CEC California Ecology and Conservation Research
Natural Reserve System UNIVERSITY OF CALIFORNIA

Evidence of niche partitioning among small mammals in the Eastern Mojave Desert from scat distribution

Jacob Ferrall[1], Lucy Malamud-Roam[2], Roxana Ramirez[3], Zishi Wu[4]

[1]University of California, San Diego; [2]University of California, Santa Cruz;
[3]University of California, Riverside; [4]University of California, Davis

Species that occupy similar ecological niches rely on niche partitioning to avoid direct competition. Our study aimed to detect niche partitioning between four abundant small mammal species residing in the Eastern Mojave Desert. By varying resource usage over space and time, the desert cottontail (*Sylvilagus audubonii*), the blacktailed jackrabbit (*Lepus californicus*), the desert woodrat (*Neotoma lepida)*, and the white-tailed antelope squirrel (*Ammospermophilus leucurus*) are able to coexist along the mountains' ridge. We investigated their niche partitioning through a scat distribution survey. We found evidence for spatial niche partitioning between jackrabbits and squirrels, and temporal niche partitioning between woodrats and cottontails. Jackrabbits and squirrels never defecated near each other, indicating a spatial difference. Cottontails scat piles increased in abundance around larger middens and were most often in closest proximity to that of woodrats, sometimes in latrines, revealing that they share the same area but avoid direct competition through temporal niche partitioning. Our study supplements understanding of how small desert mammals subsist with each other given limited resources.

Keywords: niche partitioning, small mammals, latrines, middens, scat distribution

INTRODUCTION

An ecological niche refers to a species' position in the ecosystem (Schoenherr 1992). The term encompasses all the interactions between a species and the biotic and abiotic factors that affect it. Ecological and evolutionary theory dictates that only one species can occupy an ecological niche at a time. The coexistence of two species in the same habitat is obtained through niche partitioning, the differentiating of niches and resource use so that one species does not out-compete the other. Two of the main types of niche partitioning are spatial partitioning, in which organisms occupy different spaces in the same habitat, and temporal partitioning, in which multiple species rely on the same resources but their niches are separated by the time that they are active (Albrecht 2001). Spatial niche partitioning is exemplified when closely related bird species occupy different heights on the same tree (Lara et al. 2015). Temporal niche partitioning is exemplified by owls and hawks, both of which rely on similar resources, but hunt at different times of day (Richard and Meslow, 1984). Temporal niche partitioning is common in habitats occupied by both diurnal and nocturnal species.

Niche partitioning is particularly important when the environment is harsh and resources are scarce, such as in desert ecosystems (Schoenherr 1992). A diverse array of flora and fauna compete to survive in the resource-scarce uplands of the Eastern Mojave, including many species of small mammal, who forage amongst its shrubs and cacti. The desert woodrat (*Neotoma lepida*) (henceforth "woodrat") shares a habitat with the desert cottontail (*Sylvilagus audubonii*) (henceforth "cottontail"), the black-tailed jackrabbit (*Lepus californicus*) (henceforth "jackrabbit"), and the white-tailed antelope squirrel (*Ammospermophilus leucurus*) (henceforth "squirrel") (Burt 1980). These four species occupy a similar ecological niche with overlapping diets. The woodrat's diet consists of cholla cacti (*Cylindropuntia* spp.), Mojave yucca (*Yucca schidigera*), seeds, nuts, and any available green vegetation (Burt 1980). Cottontails mostly feed on grasses but also feed on the leaves and peas of mesquite (*Prosopis* spp.), barks, fallen fruit, and twigs of shrubs (Turkowski 1975). Jackrabbits are known to forage on herbaceous vegetation such as grasses and forbs during the spring and summer, but switch to the buds, bark, and leaves of woody plants in the fall and winter (Foresman 2012). White-tailed antelope squirrels eat mostly fruit, seeds, plants, and insects (Bradley 1968). Some squirrels plant foraging preferences include Mojave yucca (*Yucca schidigera*), blackbrush (*Coleogyne ramosissima*) and catclaw acacia (*Acacia greggii*).

In this study, we assessed if woodrats, cottontails, jackrabbits, and squirrels exhibit niche partitioning to avoid direct competition for space and resources. It was difficult to directly observe animal behavior since they are easily alerted to human presence and are active at different times of the day, so we used scat and nests as indicators of animal activity. Scat sampling has been widely used for diet analysis or population estimation in carnivores and rodents, and the place of defecation effectively reflects the active area of the animals (Garrote 2014). Therefore, we used the proximity of scat piles between species to show how associated the species are. For nesting evidence, the burrows of cottontails, jackrabbits, and squirrels were hard to distinguish, but woodrats create conspicuous nests or middens out of various plant debris between rocks and under plants. In the American Southwest region, woodrats construct their middens beneath yuccas (*Yucca* spp.) and other shrubs, covering them in the spines of cholla (*Cylindropuntia* spp.) for protection (Schoenherr 1992). In addition, woodrats are territorial with a small range, and they mostly forage within 10 meters from their middens (Jameson 2004), making middens a good marker of woodrat activity. Few studies have been conducted on how woodrat middens impact the activities of other small mammals in their proximity.

We were also interested in woodrat middens because woodrats deposit scent marks around their middens to indicate territory ownership. The places where scat accumulated from repeated defecation and urination are called latrines (Kays 2002). The strong odor of latinres can mark territory, communicate sex differences to potential mates of the same species, or communicate with other species in the same environment (Hirsch et al. 2014). Many animals behave correspondingly to scent marks to either track prey or avoid predators and competitors (Arakawa 2008). Research has shown that subordinate mice species avoid the scentmark of dominant mice species to lessen intraspecific competition. Therefore, understanding how different small mammals adjust their behavior near a midden or latrine could further our knowledge of spatial niche partitioning and how coexistence in a desert ecosystem is balanced over time. We examined the scat density of small mammals around middens to evaluate if the presence of middens has an effect on the activities of non-woodrat species.

We predicted that larger woodrat middens would have more fresh woodrat scat under them, signifying more woodrat activity, and therefore the surrounding niche would be dominated by woodrats. We speculated that larger middens would have fewer scat piles of non-woodrat species around them because middens may act as a territorial marker for the woodrats (Arakawa 2008). We predicted that woodrat and cottontail scat piles would be nearer to each other than to jackrabbit or squirrel scat piles. A previous study in Idaho found only Nuttall cottontail (*Sylvilagus nuttallii*) activities around bushy-tailed woodrat (*Neotoma cinerea*) middens, despite there being three rabbit species, including jackrabbits, living in the area (Johnson and Hansen 1979). Squirrels' ability to climb trees could mean their diet often extends to the seeds of pinyon pines, which grow on elevated terrain (Bradley 1968). The difference in feeding preference may separate the location of squirrels from the rest of the species. We also hypothesized that the scat of woodrats and cottontails would most frequently be found beneath plant cover, so they can hide from predators as they defecate (Foresman 2012). Meanwhile, we expected to see the majority of jackrabbit scat in the open, as jackrabbits are too large to fit beneath most desert shrubs.

METHODS

2.1 Study System.

The study was conducted in the Eastern Mojave Desert at the Sweeney Granite Mountains Desert Research Center (34°48'N 115°37'W) (henceforth "the Granite Mountains") in February 2021. A few plant communities are characteristic of the range; single-leaf pinyon pines (*Pinus monophylla*) (henceforth "pinyons") and California junipers (*Juniperus californica*) (henceforth "junipers") speckle the mountains' ridge, and the descending wash hosts an array of desert scrub species. The flatlands surrounding the wash host an abundance of Mojave yucca (*Yucca schidigera*), creosote bush (*Larrea tridentata*), buckhorn cholla (*Cylindropuntia acanthocarpa*), and honey mesquite (*Prosopis glandulosa*). Desert woodrats (*Neotoma lepida*) are a common inhabitant of the pinyon-juniper-covered hillsides of the Eastern Mojave. They obtain necessary food and water from surrounding vegetation, as well as materials for building their middens.

2.2 Sampling Design

Plant community composition and available midden-building material, changes as one moves further from the ridge. We were curious to see if this change would impact woodrat abundance and/or behavior, so we decided to survey plots of varying distances from the ridge (Fig. 1). We surveyed eleven 30 m x 30 m plots, which we marked with transect tape. The closest distance from each plot to the ridge was recorded. The nearest plot was 10 meters from the ridge and the furthest was 250 meters. In each plot, every fresh woodrat, cottontail, jackrabbit, and squirrel scat pile that contained more than 10 pellets was identified by sight from a comprehensive walking survey and marked with a flag. Every active woodrat midden was flagged with another color. Fresh woodrat scat, as well as fresh bite marks in surrounding vegetation indicated active middens. Scat color, composition/solidity, and moisture level are all indicators of scat age (Elbroch 2012). For our study, we wanted to focus only on fresh scat, indicative of recent animal activity. We classified only dark brown except for the scat of jackrabbits, which is lighter-brown when fresh, soft, moist scat as “fresh”. A midden-centered and scat-centered survey were each conducted subsequently.

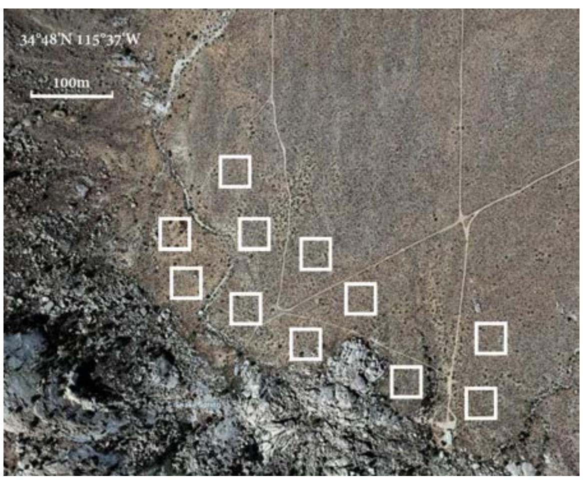

Figure 1. A satellite view of Granite Mountains taken with Google Earth with the eleven 30m x 30m plots marked by boxes. Granite Mountains are located in the Eastern Mojave Desert in California. Plots were in flatlands with varying distance to the east of a mountain ridge.

2.3 Midden-Centered Survey

The diameter of each midden at its widest point was measured with transact tape, and an estimate of the amount of woodrat scat in the midden area was recorded. In teams of two, we circled each midden and roughly estimated the amount of scat we could see surrounding or within the midden. We then recorded the average of our two estimates. In addition, we counted the number of flagged scat piles within two meters of the midden’s edge to calculate the density of scat piles around middens, noting the species that had produced each one.

2.4 Scat-Centered Survey

We identified the species of each scat pile. The round scat of cottontails and jackrabbits could be distinguished by size difference, and the scat of woodrats and cottontails could be easily identified based on size and shape (Fig. 2). After selecting a focal scat pile, we then identified the species of the nearest scat pile. We also recorded if the pile was in an open area or an area covered by vegetation.

Figure 2. Fecal pellet identification. (A) Desert woodrat: oval shape, ~1 cm in length, brown. (B) Desert cottontail: round shape, ~0.6 cm in diameter, brown (C) blacktailed jackrabbit: round shape, ~1cm in diameter, light brown (D) white-tailed antelope squirrel:oval shape, ~1.5 cm in length, black.

2.5 Statistical Tests

We used JMP Pro 15 (SAS Institute inc.) for all of our analysis. Linear regressions were used to test for a relationship between midden size and the density of scat piles of different species around the midden, as well as midden size and the number of woodrat scat pellets under the midden. An ANOVA was used to analyze if distribution of scat piles among the four species differed depending on the distance to the ridge. Chi-squared tests were used to assess if each species defecated closer to a particular other species by comparing the percentage of the nearest scat pile from a specific species to the expected value if the scats were distributed randomly. Another chi-squared test was used to examine whether the scat piles of each species had differences in being located in the open or under plant cover.

RESULTS

Larger middens had more woodrat scat in them (N=76, R^2=0.17, p<0.001) (Fig. 3A). The density of cottontail scat piles was higher around larger middens (N=76, R^2=0.051, p=0.049) (Figure 3B). The densities of woodrat (N=76, R^2=0.018, p=0.25), jackrabbit (N=76, R^2=0.005, p=0.51), and squirrel (N=76, R^2=0.007, p=0.46) scat piles were not affected by midden sizes.

Distance from the ridge did not affect the abundance of woodrat and cottontail scat piles, but did affect the abundance of jackrabbit and squirrel scat piles (N=804, F=73, p<0.001 (Fig. 4). Squirrel scat was in greater abundance closer to the ridge, and jackrabbit scat was in greater abundance further from the ridge.

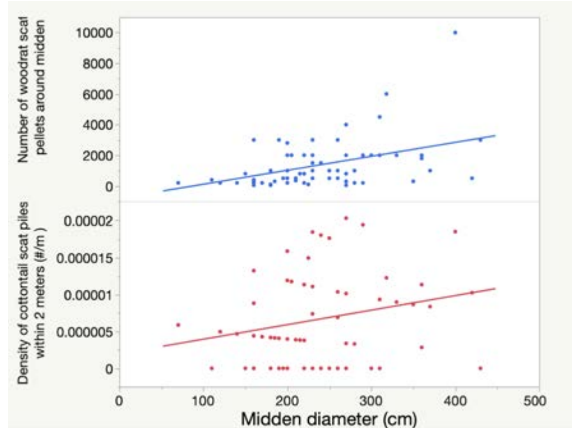

Figure 3A. (Top) Midden diameter vs. the number of woodrat scat pellets around the midden. This linear regression shows that the size of the middens had a positive relationship with the amount of woodrat scat under and around them (N=76, R^2=0.17, p<0.001).

Figure 3B (Bottom) Midden diameter vs. the density of cottontail scat piles within 2 meters of the midden. This linear regression shows that the size of the middens had a positive relationship with the density of cottontail scat piles found around each midden (N=76, R^2=0.051, p=0.049).

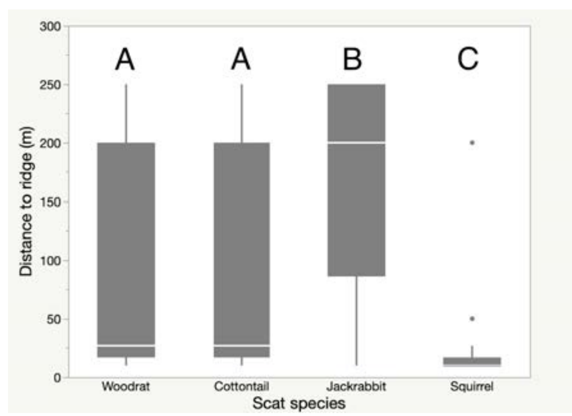

Figure 4. The distribution of scat piles for each species with respect to the distance from the ridge. Using an ANOVA, we found that squirrels defecated closer to the ridge and that jackrabbits defecated further from the ridge (N=804, F=73, p<0.001). Levels not represented by the same letter are significantly different.

Cottontail scat was more likely to be in closest proximity to that of woodrats (N=387, χ^2=420, p<0.001) and vice versa (N=124, χ^2= 40, p<0.001), than would be expected by chance (Fig. 5). Cottontails and woodrats also latrined together frequently. Jackrabbit scat was more likely to be in closest proximity to that of woodrats (N=273, χ^2=62, p<0.001) than any other of our target species. There was never an instance in-which the nearest scat to that of a jackrabbit was squirrel or vice versa. Squirrel scat was more likely to be in closest proximity to that of cottontails or woodrats (N=22, χ^2=13, p=0.0018), than would be expected by chance, with a roughly equal likelihood of either option.

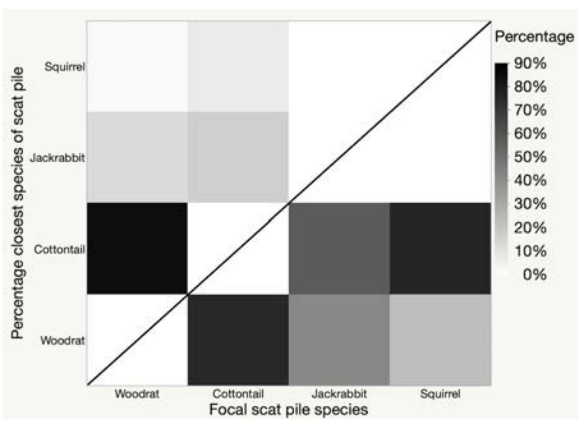

Figure 5. The percentage of closest scat pile species to each scat species. Chi-squared test showed that woodrats and cottontails prefer to defecate nearest to each other, using the expected result as if their scat randomly distributed (N=387, χ^2=420.6, p<0.001). Jackrabbits defecated closest to woodrats (N=273, χ^2=62, p<0.001). Squirrels and jackrabbits never defecated nearest to each other.

The scat of jackrabbits and squirrels was more often found in open areas, whereas the scat of cottontails and woodrats was more often found beneath the cover of vegetation (N=806, χ^2=230, p<.0001) (Fig. 6).

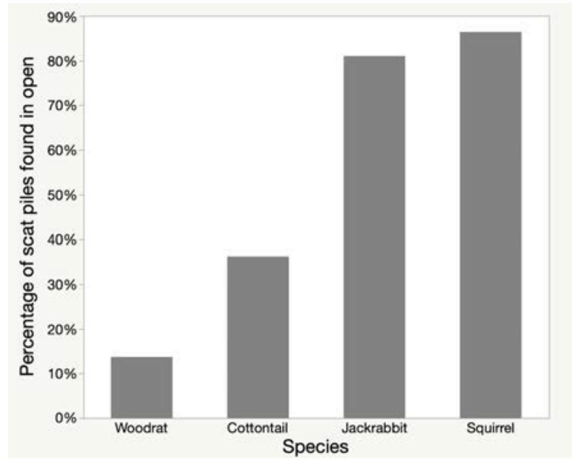

Figure 6. **The percentage of scat piles found in open areas for each species.** Jackrabbits and squirrels defecated more in open areas, and cottontails and woodrats defecated more under plant cover (N=806, χ^2=230, p<0.001).

DISCUSSION

We found strong evidence of spatial niche partitioning between squirrels and jackrabbits: squirrel scat piles were mostly found nearer to the ridge and jackrabbit scat piles were mostly found further from the ridge. The two species have little to no habitat overlap with each other and are equally impartial to woodrat and cottontail activity. We found this result interesting since the spatial scale of our study was very small, only covering around 200 meters from the ridge. Such prominent niche partitioning in a small area is due to either coevolution between jackrabbits and squirrels to avoid direct competition or a difference in their affinity with rocky habitats. Specifically, the diets of jackrabbits and squirrels during the winter are highly overlapped, but they may have different preferences. When insects are rare at this time of the year, squirrels mainly feed on plant materials such as the seeds of pine trees and the leaves of yuccas (Bradley 1968). Meanwhile, the diet of jackrabbits is mainly composed of shorter shrubs such as yucca, mesquite, and cacti, which are densely populated in the flat area at the bottom of the ridge (Foresman 2012). Therefore, the spatial niche partitioning between them could be driven by preferences in feeding between the two species. With the ability to climb trees, squirrels can access more pine seeds than rabbits and rats. They may prefer to forage more along the ridge where pinyon pines are more common, competitors are fewer, and shrubs are also accessible.

Despite the foraging area for both squirrels and jackrabbits overlapping with that of cottontails and woodrats, there was also evidence for spatial niche partitioning based on the type of area they defecated in. Cottontails and woodrats defecated mostly under cover and often together in latrines, while jackrabbits and squirrels defecated mostly in open areas. Such a behavioral difference between jackrabbits and cottontails is particularly interesting since both species belong to the family Leporidae. We speculated that partitioning was due to the differences in foraging strategies. Cottontails are known to frequently utilize protected cover, and jackrabbits are larger in size than cottontails (Vaughan 1972). This might mean the tunnels created by small rodents under shrubs are often too small for jackrabbits to enter, forcing them to feed in more open areas where plants are more easily accessible to them. Additionally, food preferences could be another factor in determining where each species defecates. The types of plants that cottontails and jackrabbits consume are highly overlapped, but a previous study showed that the proportion of plant species in their fecal pellets differed significantly: jackrabbits ingested greater proportions of grasses and woody plants while cottontails ingested more forbs (Flinders and Crawford 1977). The research was conducted in a high plain in Texas, a very different ecosystem than the Mojave Desert with vegetation mainly composed of various grass species. However, it still indicates that feeding differentiation exists between cottontails and jackrabbits. For our study system, future research could compare the proportion of cacti, mesquite, and yucca materials in fecal pellets of the two species to further our understanding on feeding differentiation between them in a desert ecosystem.

For woodrats and cottontails, their scat piles were more evenly distributed across the landscape, and no differences were found between the two species in terms of distance from the ridge. This suggested that woodrats and cottontails share the same foraging area, and this idea was further supported by the closest scat pile species. We were more likely to find woodrats being the nearest scat pile species to a cottontail scat pile than if all four species were defecating randomly on the landscape and vice versa. This is consistent with the study done on bushytailed woodrats (*Neotoma cinerea*) and Nuttall cottontails (*Sylvilagus nuttallii*) in Idaho, where among blacktailed jackrabbits, pigmy rabbits, and cottontails, only cottontails were observed near the woodrat middens (Johnson and Hansen 1979). The sharing of active areas could be an indicator of direct competition, however, there is temporal niche partitioning between cottontails and woodrats that weakens such competition. Cottontails and Woodrats have a similar diet, but woodrats are active at night while cottontails are active during the day. Furthermore, the presence of mixed scats from the two species in the latrines even suggested their tendency to defecate in the exact same area repeatedly, potentially indicating interspecific communication. The separation between diurnal and nocturnal activity amongst small mammals has previously been observed to occur among different species of spiny mice (*Acomys* spp.) through odor cues traced in their scat (Haim and Rozenfeld 1993). The shared latrines of woodrats and cottontails may signify that they too partition their niches temporally, as opposed to the spatial partitioning observed in jackrabbits and squirrels.

The interaction between woodrats and cottontails can also be reflected by cottontails increasing activity around larger middens. Contrary to our predictions that other species would be deterred by woodrat middens, we found larger middens associated with a greater density of cottontail scat piles within two meters from their edge. This is probably because larger middens are generally found under larger host plants, providing more sources for herbivory. Woodrats have small home ranges and they mostly forage within 10 meters from their middens, so the host plant of the midden acts as a food source for them (Jameson 2004). Middens are mostly found residing under yucca and cholla cacti, and both are important food resources for desert cottontails (Turkowski 1975). Additionally, the enriched soil under woodrat middens (Whitford and Steinberger 2010) could be cultivating better conditions for vegetation around the midden, thus attracting more cottontails that feed on the vegetation around the midden. A possible future course of study could focus on this phenomenon and investigate the effects of woodrat middens on their surrounding plant community. Furthermore, comparing the fecal pellet composition between woodrats and cottontails in a desert environment could be a good indicator of whether their feeding preferences are significantly different.

Larger middens had more woodrat scat under them, so it is possible that cottontails might be tracking the scent mark of woodrats to find middens in which they can feed upon the host plant. If there is interspecies communication to cottontails occurring from the scent of woodrat scat, then it may be revealed by examining their latrines (Schoener 1973). If interspecies communication is found, it implies that the latrines are used to facilitate temporal niche partitioning. Evidence of different species sharing latrines to convey information of their presence was found in some solitary carnivores such as pampas cats *(Leopardus pajeros)* and culpeos *(Lycalopex culpaeus)*, as well as honey badgers *(Mellivora capensis)* and meerkats *(Suricata suricatta)* (Berg 2003; Jordan 2005). Observing how many scat pellets from each species are in a latrine across several seasons can reveal if the species uses the latrine to communicate to the opposite sex of their own species, with potentially more pellets during mating season. If the woodrats and cottontails consistently use the same latrine with equivalent frequency year-round, then there may be interspecies communication between them rather than only intraspecies communication for mating.

ACKNOWLEDGMENTS

This work was performed at the University of California's Sweeney Granite Mountains Desert Research Center, doi: 10.21973/N3S942. We would like to extend our gratitude to Sarah Kingston and Tim Miller for the opportunity to conduct our own research and enhance our knowledge of the natural world.

REFERENCES

Albrecht, M. & Gotelli, N. J. 2001. Spatial and temporal niche partitioning in grassland ants. *Oecologia* **126:**134–141.

Arakawa, H., Blanchard, D. C., Arakawa, K., Dunlap, C., & Blanchard, R. J. 2008. Scent marking behavior as an odorant communication in mice. *Neuroscience and Biobehavioral Reviews* ***32*(7):**1236–1248.

Berg, J. E. 2003. The carnivore assemblage of La Payunia Reserve, Patagonia, Argentina: Dietary niche, prey availability, and selection. The University of Montana, Missoula, MT, USA.

Bradley, G. W. 1968. Food habits of the antelope ground squirrel in southern Nevada. *Journal of Mammalogy* **49(1):**4–21.

Burt, W. H., R. P. Grossenheider. 1980. *Mammals*. Houghton Mifflin Company, New York, New York, USA.

Campos, H., Boeing, W.J. and Throop, H.L. 2019. Decaying woodrat (*Neotoma* spp.) middens increase soil resources and accelerate decomposition of contemporary litter. *Journal of Arid Environments* **171**.

Elbroch, M., Kresky, M., & Evans, J. 2012. *Field guide to animal tracks and scat of California*. University of California Press, Berkeley, California, USA.

Flinders, J. T., & Crawford, J. A. 1977. Composition and degradation of jackrabbit and cottontail fecal pellets, Texas High Plains. *Journal of Range Management* **30(3):**217–220.

Foresman, K.R. 2012. *Mammals of Montana*. Second edition. Mountain Press Publishing, Missoula, Montana, USA.

Garrote, G., de Ayala, R.P. & Tellería, J.L. 2014. A comparison of scat counts and camera-trapping as means of assessing Iberian lynx abundance. *Eur. J. Wildl. Res.* **60:**885–889

Haim, A., & Rozenfeld, F. M. 1993. Temporal segregation in coexisting *Acomys* species: The role of odour. *Physiology & Behavior* **54(6):**1159–1161.

Hirsch, B. T., S. Prange, S. A. Hauver, S. D. Gehrt. 2014. Patterns of latrine use by raccoons (*Procyon lotor*) and implication for *Baylisascaris procyonis* transmission. *J. Wildl. Dis.* **50(2):**243–249.

Jameson, E. W., Jr. and Peeters, H. J. 2004. *Mammals of California*. University of California Press, Berkeley, California, USA.

Johnson, M. K. and Hansen, R. M. 1979. Foods of cottontails and woodrats in south-central Idaho. *Journal of Mammalogy* **60(1):**213–215.

Jordan, Neil R. 2005. Meerkat latrines: cooperation, competition and discrimination. Thesis (MSc) University of Stellenbosch.

Kays, R. W., and D. E. Wilson. 2002. *Mammals of North America*. Princeton University Press, Princeton, New Jersey, USA.

Lara, C., Pérez, B., Castillo-Guevara, C. et al. 2015 Niche partitioning among three tree-climbing bird species in subtropical mountain forest sites with different human disturbance. *Zool. Stud.* **54(28)**.

Richard T. Reynolds, and E. Charles Meslow. 1984. Partitioning of food and niche characteristics of coexisting accipiter during breeding. *The Auk* **101(4):**761–779.

Schoenherr, A. 1992. *A natural history of California*. University of California Press, Berkeley, California, USA.

Schoener, T. 1973. Population growth regulated by intraspecific competition for energy or time: Some simple representations. *Theoretical Population Biology* **4:**56–84.

Turkowski, F. 1975. Dietary adaptability of the desert cottontail. *The Journal of Wildlife Management* **39(4):**748–756.

Vaughan, T. 1972. *Mammalogy*. W. B. Saunders Company, Philadelphia.

Whitford, W.G. and Y. Steinberger. 2010. Packrats (*Neotoma* spp.): Keystone ecological engineers? *Journal of Arid Environments* **74:**1450–1455.