beetle larvae (Lycidae) in all of the shrub habitats. There were five arthropod taxa that occupied all middens in the creosote-bush shrubland, and 12 arthropod taxa that occupied all middens in the tarbush shrubland. Soils associated with pack-rat middens had significantly higher soil organic-matter content than reference soils. Nitrogen mineralization was significantly higher in soils associated with pack-rat middens than in reference soils. *Neotoma* spp. create habitats with moderate microclimates that are essential for several invertebrates, thus contributing to maintenance of biodiversity. The effects of middens on soil organic matter and nitrogen mineralization create nutrient-rich patches. *Neotoma* spp. affect biodiversity and critical ecosystem processes, thus supporting the designation of keystone ecological engineers.

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1. Introduction

Animals that modify the structure and/or function of ecosystems have been described as ecosystem engineers. Ecosystem engineers directly or indirectly affect the availability of resources to other species by changing some biotic and abiotic components of the environment. These changes modify, maintain, or create habitats for ecological engineers themselves or other species (Jones et al., 1994). In arid regions, animals that create soil disturbances have been identified as important ecosystems engineers. Soil modifications by animals include pits which serve as collection areas for seeds and organic debris (Whitford, 1998), soil tunnels and chambers that affect water infiltration (James et al., 2008), and burrows and mounds that affect water infiltration, soil nutrients, abundance, and diversity of plants and soil biota (Eldridge et al., 2009; Ginzburg et al., 2008; Ukabi et al., 2009; Whitford and Kay, 1999; Whitford et al., 2008). Some ecosystem engineers, such as beavers building dams on streams, have pervasive, cascading effects on other organisms and physical/chemical processes that

have earned those species designation as keystone ecosystem engineers (Brown, 1995). Mammals that collect plant parts and other materials to build structures within which the animals reside may be the terrestrial equivalent of beavers and may function as keystone ecosystem engineers.

In North American deserts, several species of rodents, *Neotoma* spp., build houses or middens of sticks plus other plant materials, dried dung, and frequently include shiny man-made objects in their middens (Vaughan, 1990). This behavior has earned members of this genus the common name pack rats. *Neotoma* spp. are widely distributed in North American deserts and the nest midden structures have been shown to vary considerably depending upon the availability of suitable shelter of rock or vegetation for the location of the nests. Two pack-rat species inhabit the Chihuahuan Desert areas of southern New Mexico: the white-throated woodrat, *Neotoma albigula*, and the plains woodrat, *Neotoma micropus*. *N. albigula* has expanded its range from the rocky slopes of mountains and rocky drainages into the desert grasslands, which are the historical habitats of *N. micropus*, and into the shrub-dominated plant communities that have replaced desert grasslands over the past one and a half centuries (Wright, 1973; Whitford, 1976). *N. micropus* continues to occupy some of the shrublands that were grasslands in the past (Whitford and Steinberger, 1989). *N. micropus* middens in shrubland habitats are similar to those of

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N. albigula, and are different from *N. micropus* nest structures in plains grassland habitats. The species composition and life form of the dominant vegetation constrain the materials that are available to pack rats for midden construction. In this study, the density and structural materials of pack-rat middens were estimated in several vegetation communities on two shrub-dominated watersheds.

The stick nests of *Neotoma* spp. are similar to those of the Stick-nest rats (*Leporillus* spp.) of Australia (Copley, 1999; Nelson et al., 1990) and nests of three Southern African rodents (*Acomys spinosissimus*, *Thallomys nigricauda*, and *Athomys namaquensis*) (Skinner and Smithers, 1990). It is plausible that the stick nests of rodents in other deserts would have similar effects on the structure and function of the ecosystems in which they occur. The stick nests of *Neotoma* spp. have been reported as an essential habitat for pseudoscorpions (Francke and Villegas-Guzman, 2006) but there are no records of other arthropod inhabitants of pack-rat middens. Desert pack-rat middens have been reported to provide a moderate thermal environment that may make the stick nests a desirable habitat for other animals (Thies et al., 1996). If pack-rat houses provide a moderate thermal environment, they may also moderate the relative humidity of the midden interior. If pack-rat middens do provide moderate microclimates in environments characterized by high temperatures and low relative humidity, *Neotoma* spp. houses would represent the activities of an ecosystem engineer that help maintain or enhance biodiversity. One part of this study was designed to test this hypothesis.

Since pack-rat middens are occupied by successive generations that add materials to the middens, the immediate surroundings of the middens should be fertilized by the feces and urine of the occupants. We measured rates of nitrogen mineralization in soils adjacent to middens in comparison to reference sites as a test of this hypothesis.

2. Methods

2.1. Site description

Studies were conducted on two watersheds of the Doña Ana Mountains located at the Chihuahuan Desert Rangeland Research Center and the USDA-ARS Jornada Experimental Range approximately 40 km NNE of Las Cruces, NM. The watersheds are composed of several plant communities occupying different topographic positions. The plant community of the montane toe slopes is a black-grama (*Bouteloua eriopoda*), Lehmann's love grass (*Eragrostis lehmanniana*) grassland with abundant large platyopuntia, (*Opuntia phaeacantha*). The piedmont (bajada) below the toe-slope grassland is dominated by creosote-bush (*Larrea tridentata*) on sandy or sand-gravel soils. The piedmont is dissected by numerous small drainage channels, the margins of which support fairly large multi-stemmed mesquite (*Prosopis glandulosa*), large patches of banana yucca (*Yucca baccata*), and apache plume (*Fallugia paradoxa*). One of the watersheds drains into a small ephemeral lake with a 30-m-wide dense thicket of mesquite along the lake margin. The other watershed has a mixed shrub community of creosote-bush and tarbush (*Flourensia cernua*) on the lower slopes of the piedmont. The mixed shrub community merges into tarbush shrubland on the lowest slopes of the watershed.

2.2. Midden densities

Pack-rat midden densities were estimated on 10 plots of 50 m × 100 m established along 1-km transects in each of three major shrub habitats on the watersheds: creosote-bush shrubland, tarbush shrubland, and mesquite fringe of the lake basin. The 1-km transects were established with 21 numbered stakes spaced at 50-

m intervals. Plots were selected on the right or left of the center line by coin toss and the 50 m × 100 m plots flagged. Pack-rat middens were identified by systematic surveys of each plot. The intensive surveys provided absolute numbers of pack-rat middens in each 0.5 ha plot.

Shrub cover and composition were estimated for each plot by the line intercept method. Thirty-meter lines were stretched from three randomly selected meter points on a tape stretched between the center line stakes.

2.3. Size and structure of middens

The size of nine middens, selected at random, in each plant community was determined by measuring two diameters of the midden and the height above the soil surface of the nest mound. The volume of each midden was calculated as one half the volume of a prolate spheroid. The materials incorporated into the structure of middens in the toe-slope grassland and tarbush shrubland were sampled by dismantling the structure, sorting the materials into general classes, i.e., sticks, grass, leaves, dung, *Opuntia* spp. cladodes, and unidentifiable objects. The mass of materials in a midden was measured using a large capacity scale on nine middens in the tarbush shrubland, creosote-bush shrubland, and the toe-slope grassland, and two middens in the playa mesquite fringe. Only two middens were dismantled in the playa mesquite fringe in order to minimize the effect on other on-going studies in that area. Before the middens were dismantled, 20 sticks were removed from the surface layer and the mid-length diameter was measured with calipers. When half of the original height of the midden was reached, 20 sticks were removed from that layer and the mid-length diameter measured.

2.4. Midden microclimate and soil

Air relative humidity and temperature were measured in five middens on the creosote-bush bajada, five middens in the tarbush community, and two middens in the playa fringe mesquite over a two-week period in mid-October. After the outer midden material was removed, the relative humidity and temperature of the inner nest were measured with a digital hygrometer and thermometer, respectively. Ambient air temperature and relative humidity were measured in the shade at 15 cm above the soil surface. The diurnal pattern of humidity and temperature in intact middens was measured in early September with a digital hygrometer and thermometer, respectively.

Percentage of soil organic matter was measured in soil cores (0–5-cm and 5–10-cm depths) taken from the middle of seven dismantled pack-rat middens on the creosote-bush piedmont. Reference cores were taken at a distance of 3 m from each midden on a random compass heading. Soil cores were dried to a constant weight and placed in a muffle furnace at 300 °C for 24–36 h.

2.5. Nitrogen mineralization

Nitrogen mineralization rates were measured by anion and cation exchange resin bags placed at the margins of pack-rat middens and reference areas equal to the area of the middens. Seven woodrat middens were randomly selected using a random number table to numbers previously assigned to 38 middens in toe-slope grassland and the upper creosote-bush piedmont. A reference area equal to the diameter of the midden was obtained by finding an *Opuntia* spp. or *Yucca baccata* at half the average distance between pack-rat nests (16.4 m). Resin bags were placed in each cardinal direction at the edges of the pack-rat middens and the reference "midden". The resin bags were placed in holes at a 10-cm

depth and covered with the soil removed in the excavation. Resin bags were left in the field for different time periods and new sets of bags were installed in the middle of the summer monsoon season in order to measure maximum mineralization rates.

Resin bags were constructed of relatively hydrophilic, unbleached, tubular nylon stocking material obtained from L'eggs Products Inc. (Mesilla Park, NM). Eight grams of Dowex 1-X8 anion exchange resin was placed in 12-cm lengths of stocking material and sewn closed at both ends, providing bags of 50 cm² area. Anion bags were charged by three successive washes of 0.5 M NaHCO₃ (Lajtha, 1988). Excess water was removed by centrifuging in a salad spinner. The charged resin bags were refrigerated at 3–5 °C until use.

Collected resin bags were rinsed with deionized water to remove adhering soil, and the excess water was removed by gentle centrifuging. Ions were extracted by submerging the intact bags in 100 ml 2.0 M KCl overnight, followed by filtration through Whatman no. 42 paper. Resin collected in filters was oven-dried (50 °C) and weighed. NO₃ + NO₂-N were measured by an automated Cd reduction procedure (Henriksen and Selmer-Olsen, 1970).

The data were analyzed by analysis of variance, and differences among means were examined by Duncan's multiple range test (Kirk, 1968).

2.6. Arthropod fauna of middens

Five middens were sampled in the tarbush and creosote-bush areas and only two middens were sampled in the playa fringe habitat. Middens were selected to represent the range of sizes characteristic of the vegetation community because of two other studies being conducted in that area. An 80-cm sheet metal barrier buried to a depth of 20 cm was erected around each midden prior to the initiation of the deconstruction of the midden. Arthropods were collected as they emerged during the dismantling of the middens. All invertebrates collected were placed in 70% ethanol and returned to the laboratory for identification. Resident pack rats were able to scramble over the barrier and were not captured.

3. Results

3.1. Midden densities

The highest density of *Neotoma* spp. middens was in the creosote-bush bajada habitat, where most of the nests were within large *Yucca baccata* patches or large *Opuntia phaeacantha* patches at the edges of small drainage channels (Table 1). The lowest abundance of *Neotoma middens* was in the tarbush shrubland and playa fringe mesquite communities.

3.2. Size and structure of middens

The size distribution of *Neotoma* spp. middens varied significantly among the plant communities in which they occurred. *Neotoma* spp. middens in the creosote-bush shrubland were significantly larger than the middens in the tarbush shrubland and

toe-slope grassland ($F_{3,32} = 15.74, p < 0.0001$) (Table 2). The average mass of wood and other materials in the middens was higher in the playa fringe mesquite habitat and the creosote-bush shrubland than in the toe-slope grassland and tarbush shrubland ($F_{2,24} = 44.7, p < 0.0001$).

The materials in the middens represented the materials available within a 50-m radius of the midden site. Seven of the nine middens in the toe-slope grassland were built within large clumps of the platyopuntia, *Opuntia phaeacantha*, which accounted for between 30% and 50% of the mass of materials in those structures. Other woody species (*Ephedra trifurca*, *Gutierrezia sarothrae*, *Yucca elata*, and *Larrea tridentata*) plus unidentifiable sticks accounted for most of the remaining mass of materials in the nest structure in the toe-slope grassland. In the tarbush shrubland, no plant species were represented in all of the middens sampled, and stems of several species accounted for more than half of the mass of materials in the nest structures of different nests (tarbush, *Flourensia cernua*, crucifixion thorn, *Koerberlinia spinosa*, wolfberry, *Lycium pallidum*, and pencil cholla, *Opuntia leptocaulis*). The three largest middens in the tarbush shrubland were under large *K. spinosa* and the smaller middens were located in old badger, *Taxidea taxus*, excavations. The middens in the creosote-bush shrubland were located at the edges of small washes under mesquite (*P. glandulosa*) shrubs or within large patches of banana yucca, *Yucca baccata* or platyopuntias (*Opuntia* spp.). These middens were constructed primarily of stems and branches of *L. tridentata*, *P. glandulosa*, *G. sarothrae*, and desert willow, *Chilopsis linearis*. The average diameter of sticks from the external layer of middens was nearly twice that of sticks from the layer at mid-height ($F_{5,30} = 11.48, p < 0.0001$) (Fig. 1).

3.3. Midden microclimate and soils

In early September, when air temperatures reached a maximum of 37 °C, the difference between the relative humidity in the nest interior (approximately 20 cm below the surface of the midden) and the external air relative humidity values ranged from 0 to 28% and the temperature of the nest interior ranged from –1 °C below the ambient air temperature in the morning to –10 °C by late afternoon (Fig. 2). In mid-October, when maximum ambient temperature remained below 30 °C, the average relative humidity of the interior of the middens was significantly higher than the external ambient humidity ($F_{1,22} = 8.03, p < 0.05$). The interior relative humidity was 15.3 ± 10.4% higher than that of the external ambient air. However there were no significant differences in nest interiors and external air temperatures (Fig. 2). The interior air temperature of eight of the 12 nest middens measured was an average 0.9 ± 0.3 °C higher than the ambient temperature, and in four nest middens the interior temperature was an average of 0.9 ± 0.3 °C lower than the ambient air temperatures.

The percentage of organic matter of soils collected from below the middens (0–5 cm: 2.47 ± 0.63, 5–10 cm: 1.85 ± 0.57) was

Table 1

Percentage of cover ± standard deviation of the dominant shrub or grass; total shrub or grass cover and average number of *Neotoma* spp. middens ha⁻¹ in four plant communities on Chihuahuan Desert watersheds.

Plant community	Dominant	Total cover	Middens ha ⁻¹
Creosote-bush bajada	19.2 ± 11.8	25.7 ± 10.8	7.2 ± 4.8
Tarbush shrubland	15.8 ± 6.9	18.6 ± 8.8	2.0 ± 2.6
Playa fringe mesquite	14.6 ± 5.3	21.1 ± 4.0	24.8 ± 18.9
Toe-slope grassland	12.6 ± 10.6	20.2 ± 15.3	6.6 ± 2.6

Table 2

The average diameter, height, volume and mass ± standard deviation of *Neotoma* spp. middens in four plant communities on Chihuahuan Desert watersheds. Numbers followed by the same letter are not significantly different.

Plant community	Diameter (cm)	Height (cm)	Volume (m ³)	Mass kg
Creosote-bush shrubland	97.3 ± 21.5a	63.3 ± 18.7a	0.99 ± 0.57a	22.0 ± 7.3a
Tarbush shrubland	73.7 ± 43.5b	20.3 ± 6.9b	0.08 ± 0.09b	5.1 ± 1.6b
Playa fringe mesquite	100.0 ± 10.3a	56.7 ± 5.6a	0.68 ± 0.14a	30.8 ± 8.1
Toe-slope grassland	73.3 ± 24.4b	32.8 ± 10.9b	0.20 ± 0.18b	4.9 ± 1.3b

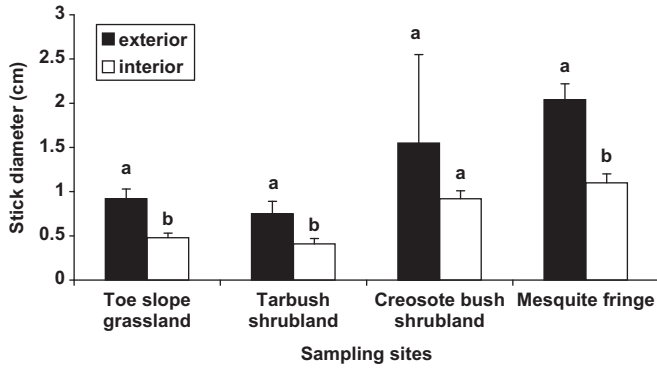


Fig. 1. Comparison of stick diameters from the exterior of *Neotoma* spp. middens compared with stick diameters from the middle of the middens in four different pack-rat habitats.

significantly higher than that of soils collected in reference areas 3 m from middens (0–5 cm: 0.92 ± 0.37 , 5–10 cm: 0.92 ± 0.56) ($F_{3,24} = 13.5$, $p < 0.0001$). The pattern was similar for two middens from the playa fringe area (average percent of organic matter in the upper 10 cm was 2.52) compared to the average percent of organic matter in the upper 10 cm of reference soils (1.01).

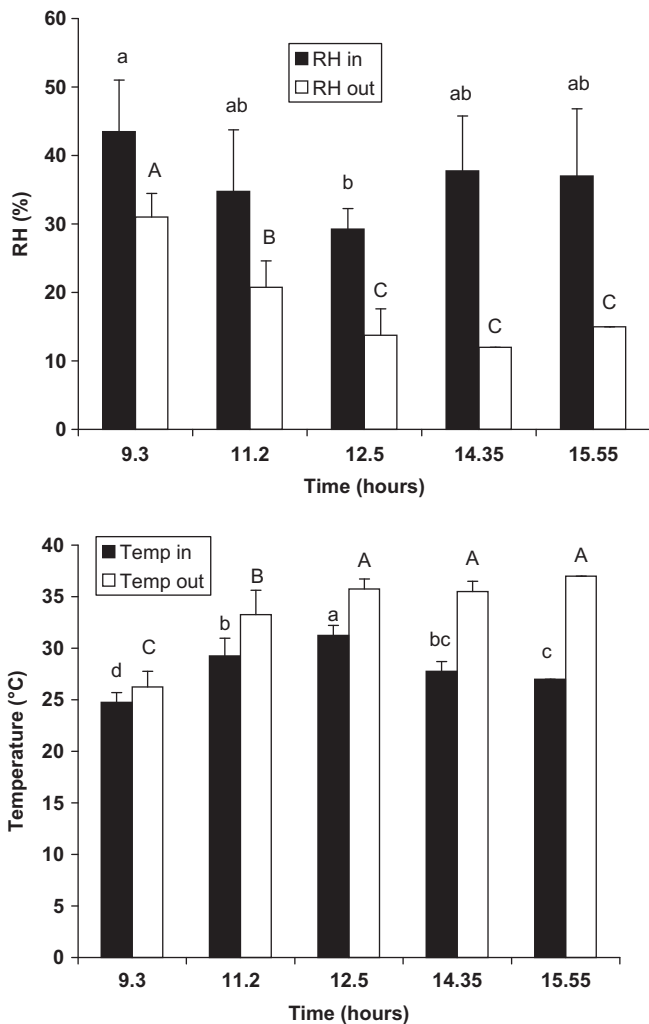


Fig. 2. Temporal pattern of temperature and relative humidity within the interior of *Neotoma* spp. middens and in the shade outside the middens at 15 cm above the soil surface.

3.4. Nitrogen mineralization

Nitrogen mineralization to nitrate was higher in the soils from the margins of pack-rat middens than in reference soils in both the eight- and four-week incubations (Fig. 3). From January 1 – July 25, there were seven rainfall events > 5 mm that produced a total of 50.3 mm, of which 26.7 mm occurred in 5 events in July. During that period, there were 13 events smaller than 5 mm that produced a total of 26.1 mm.

3.5. Arthropod fauna of middens

Pack-rat middens provided refuge microhabitat for more than 40 arthropod taxa (Table 3). Although the taxonomic richness of the arthropods inhabiting the *Neotoma* spp. nests in the tarbush community was lower than that in the creosote-bush community, the diversity index of arthropods in middens in the tarbush area was higher than that in the creosote-bush area. If taxa that were recovered from less than 4 of the 5 middens sampled are considered occasional or opportunistic residents of *Neotoma* spp. nests, there were fewer obligate resident taxa (5 taxa) in middens in the creosote-bush habitat than in pack-rat nests (12 taxa) in the tarbush area. The *Neotoma* spp. middens were an important microhabitat for crickets (*Gryllus* sp.), wolf spiders (*Lycosa* spp), and lycid beetle larvae (Lycidae) in all of the shrub habitats (Table 3). More arthropods (479) were captured from the pack-rat middens in the tarbush area than in the creosote-bush area (338 arthropods). Although middens in the tarbush shrubland were significantly smaller than those in the creosote-bush shrubland (Table 3), middens in the tarbush area provided habitat for more individuals and for more taxa that appeared to be obligate residents than middens in the creosote-bush shrubland.

4. Discussion

Support for designating *Neotoma* spp. keystone ecosystem engineers in arid ecosystems is provided by their effect on biodiversity in providing refuge habitat for numerous arthropod taxa, by the effects of their middens on nitrogen mineralization in soils surrounding their middens, and by the cascading effects on ecosystem structure and processes by the pack rats and their houses. The elevated humidity and temperature moderation of the midden interior provide a moderate microclimate for many invertebrates and some vertebrates. Vertebrates that have been reported to utilize pack-rat middens include: ornate box turtle, *Terrapene ornata*, the side-blotch lizard, *Uta stansburiana*, gopher snake, *Pituophis melanoleucus*, the cactus mouse, *Peromyscus eremicus*, and deer mouse, *Peromyscus maniculatus* (Vaughan, 1990). These vertebrates are common in the vegetation communities included in

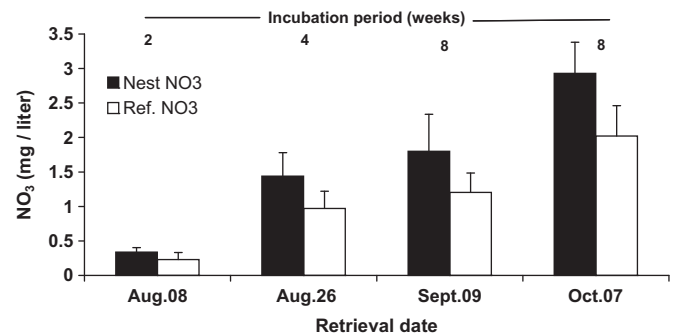


Fig. 3. Nitrate concentration in anion exchange resin bags from the margins of *Neotoma* spp. middens and from reference soils 3 meter from the margin of the midden.

Table 3

Arthropods captured from five dismantled *Neotoma* spp. middens in the creosote-bush community (Latr), five dismantled middens in the tarbush community (Ffce) and two middens in the ephemeral lake margin community (Pla). No = total number of individuals of a taxon, NoM = number of middens in which that taxon occurred.

Taxon	Latr No	Latr NoM	Ffce No	Ffce NoM	Pla No	Pla NoM
Insecta						
Hemiptera						
Cydnidae	20	4	0	0	0	0
Reduviidae	11	3	1	1	2	1
Other Hemiptera	3	3	8	5	0	0
Diptera						
Stratiomyidae (larvae)	35	4	3	2	1	1
Coleoptera						
Alleculidae	1	1				
Carabidae	6	3	10	3	2	1
Chrysomelidae	2	1	4	1	0	0
Cleridae	1	1	0	0	0	0
Curculionidae	1	1	10	4	1	1
Curculionidae <i>Peritaxia hispidahom</i>	6	3	0	0	0	0
Elateridae	0	0	7	3	2	1
Histeridae	2	2				
Lycidae (larvae)	27	5	9	5	2	1
Meloidae, <i>Epicauta</i> spp.	1	1	1	1	1	1
Scarabaeidae	33	4	16	2	0	0
Scarabaeidae, <i>Canthon</i> spp.	11	3	0	0	0	0
Tenebrionidae	5	3	17	5	0	0
Tenebrionidae, <i>Eusattus</i> sp.	0	0	7	2	0	0
Tenebrionidae, <i>Eleotes</i> sp. (larvae)	7	3	7	3	4	2
Tenebrionidae, <i>Trioyophus</i> sp.	6	3	0	0	0	0
Orthoptera						
Gryllidae, <i>Gryllus</i> sp.	39	4	11	4	15	2
Mogoplistinae, <i>Cycloptilum</i> sp.	7	1	22	4	9	2
Mogoplistinae, <i>Hoplophyrum</i> sp.	4	2	86	5	9	2
Mogoplistinae, Gryllacrididae <i>Ceuthophilus pallidus</i>	5	1	47	5	0	0
Mantidae	0	0	6	5	0	0
Polyphagidae <i>Eremoblatta subdiaphana</i>	7	3	23	4	10	2
Araneae						
Agelenidae	1	1	11	5	3	2
Agelenidae, <i>Agelenopsis aparata</i>	1	1				
Clubionidae, <i>Castianeira</i> sp.	0	0	2	2	0	0
Dictynidae	3	2	3	2	2	2
Erembatidae	2	2	0	0	0	0
Gnaphosidae	5	2	34	5	7	2
Gnaphosidae, <i>Casonia sincera</i>	0	0	4	3	0	0
Gnaphosidae, <i>Drassodes</i> sp.	0	0	16	2	2	1
Gnaphosidae, <i>Herpyllus propinus</i>	0	0	0	0	1	1
Gnaphosidae, <i>Zelotes lasalanus</i>	2	2	1	1	0	0
Gnaphosidae, <i>Zelotes tuobus</i>	0	0	4	2	1	1
Lycosidae, <i>Lycosa</i> sp.	1	1	1	1	0	0
Lycosidae, <i>Paradosa</i> sp.	27	4	22	5	7	1
Oxyopidae, <i>Oxyopes tridens</i>	4	2	2	2	0	0
Phalangiidae	4	3	0	0	0	0
Philodromidae, <i>Apollophanes</i> sp.	1	1	0	0	2	1
Pholcidae, <i>Psilochorus</i> sp.	4	2	8	2	8	2
Salticidae, <i>Habronattus conjunctus</i>	4	2	1	1	1	1
Salticidae, <i>Habronattus</i> sp.	4	2	6	5	8	2
Theridiidae, <i>Latrodectus hespens</i>	4	3	5	2	0	0
Thomisidae, <i>Xysticus</i> sp.	5	3	1	1	0	0
Microcorphis						
Machilidae	0	0	13	3	0	0
Thysanura	2	2	0	0	0	0
Lepidotrichidae	1	1	3	2	0	0
Lepismatidae	7	3	0	0	1	1
Pseudoscorpiones						
<i>Larca granulato</i>	10	3	0	0	0	0
Scorpiones						
	6	3	3	2	3	2
Uropygi						
<i>Mastigoproctus gigantus</i>	0	0	2	1	0	0
Scolopendromorpha						
	0	0	24	3	2	1
Taxonomic richness	44		40		25	
Diversity index H'	2.54		3.10		2.78	

this study (Whitford, 1976; Peterson and Whitford, 1987; Whitford and Steinberger, 1989). The middens provide a protective shelter for the nests that are constructed of shredded bark, grass, and *Yucca* spp. leaf fibers. The nests provide habitat for many species of microarthropods that were not captured by the methods used in this study. Nests of *Neotoma* spp. have been reported to harbor many species of oribatid and prostigmatid mites, psocopterans, collembolans and termites (Cudmore, 1986; Zak and Whitford, 1988).

Neotoma spp. not only contribute to the biodiversity of the ecosystems in which they build houses, they contribute to that biodiversity by serving as dispersal agents for taxa that utilize the midden microhabitat. The more than thirty species of pseudoscorpions that coexist with pack rats are considered phoretic on *Neotoma* spp. (Francke and Villegas-Guzman, 2006). Phoresy is passive dispersal that occurs when one species hitches a ride on another to reach a new habitat. Thus *Neotoma* spp. not only build structures that provide habitat for pseudoscorpions, young rats carry pseudoscorpions from their natal midden to a new nest. *Neotoma* spp. middens are also reported to provide mesic microhabitats favorable for fungal growth in xeric environments. Pack rats may be responsible for dispersing the basidiomycete, *Marasmius inaquosi*, to the suitable microhabitat of the midden (Desjardin et al., 1992).

Neotoma albigula has been reported to have an indirect effect on mule deer, *Odocoileus hemionus*, by stripping bark from skunkbrush, *Rhus trilobata*, thereby controlling the spread of this shrub, which reduces the abundance of shrub species that are browsed by deer (Hanson and McCulloch, 1955). We have observed bark stripping by *Neotoma* spp. on multi-stem mesquite, *Prosopis glandulosa*, which has resulted in the mortality of many of the stems (unpublished data). It is possible that the stem mortality reduces the vigor of the shrub and competitive advantage of the shrubs with the perennial grasses. The behavior of pack rats requires further investigation to document the indirect effects of these animals on ecosystem properties and processes.

Higher nitrogen mineralization in soils at the margins of pack-rat middens is attributed to the higher soil organic-matter content of midden-influenced soils relative to reference soils. Total soil nitrogen and mineral nitrogen have been found to be proportional to the soil organic-matter concentration in a variety of Chihuahuan Desert ecosystems (Whitford et al., 1987). Total soil nitrogen was reported to be significantly higher in pack-rat middens ($1334 \pm 835 \text{ mg kg}^{-1}$ of soil) than in reference soils ($537 \pm 67 \text{ mg kg}^{-1}$ of soil) as was the percentage of soil organic matter (Zak and Whitford, 1988). The increase in soil organic matter in pack-rat midden soils develops from the slow decomposition of sticks and other materials from which the middens were constructed and the deposition of fecal pellets at the edges of the nests near the multiple entrances. The smaller-diameter stems at mid-level in the middens provide an indirect measure of the decomposition of those items. Subterranean termites build foraging galleries on the upper- and mid-level woody structural materials in the middens and are responsible for the removal of most of the material from the midden wood. Termite galleries have higher nitrogen content than the soils in the environment (Whitford, 1991).

The differences in densities of pack-rat middens and size distribution of those middens are attributed to the structure of the ecosystems in which they occur. Pack rats have been shown to be habitat-limited (Brown et al., 1972; Cameron and Rainey, 1972; Whitford, 1976). The low density and small size of *Neotoma* spp. middens in the tarbush area is attributed to the sparse distribution of suitable habitats. In the tarbush shrubland, the shrubs that provided suitable habitat for pack-rat middens were large (>2 m height) crucifixion thorn, *Koeberlinia spinosa*, which occur at a density of less than one per hectare. The density of pack-rat

middens in the toe-slope grassland is directly related to the abundance of large patches (1.5–3.0 m long dimension) of the platyopuntia, *O. phaeacantha*, which was the preferred habitat for *Neotoma* spp. The abundance of ephemeral stream channels lined with large mesquite, cacti, and *Y. baccata* provided suitable habitat for the numerous pack-rat middens in creosote-bush shrubland (Ellison and van Riper, 1998). The large (>2 m height and canopy diameter) mesquite on the margins of the playa lake provided ideal habitat for *Neotoma* spp.

The size of *Neotoma* spp. houses appears to be related to the availability of suitable construction materials within a 50 m radius of the nest (Vaughan, 1990). Woody debris is scarce, and the only cactus in tarbush shrublands is *O. leptocaulis*, which occurs at less than ten plants per hectare. The largest middens in tarbush shrublands were under the tall crucifixion thorn, *K. spinosa*, and more than half of the material in these middens was stems of *K. spinosa* that had been cut-off by the resident rats. Shrubs are sparse in the toe-slope grasslands (<30 shrubs per hectare). The grassland shrubs, primarily *L. tridentata* and *E. trifurca*, are pruned by rabbits during the dry winters and this is the primary source of woody debris available to pack rats for midden construction (Steinberger and Whitford, 1983). Creosote-bush (average 1206 kg ha⁻¹) and mesquite (7187 kg ha⁻¹) shrublands have large quantities of dead wood available and that has resulted in the large middens in these habitats (Zak and Whitford, 1988). Much of this woody debris is creosote-bush stems pruned by jackrabbits (*L. californicus*) and mesquite stems pruned by stem girdler beetles, *Oncideres* spp. (Duval and Whitford, 2008).

The higher humidity and moderate temperatures in the center of pack-rat middens provide an environment that enhances the growth of wood-decomposing fungi (Zak and Whitford, 1988). Stem surfaces that have been partially decomposed are the only wood removed by termites (Mackay et al., 1985). Termites remove less than 0.5 mm of material from stems that are either standing dead within shrub canopies or on the soil surface but consume a larger amount of the partially decomposed material from stems in the interior of pack-rat middens (Zak and Whitford, 1988). Accelerated decomposition of wood in the interior of middens represents another important ecosystem process that is modified by *Neotoma* spp.

The construction of mounds of dried plant materials that provide protection from predators and moderate interior climates is a characteristic known to be shared by rodent species in other arid regions of the world (Copley, 1999; Skinner and Smithers, 1990). It is probable that structures built by other murid rodents in arid regions provide refuge microhabitats for other vertebrates and for many invertebrates. The accumulation of plant debris into the mound structures provides the carbon inputs for increased soil organic matter and, subsequently, increased nitrogen content. Because of the potential similarity in effects on ecosystem structure and processes and on biodiversity, it would be valuable to examine these rodents and their houses in order to test their status as keystone ecosystem engineers.

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