2023 NORTHEASTERN NATURALIST 30(1):41–58

# Activity Patterns of Allegheny Woodrats (*Neotoma magister*) and Two Potential Competitors in Virginia

Karen E. Powers[1,*], Emily D. Thorne[2], Logan R. Platt[1],
Kayla M. Nelson Anderson[1], Logan M. Van Meter[1], Chris M. Wozniak[1],
Richard J. Reynolds[3], and W. Mark Ford[4]

**Abstract -** *Neotoma magister* (Allegheny Woodrat) is a nocturnal, emergent rock-habitat specialist (i.e., inhabits rocky outcrops, boulderfields, and caves). Woodrat populations have declined range-wide due to habitat fragmentation, endoparasites, and interspecific competition. We estimated the diel activity curves of Allegheny Woodrats and assessed the effects of habitat type (exposed rock habitat/cave-exterior vs. cave-interior) and season (spring, summer, and fall) on curve shape. We also investigated the effect of 2 granivorous competitors' presence and activity curves (*Peromyscus* spp. and *Tamias striatus* [Eastern Chipmunk]) on woodrat activity. Additionally, we investigated whether the presence or absence of *Procyon lotor* (Raccoon), a primary carrier of *Baylisascaris procyonis* (Raccoon Roundworm), significantly affects the presence or absence of Allegheny Woodrats. We used remote-detecting cameras to document the diel cycles of Allegheny Woodrats and 2 competitors across 83 sites in western Virginia and 2 sites in West Virginia from 2017 to 2022. For 13,002 recorded events, we detected woodrats at 36 of 85 sites (3778 camera events). We observed a higher proportion of daytime activity by woodrats within cave interiors than cave exteriors. Allegheny Woodrat activity curves differed among seasons, with the greatest differences observed between summer and fall and with ~80% activity overlap. These activity curves differed significantly when co-occurring with versus not co-occurring with a competitor. Additionally, Allegheny Woodrats showed an inverse activity rate with *Peromyscus* spp. Thus, our results suggest that competition avoidance via temporal partitioning occurs between these species. Allegheny Woodrats and Raccoons occurred together more often than expected suggesting the presence of woodrats is currently not reduced by the presence of Raccoons. Our remote-detecting camera data help elucidate relationships of Allegheny Woodrats with presumptive competitors, and open avenues for further investigation in Virginia.

## Introduction

*Neotoma magister* Baird (Allegheny Woodrat) is a rodent that inhabits emergent rock habitats (i.e., rocky outcrops, colluvial boulders, and caves) primarily along the Appalachian Mountains and the Interior Low Plateau of the United States (Poole 1940). Populations have been extirpated from much of the northeastern extent of their range, including Massachusetts, Connecticut, and New York (Castleberry

---

[1]Biology Department, Radford University, Radford, VA 24142. [2]Department of Fish and Wildlife Conservation, Virginia Tech, Blacksburg, VA 24061. [3]Virginia Department of Wildlife Resources, Verona, VA 24482. [4]US Geological Survey, Virginia Cooperative Fish and Wildlife Research Unit and Department of Fisheries and Wildlife Conservation, Virginia Tech, Blacksburg, VA 24061. [*]Corresponding author - kpowers4@radford.edu.

Manuscript Editor: Thomas French

et al. 2006). Though still widespread, Allegheny Woodrat populations reportedly have been declining in Pennsylvania, Virginia, and West Virginia, and only a few colonies remain in New Jersey, Indiana, and Ohio (Ford et al. 2006, Mengak 2002, Timm et al. 2019, Wright 2008). In Virginia, Allegheny Woodrats are listed as a Tier IV species of "moderate conservation need" (VDGIF 2015). However, more recent work at >75 locales (Kanine et al. 2018, Lombardi et al. 2022, Thorne et al. 2022) suggests that Virginia remains a relative stronghold for the species.

Synergistic threats to Allegheny Woodrats across their range include habitat fragmentation, decline in *Quercus* spp. (oaks), parasites, and predation (LoGiudice 2006, 2008; Powers et al. 2020a, b; Smyser et al. 2012). Habitat fragmentation is a primary concern when gene flow within metapopulations is inhibited (Kanine et al. 2018). Forest alterations affect Allegheny Woodrat metapopulation gene flow by disrupting colony demographics and immigration and emigration among colonies, thereby reducing genetic variability and fitness (Castleberry et al. 2001). Another major threat is a potentially lethal endoparasite, *Baylisascaris procyonis* (Stefanski & Zarnowski) (Raccoon Roundworm), which is spread through *Procyon lotor* (L.) (Raccoon) scat. Raccoon Roundworm presence has been tied to declines in woodrat abundance (Page et al. 2012) or local extinctions (e.g., Balcom and Yahner 1995, LoGiudice 2003) and has been hypothesized to have been the most contributory factor for decline of Allegheny Woodrats in the Northeast (Birch et al. 1994).

Although not a direct threat to Allegheny Woodrat populations, competition for resources with other granivorous species can force these woodrats to partition limited resources (Ford et al. 2006). Castleberry et al. (2002) identified 147 unique items in the diets of Allegheny Woodrats, suggesting they are generalist granivores/frugivores. With such a variety of food items (e.g., hypogeal fungi, angiosperm leaves, berries, acorns and other hard mast; Castleberry and Castleberry 2008, Castleberry et al. 2002) comprising their diet, this creates a substantial list of interspecific competitors for seasonally limited food resources. Furthermore, Allegheny Woodrats cache their food, particularly hard mast (i.e., acorns), and their seasonal reliance for this limited resource places them in competition with both substantially larger and similarly sized mammals. Potential mammalian food competitors occupying emergent rock outcrops in western Virginia include, but are not limited to, other cricetids such as *Peromyscus leucopus* (Rafinesque) (White-footed Mouse), *Peromyscus maniculatus* (Wagner) (Deer Mouse) (treated collectively in this paper as *Peromyscus* spp.), and voles, sciurids such as *Tamias striatus* (L.) (Eastern Chipmunk), tree squirrels, *Marmota monax* (L.) (Woodchuck), rabbits (*Sylvilagus floridanus* (J.A. Allen) [Eastern Cottontail] and *Sylvilagus obscurus* Chapman, Cramer, Deppenaar and Robinson [Appalachian Cottontail]), *Odocoileus virginianus* (Zimmermann) (White-tailed Deer), and *Ursus americanus* Pallas (American Black Bear) (Campbell et al. 2010; Castleberry 2008; Castleberry et al. 2001, 2006; Clair 2015).

The relative impact of food competitors remains unresolved, but it may be measured in woodrats via alterations to diel activity patterns. Further, these patterns may differ according to woodrats' use of cave interiors, a habitat with a more limited suite of competitors. Cave interiors provide shelter and lower risk for predation, but a lack of food resources necessitates foraging in exterior habitats (Barr 1967, Romero 2009, Venarsky et al. 2014). As such, diel activity patterns of woodrats within cave interiors may vary from external habitats due to a necessary increased foraging time and/or a reduced risk of depredation. Past woodrat-activity studies typically were limited to cave-exterior (emergent outcrop) habitats, describing patterns that varied by season (i.e., day length; Castleberry 2008) and subsequent food availability. In summer months, Allegheny Woodrats typically exhibit 2 peaks in activity per evening, with movement beginning ~30 min after sunset, decreasing gradually throughout the night, and spiking again prior to sunrise (Castleberry et al. 2006). Poole (1940) reported peaks in summer activity around midnight. Only Poole (1940) has anecdotally described cave-interior activity; he noted relatively more daytime movement in woodrats. However, these cave-interior diel trends have not been quantified. Moreover, White-footed Mice, Deer Mice, and possibly *Microtus chrotorrhinus* (Miller) (Rock Vole) also inhabit cave interiors (Castleberry et al. 2006). When co-occurring within caves, these rodents may collectively adjust diel activity to reduce competition.

Given the unknowns about competition, especially considering differing microhabitats (cave-interior versus exterior), the aims of our study were to estimate the diel activity pattern of Allegheny Woodrats and understand the relationships between woodrat activity, habitat type, seasonality, and interspecific occurrence. Our first objective was to assess potential differences in woodrat activity curves between cave-exterior and cave-interior habitats. We predicted that greater diurnal activity would be observed within cave interiors than outside of caves because caves potentially offer a habitually dark environment, lower resource profitability, lower direct competition with other species, and lower daytime predation risk. Our second objective was to assess the effects of season (spring, summer, and fall) to better understand the relationship between seasonal differences in night length and woodrat activity. We predicted that woodrat activity curves would be flatter and wider in spring (mid-March–May) and fall (September–mid-November) when nights are longer and more narrow during summer months (June–August) when nights are shorter. We did not investigate winter months, when Allegheny Woodrats rely on cached food resources and thus rarely leave their dens (Castleberry and Castleberry 2008, Hornsby et al. 2005). Our third objective was to examine whether Allegheny Woodrat activity curves quantitatively changed in the presence of potential competitors. We predicted that: (1) the ubiquitous presence of some direct competitors (i.e., *Peromyscus* spp. or Eastern Chipmunks) would lead to temporal partitioning between the species; and (2) Allegheny Woodrat activity rates would be inversely related to activity rates of competing species. Our final objective was to assess the effect of Raccoon presence on Allegheny Woodrat presence. We predicted that Allegheny Woodrats and Raccoons would co-exist at sites less often than expected due to the susceptibility of woodrats to Raccoon Roundworm.

## Field-Site Description

We surveyed 83 emergent rock habitats across 17 counties (Alleghany, Augusta, Bath, Botetourt, Craig, Fauquier, Giles, Montgomery, Nelson, Page, Roanoke, Rockbridge, Rockingham, Russell, Scott, Wythe, and Wise) in northern, central, and western Virginia in the Blue Ridge and Ridge and Valley provinces of the central Appalachian Mountains. We also included 2 sites in Jefferson County in eastern West Virginia, on the border with Loudoun County, VA. We collectively considered these 85 sites "Virginia" sites for the remainder of this discussion. Virginia sites were located in the George Washington–Thomas Jefferson National Forest, multiple state parks (Natural Bridge State Park, Natural Tunnel State Park), and other state-owned lands (e.g., Short Mountain Wildlife Management Area) as well as private lands. The habitats we surveyed included closed-canopied rocky outcrops (i.e., clifflines and rockhouse formations), caves (interior and around entrances), and open-canopied, colluvial boulderfields. Dominant landcover typically was mature secondary-growth forest. Depending on elevation and aspect, forest types included Appalachian oaks and mixed *Pinus* spp. (pines) with smaller patches of mesic species (e.g., *Acer saccharum* Marsh. [Sugar Maple], *Liriodendron tulipifera* L. [Yellow Poplar], *Fagus grandifolia* Ehrh. [American Beech]), and *Tsuga canadensis* (L.) Carrière (Eastern Hemlock). Dense shrub layers of *Kalmia latifolia* L. (Mountain Laurel) and *Rhododendron maximum* L. (Rosebay Rhododendron) were common (Kniowski and Ford 2018). Elevations varied from ~200 to 1200 m asl.

## Methods

### Camera deployment

Depending on site and whether the location was a component of long-term monitoring or initial survey, we deployed remote-detecting cameras providing time and date data across 85 sites. Given site size, accessibility, weather limitations, as well as subproject goals, we deployed between 2 and 18 cameras/site for 1–52 nights/site. In most of our summer studies that paired cameras with active live-trapping, we deployed cameras at sites for 3–4 consecutive nights, unless extreme weather or other access limitations reduced our efforts. When monitoring sites with cameras in the absence of live traps, we extended deployment times up to 52 nights with fewer cameras. We surveyed these sites from March to November in 2017 (28 sites, 29 unique camera deployments; 595 camera trap-nights [1 trap-night = 1 camera set for 1 night at 1 site]), 2018 (35 sites, 37 unique deployments, 633 trap-nights), 2019 (27 sites, 39 unique deployments, 2440 trap-nights), 2020 (14 sites, 15 unique deployments, 279 trap-nights), 2021 (22 sites, 22 unique deployments, 667 trap-nights), and 2022 (14 sites, 17 unique deployments, 559 trap-nights). We visited sites 1–5 times throughout the study, and no sites were visited in all 6 years. Camera types varied by site, and included a mixture of Reconyx HyperFire (Model HC500, Holeman, WI), Bushnell Trophy Cam HD (Model 119739, Overland Park, KS), and Stealth Cams (Model STC-G45NGX, Grand Prairie, TX).

We set cameras to capture images on and around apple-baited Tomahawk traps (#1 or #2, Tomahawk Live-Trap Co., Tomahawk, WI; all years except 2019), bait piles (1 cup livestock sweet feed [Multitext 12.5% multi-purpose livestock feed, Augusta Cooperative Farm Bureau, Staunton, VA]; primarily 2019 [see Thorne et al. 2022], few in 2021), or unbaited cameras without traps (primarily 2019). We set remote cameras to take a rapid set of 3 photos followed by a 1-min latent period.

### Species identifications and detection histories

We documented activity patterns for each species by recording the time stamp of each detection event. A detection event consisted of at least 1 image of at least 1 individual of a species within a 1-min timeframe. Within this 1-min time frame, we recorded the maximum number of individuals sighted per species in a single image. We identified every mammal to the species level, when possible. We identified some mammals to the genus level, i.e., *Peromyscus* and all soricids, when species-specific features could not be discerned in the image. In agreement with multiple rodent and mesocarnivore studies, we defined a single event as a 1-minute sequence at 1 camera at 1 site (e.g., De Bondi et al. 2010, Higdon and Gompper 2020, Meek et al. 2012, Webster et al. 2021).

Because some of our camera efforts accompanied live-trapping for a concurrent project, with cameras facing a trap, we documented all events up to and including the minute in which the animal was captured in the trap. When a trapped animal could no longer escape the view of the camera, we did not document its activity while in the trap. However, for all other animals observed outside of the trap, their activity continued to be recorded as unique events. This study was performed under the auspices of Virginia Tech Institutional Animal Care and Use Committee (IACUC) protocol # 20-039, and Radford University IACUC protocols #FY17-07 and FY20-08.

### Statistical analyses

We used the recorded timestamps of the detection events of each species to assess activity curves. Lashley et al. (2018), supported by previous work (Rowcliffe et al. 2014), suggested that activity curves should include a minimum of 100 events to increase accuracy of the models. To err on the side of caution, we limited further competitor analyses to those taxa with >300 camera events. Additionally, because this study was conducted across several months (March–November) each year and across a large range of geographic locations, we accounted for seasonal and geographical differences in night length. To do this, we converted the "clock time" (2400 timestamp on camera image) recorded on images captured from the remote-detecting cameras to "sun time" using the 'sunTime' function (Nouvellete et al. 2011) in the Program R package 'overlap' version 0.3.3 (Meredith and Ridout 2014).

To investigate potential differences in Allegheny Woodrat activity among habitat types, we fit non-parametric kernel density activity curves for observations collected within cave interiors, outside cave entrances, and at exposed rock outcrops for Allegheny Woodrats following methods of Ridout and Linkie (2009). We tested for homogeneity among activity curves using Watson's non-parametric two-sample test (Watson 1962) using Program *R* package 'circular' v. 0.4-93

(Agostinelli and Lund 2017). Further, we estimated the coefficient of overlap of the activity curves for sample sizes >50 ($\Delta_4$; Schmid and Schmidt 2006) for each habitat type pair for each species. We then estimated 95% confidence intervals surrounding the estimates using 10,000 bootstrap samples (Linkie and Ridout 2011).

To assess the effect of seasons, we first categorized our camera observations into spring (mid-March–mid-June), summer (mid-June–August), and fall (September–November) following methods of Castleberry et al. (2002). We then estimated woodrat activity curves for each season and tested for homogeneity between seasons. We also estimated $\Delta_4$ and the 95% confidence intervals surrounding $\Delta_4$ for each pair of seasons.

To quantify the potential for resource competition between Allegheny Woodrats and 2 potentially competing species (i.e., *Peromyscus* spp. and Eastern Chipmunks), we investigated temporal overlap between woodrats and their competitors. We compared the activity curve of woodrats when a competing species was present at a site to the activity curve of woodrats when a competing species was presumed absent from a site. To do this, we subset the Allegheny Woodrat observations into 2 categories: (1) woodrat observations at sites where a potentially competing species (either *Peromyscus* spp. or Eastern Chipmunk) was co-detected (competitor-present sites), and (2) woodrat observations at sites where that competing species was not co-detected and thus presumed absent (competitor-absent sites). We then estimated activity curves for Allegheny Woodrats at competitor-present sites and competitor-absent sites with respect to each competing species. We also tested for homogeneity between competitor-present and competitor-absent curves and estimated $\Delta_4$ and the 95% confidence intervals with respect to each competing species.

We then assessed the effect of competitor activity rates on the activity rates of woodrats using generalized linear models (GLMs) in Program R package 'stats' v. 4.2.2 (R Core Team 2022). We calculated each species' site-specific activity rate by dividing the number of image-capture events for a particular species detected by our remote cameras by the total number of species/genera-wide capture events at that site. We determined a significant effect of competitor activity rate on woodrat activity rate when $P$-value $\leq 0.05$.

Lastly, to determine if Raccoon and Allegheny Woodrat presence or absence were related, we summed the number of sites with: (1) Raccoon-presence only, (2) woodrat-presence only, (3) both species present, and (4) neither species present. We then conducted a chi-squared test of independence to test for a non-random relationship between Allegheny Woodrat and Raccoon presence in Program R package 'stats'.

## Results

We recorded 13,002 events across our 6-year study, of which 11,387 events detected an Allegheny Woodrat, *Peromyscus* spp., or Eastern Chipmunk. We documented Allegheny Woodrats at 36 of 85 sites ($n = 3778$ camera events) plus 19 other terrestrial mammalian species. Although potential competitors included 12 mammalian species/genera in this study, only 2, *Peromyscus* spp. ($n = 6521$) and Eastern

Chipmunks ($n = 1088$), were documented in >300 camera events (Appendix 1). Less common competitors included Woodchucks ($n = 288$), *Sciurus carolinensis* Gmelin (Gray Squirrel; $n = 224$), American Black Bears ($n = 148$), *Myodes gapperi* (Vigors) (Southern Red-backed Vole; $n = 71$), White-tailed Deer ($n = 67$), and Appalachian Cottontails ($n = 65$) (Appendix 1). Rodent or lagomorph competitors with <50 camera events included jumping mice, voles in the genus *Microtus*, *Glaucomys volans* (L.) (Southern Flying Squirrel) and Eastern Cottontails. Presumed non-competitors included *Didelphis virginiana* Kerr (Virginia Opossum; $n = 199$) and shrews ($n = 10$).

Of the 9 species of mammalian predators documented, there were 4 canids (*Canis latrans* Say [Coyote], *Canis lupus familiaris* L. [Domestic Dog], *Vulpes vulpes* [L.] [Red Fox], *Urocyon cinereoargenteus* [Schreber] [Gray Fox]), 2 felids (*Lynx rufus* [Schreber] [Bobcat], *Felis catus* L. [Domestic Cat]), 2 mephitids (*Mephitis mephitis* [Schreber] [Striped Skunk], *Spilogale putorius* [L.] [Eastern Spotted Skunk]), and 1 mustelid (*Mustela frenata* Lichtenstein [Long-tailed Weasel]). Of these 9 species, 8 were documented ≤7 times, and Long-tailed Weasels were documented just 18 times.

### Objective 1: Effects of habitat on Allegheny Woodrat activity

Allegheny Woodrat activity curves differed among habitat types, specifically between cave interiors and emergent rock outcrops ($U^2 = 5.26$, $P < 0.001$) with $\Delta_4 = 0.73$ (95% confidence interval [CI] = 0.71–0.76) and between cave interiors and outside of cave entrances ($U^2 = 0.68$, $P < 0.001$) with $\Delta_4 = 0.71$ (95% CI = 0.62–0.80). Daylight activity was greater within cave interiors than outside cave entrances or at exposed rock outcrops. Woodrat activity curves did not differ between outside cave entrances and exposed rock outcrops ($U^2 = 0.16$, $P > 0.05$) with $\Delta_4 = 0.85$ (95% CI = 0.77–0.92); thus, we pooled data from outside cave entrances and exposed rock outcrops into 1 category ("cave-exterior") and excluded cave-interior data for all further analyses. Overlap of the pooled cave-exterior activity curve and the cave-interior activity curve was $\Delta_4 = 0.82$ (95% CI = 0.79–0.85), and the 2 curves differed significantly ($U^2 = 2.76$, $P < 0.001$; Fig. 1).

### Objective 2: Effects of season on Allegheny Woodrat activity

Allegheny Woodrat activity curves differed among all seasons. The spring and summer activity curves differed significantly ($U^2 = 0.64$, $P < 0.001$) with ($\Delta_4 = 0.87$, 95% CI = 0.83–0.91, Fig. 2A); however, the summer and fall activity curves were the most different ($U^2 = 0.77$, $P < 0.001$) with $\Delta_4 = 0.85$ (95% CI = 0.81–0.90, Fig. 2B). The spring and fall activity curves were the most similar ($U^2 = 0.36$, $P < 0.01$) and showed the greatest amount of overlap ($\Delta_4 = 0.91$, 95% CI= 0.86–0.95, Fig. 2C). While woodrat activity during spring and summer was mostly nocturnal, a greater number of daylight observations occurred during spring than during fall.

### Objective 3: Allegheny Woodrat–competitor interactions

When comparing the activity curve of woodrats at *Peromyscus* spp.-present sites to woodrat activity curves at *Peromyscus* spp.-absent sites, we found a significant difference in curve shape ($U^2 = 0.25$, $P < 0.05$), with $\Delta_4 = 0.84$ (95% CI = 0.75–0.90, Fig. 3A). We observed more daytime activity by woodrats when *Peromyscus* spp. were absent than when present.

Unlike the relationship between woodrats and *Peromyscus* spp., we did not find a significant difference in woodrat activity between chipmunk-present and chipmunk-absent sites (Fig. 3B).

Mean activity rate of Allegheny Woodrats across all sites was 0.16 (SE = 0.02). The activity rate of Eastern Chipmunks was similarly low at 0.16 (SE = 0.02) while activity rate of *Peromyscus* spp. was much greater at 0.54 (SE = 0.02). We found a significant inverse effect of *Peromyscus* spp. activity rate on woodrat activity rate ($\beta = -0.33$, SE = 0.07, $t = -4.36$, $P < 0.001$; Fig. 4A). However, we found no significant relationship between the activity rates of Allegheny Woodrats and Eastern Chipmunks ($\beta = -0.06$, SE = 0.14, $t = -0.40$, $P = 0.69$; Fig. 4B).

### Objective 4: Allegheny Woodrat and Raccoon presence

We documented Raccoons in 433 camera events at 46 of 85 sites. Of these sites, they co-existed with Allegheny Woodrats at 24 sites ($n = 216$ Raccoon camera events). Raccoons were found at 22 sites where woodrats were absent. Woodrats ($n = 2062$ events) existed at 12 sites lacking Raccoon detections. In contrast to our prediction, Allegheny Woodrats and Raccoons occurred together more often than expected by chance ($\chi^2 = 3.96$, df =1, $P = 0.05$).

## Discussion

In general, Allegheny Woodrat activity was largely nocturnal both at cave-interior and cave-exterior habitats. However, we observed significantly more daytime activity by woodrats within caves than outside of caves. The observations of greater proportion of daytime activity within caves by woodrats may be a behavioral response to lower predation risk within caves. Rodents, including Allegheny Woodrats, are frequently preyed upon by nocturnal predators such as owls, weasels, and foxes (Hockman and Chapman 1983, Morris and Davidson

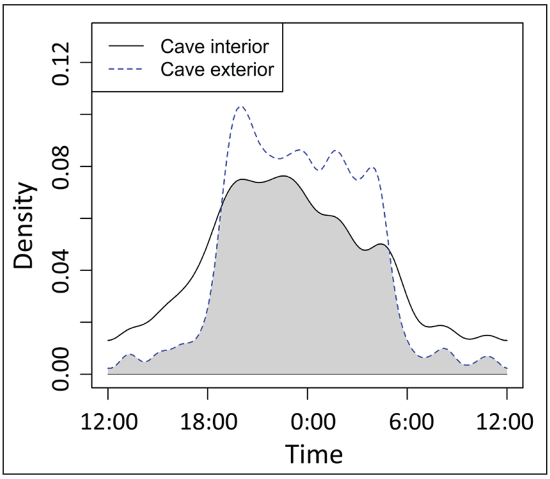

Figure 1. Temporal activity curve and overlap of activity within cave interiors and outside of caves for *Neotoma magister* (Allegheny Woodrat) from 83 sites in western Virginia and 2 in eastern West Virginia, 2017–2022.

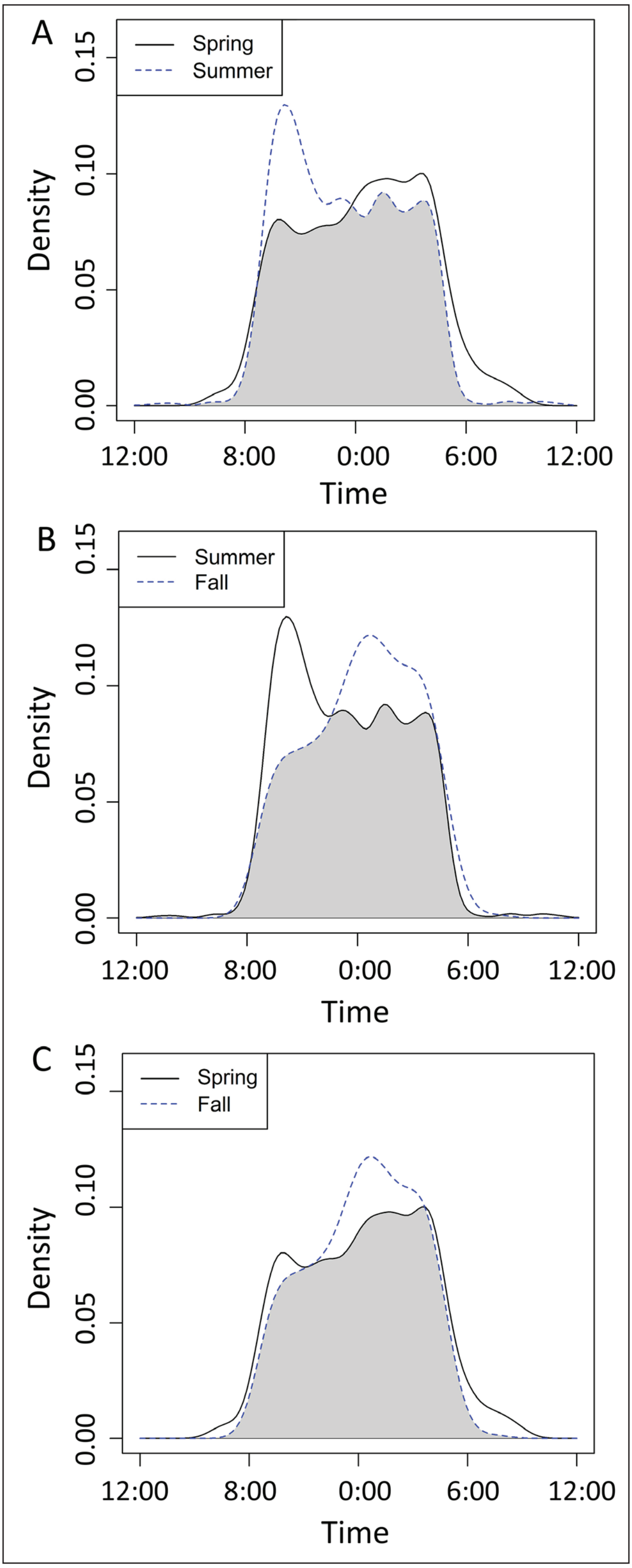

Figure 2. Temporal activity curve and overlap of activity for (A) spring–summer, (B) summer–fall, and (C) spring–fall for *Neotoma magister* (Allegheny Woodrat) from 83 sites in western Virginia and 2 in eastern West Virginia, 2017–2022.

2000, Poole 1940, Powers et al. 2020a), but can also be susceptible to diurnal predators, such as hawks (K.E. Powers, pers. observ.) and snakes (Poole 1940). Thus, cave interiors may offer refuge from predation for foraging woodrats both at night and during daylight hours. Further, the more stable microclimate within cave interiors may provide refuge from precipitation or thermally challenging temperatures to which an individual would otherwise be exposed in the ambient environment (Poulson and White 1969).

Additionally, we found that Allegheny Woodrat activity remained generally nocturnal during all seasons; however, the timing of peak activity differed among seasons. As predicted, the spring and fall activity curves were wider than the summer curve, though this pattern was more pronounced in spring than fall. Generally, peak activity during spring and fall occurred after midnight. Whereas during summer, the curve was narrower and peak activity occurred between sunset and midnight. The near-constant activity throughout the night during spring may

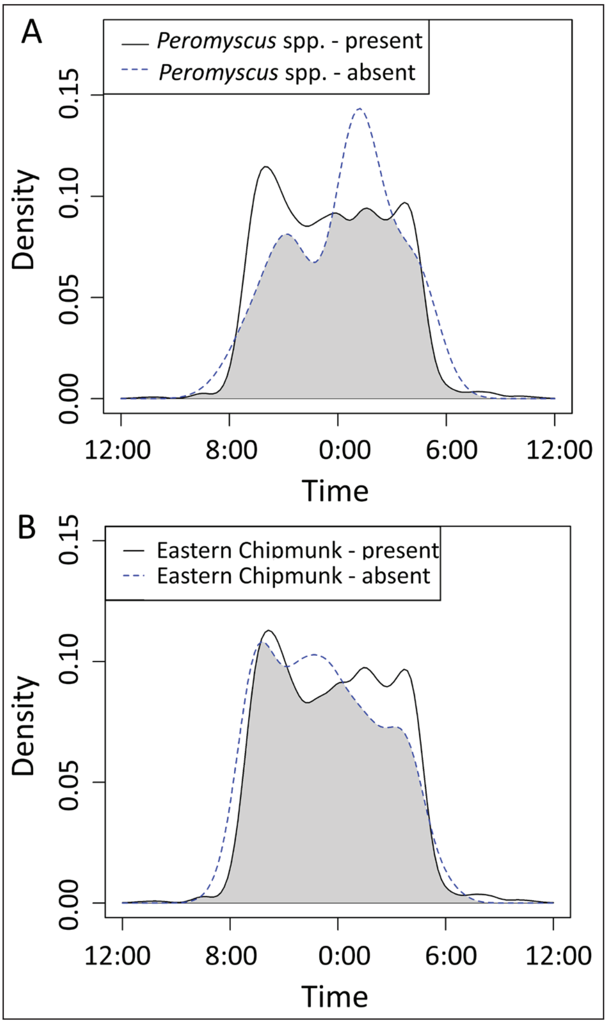

Figure 3. Temporal activity curve and overlap of activity for *Neotoma magister* (Allegheny Woodrat) at (A) *Peromyscus* spp.-present and *Peromyscus* spp.-absent sites and (B) *Tamias striatus* (Eastern Chipmunk)-present and Eastern Chipmunk-absent sites across 83 sites in western Virginia and 2 in eastern West Virginia, 2017–2022.

be due to breeding activity, which peaks during April and May (Mengak 2002). Moreover, more-frequent foraging bouts may be necessary to fulfill foraging needs during the onset of new spring food sources (soft mast, vegetation) and dwindling winter-cache food sources (Castleberry et al. 2002). Conversely, summer activity may peak earlier in the night as foraging needs may be fulfilled in the first few hours past sunset, allowing woodrats to return to their den to feed and rest (Wiley 1971). This pattern may be a particularly beneficial behavior for females with nursing offspring. Similar to our findings, Stovall and Hayeslette (2013) found fall Allegheny Woodrat activity to peak between 0200 and 0300 h, with activity after 0500 h only occurring during these months. Though neither our study nor Stovall and Hayslette (2013) assessed the influence of age on Allegheny Woodrat activity, Wiley (1971) found that subadult *Neotoma floridana* (Ord) (Eastern Woodrat) activity peaks after

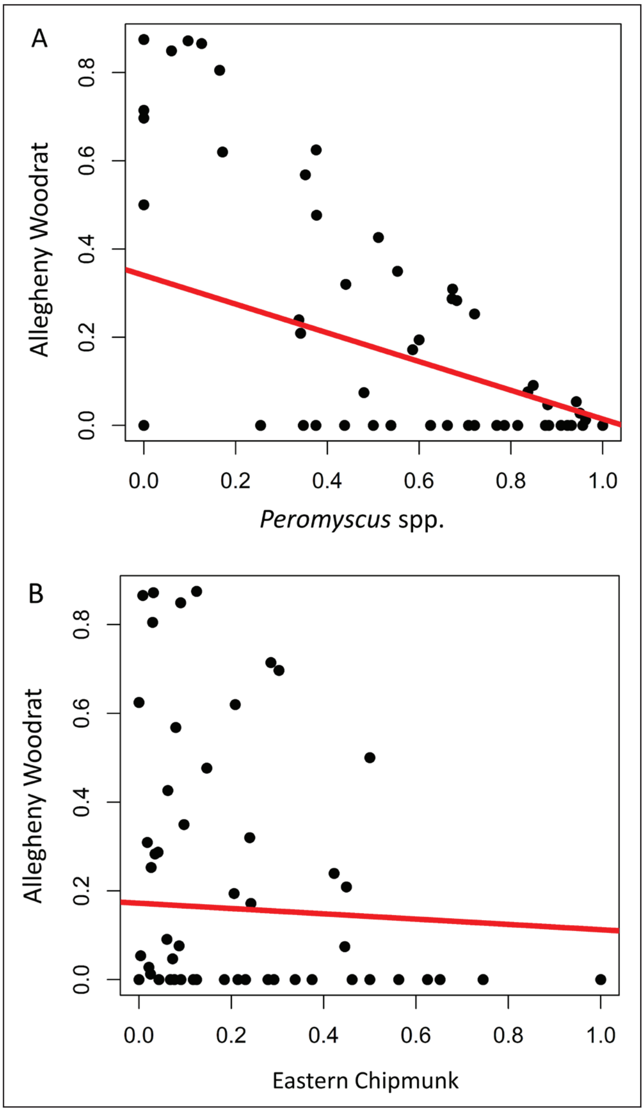

Figure 4. Relationship between *Neotoma magister* (Allegheny Woodrat) activity rates and that of 2 potential competitors: (A) *Peromyscus* spp. and (B) *Tamias striatus* (Eastern Chipmunk), based on remote camera detections at 83 sites in western Virginia and 2 in eastern West Virginia, 2017–2022. Activity rates for each species calculated as the number of image capture events/site divided by the total number of species/genera-wide capture events for that site.

midnight, likely in response to competition from dominant adult Eastern Woodrats. Thus, the post-midnight activity peak by Allegheny Woodrats during late summer or fall may be representative of juvenile and subadult individuals, whereas activity observed earlier in the night may be representative of adult individuals, a hypothesis that warrants further investigation.

Our results suggest competition avoidance via temporal partitioning occurs between Allegheny Woodrats and *Peromyscus* spp. Although direct physical altercations among *Neotoma* and other granivorous species is rare in captive situations (e.g., Howe 1978), and even more unlikely in field environments (Cameron 1971), temporal partitioning may be alleviating such direct competition. Because both species are largely nocturnal, we did not expect to see excessive adjustments to diel activity patterns of woodrats (e.g., shift from nocturnal to diurnal) when the 2 species occur sympatrically. As such, the shift in woodrat activity curves was minor but notable. The activity curve of woodrats at *Peromyscus*-present sites and *Peromyscus*-absent sites only overlapped by 84%. At *Peromyscus*-absent sites, the woodrat activity curve was wider with activity occurring before sunset and after sunrise. Additionally, peak woodrat activity at these sites occurred between midnight and 0300 h. At *Peromyscus*-present sites, woodrats activity appeared more restricted to dark hours. These fine-scale differences may facilitate coexistence in the specialists' habitat. However, it is important to note that both Allegheny Woodrats and *Peromyscus* spp. were detected at most sites in our study, and the sample size of Allegheny Woodrats at *Peromyscus*-absent sites was quite low compared to the sample size of woodrat observations at *Peromyscus*-present sites; it is possible that the observed activity curve is a spurious artifact of small sample size. Future efforts to assess interspecific competition between Allegheny Woodrats and *Peromyscus* spp. should include finer-scale observations of behavioral interactions and resource use.

Our prediction that activity rates of Allegheny Woodrats would be inversely related to activity rates of *Peromyscus* spp. was supported, suggesting that they are strong competitors in these karst habitats. Allegheny Woodrats and *Peromyscus* spp. could be described as foraging generalists, feeding opportunistically on seasonally abundant food types, such as soft fruits in the summer and nuts in the fall (Castleberry and Castleberry 2008, Randolph 1980, Wolff et al. 1985). Castleberry et al. (2003) proposed that due to Allegheny Woodrats' relatively larger body size, they are likely to competitively exclude other physically smaller species such as *Peromyscus* spp. Freeman (1974) suggested that this was the case for intrageneric *Neotoma albigula* Hartley (White-throated Woodrat) outcompeting the smaller *N. stephensi* Goldman (Stephen's Woodrat) for food and den-sites. However, Holbrook's (1979) removal studies of Stephen's Woodrats and 2 species of *Peromyscus*, and Sasso and Gaines' (2002) study of *Neotoma floridana smalli* Sherman (Key Largo Woodrat) and *Peromyscus gossypinus allapaticola* Schwartz (Key Largo Cotton Mouse) suggested that habitat specialization can be a greater influence than size difference. Small sample size and subsequent low power in wildlife studies is a common concern (Bissonette 1999). Due to the low sample size for nearly all other competitors, we could not analyze species-specific reactions of

Allegheny Woodrats with, for example, Appalachian Cottontails that, although are not emergent rock specialists per se, are a similar-sized species that occurs in these habitat types.

Our Raccoon and Allegheny Woodrat co-occurrence data were not what we expected; at sites further north in their geographic range, greater detections of Raccoons and Raccoon Roundworm were tied to decreased abundance (Page et al. 2012) or complete extirpation (Balcom and Yahner 1995, LoGiudice 2003) of Allegheny Woodrats. Our findings that co-occurrence was more common than expected by chance may anecdotally suggest that Raccoon Roundworm is not prevalent in Virginia. However, the lack of surveys to detect *Baylisascaris procyonis* in Virginia leaves us with more questions than answers. In summer 2022, we initiated collections of Raccoon scat to detect *Baylisascaris procyonis* from many of these study sites; our on-going analyses may better explain these patterns.

Remote cameras provide a passive method of data collection with minimal disturbance and relatively low labor requirements (Rowcliffe et al. 2008). Continued use of cameras to survey for uncommon Allegheny Woodrats in rough terrain remains a high priority in Virginia, and this survey method helps other states manage this species where it is imperiled (Castleberry et al. 2014). We recommend repeated surveys at the same sites, given the transient nature of woodrats at many of our study sites. Although the cameras' main goal was to detect woodrats, our use of ancillary remote-detecting camera photos emphasizes their value in documenting biodiversity in these karst habitats (McCarthy et al. 2010), and further helped us quantify relationships of Allegheny Woodrats with 2 presumptive competitors. Such information helps us elucidate threats to persistence of woodrat populations.

## Acknowledgments

Funding was provided by Virginia Department of Wildlife Resources through a Wildlife Restoration Program Grant from the US Fish and Wildlife Service. Funding and equipment support were provided by Virginia Tech and Radford University. We thank M. Beckner, J. Bentley, K. Black, J. Blevins, J. Brown, C. Bryan, J. Crotts, H. Custer, M. Dimas, K. Ellis, S. Felty, H. Greer, S. Hannabass, N. Harris III, R. Harris, A. Leon, E. Luehr, N. McDonald, B. Mullen Griffith, R.J. Powers, and S. Powers for field assistance. We are grateful to multiple landowners for allowing access to privately owned sites. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government. Data are not publicly available at this time from Virginia Department of Wildlife Resources.

## Literature Cited

Agostinelli, C., and U. Lund. 2017. R package 'circular': Circular statistics (version 0.4-93). Available online at https://r-forge.r-project.org/projects/circular/. Accessed 7 August 2022.

Balcom, B.J., and R.H. Yahner. 1995. Microhabitat and landscape characteristics associated with the threatened Allegheny Woodrat. Conservation Biology 10(2):515–525.

Barr Jr., T.C. 1967. Observation on the ecology of caves. American Naturalist 101(922):475–491.

Birch, G.L., G.A. Feldhamer, and W.G. Dyer. 1994. Helminths of the gastrointestinal tract of Raccoons in southern Illinois with management implications of *Baylisascaris procyonis* occurrence. Transactions of the Illinois State Academy of Science 87(3):165–170.

Bissonette, J.A. 1999. Small sample size problems in wildlife ecology: A contingent analytical approach. Wildlife Biology 5(1):65–71.

Cameron, G.N. 1971. Niche overlap and competition in woodrats. Journal of Mammalogy 52(2):288–296.

Campbell, J.W., M.T. Mengak, S.B. Castleberry, and J.D. Mejia. 2010. Distribution and status of uncommon mammals in the southern Appalachian Mountains. Southeastern Naturalist 9(2):275–302.

Castleberry, N.L., and S.B. Castleberry. 2008. Food selection and caching behavior. Pp. 93–106, *In* J.D. Peles and J. Wright (Eds.). The Allegheny Woodrat: Ecology, Conservation, and Management of a Declining Species. Springer-Verlag Publishers, New York, NY. 234 pp.

Castleberry, N.L., S.B. Castleberry, W.M. Ford, P.B. Wood, and M.T. Mengak. 2002. Allegheny Woodrat (*Neotoma magister*) food habits in the central Appalachians. American Midland Naturalist 147(1):80–92.

Castleberry, S.B. 2008. Home range, movements, and habitat selection. Pp. 63–74, *In* J.D. Peles and J. Wright (Eds.). The Allegheny Woodrat: Ecology, Conservation, and Management of a Declining Species. Springer-Verlag Publishers, New York, NY. 234 pp.

Castleberry, S.B., W.M. Ford, P.B. Wood, N.L. Castleberry, and M.T. Mengak. 2001. Movements of Allegheny Woodrats in relation to timber harvesting. Journal of Wildlife Management 65(1):148–156.

Castleberry, S.B., N.L. Castleberry, P.B. Wood, W.M. Ford, and M.T. Mengak. 2003. Fleas (Siphonaptera) of the Allegheny Woodrat (*Neotoma magister*) in West Virginia with comments on host specificity. American Midland Naturalist 149(1):233–236.

Castleberry S.B., M.T. Mengak, and W.M. Ford. 2006. *Neotoma magister*. Mammalian Species 789:1–5.

Castleberry, S.B., M.T. Mengak, and T.E. Menken. 2014. Comparison of trapping and camera survey methods for determining presence of Allegheny woodrats. Wildlife Society Bulletin 38:414–418.

Clair, C.D. 2015. Allegheny Woodrat (*Neotoma magister*) distribution across Pennsylvania. M.Sc. Thesis. Indiana University of Pennsylvania, Indiana, PA. 78 pp.

De Bondi, N., J.G. White, M. Stevens, and R. Cooke. 2010. A comparison of the effectiveness of camera trapping and live trapping for sampling terrestrial small-mammal communities. Wildlife Research 37:456–465.

Ford, W.M., S.B. Castleberry, M.T. Mengak, J.L. Rodrigue, D.J. Feller, and K.R. Russell. 2006. Persistence of Allegheny Woodrats, *Neotoma magister*, across the mid-Atlantic Appalachian Highlands landscape, USA. Ecography 29:745–754.

Freeman, J. 1974. Competition between two species of woodrats, *Neotoma stephensi* and *Neotoma albigula*. M.Sc. Thesis. Northern Arizona University, Flagstaff, AZ. 70 pp.

Higdon, S.D., and M.E. Gompper. 2020. Rest-site use and the apparent rarity of an Ozark population of Plains Spotted Skunk (*Spilogale putorius interrupta*). Southeastern Naturalist 19:74–89.

Hockman, J.G., and J.A. Chapman. 1983. Comparative feeding habits of Red Foxes (*Vulpes vulpes*) and Gray Foxes (*Urocyon cinereoargenteus*) in Maryland. American Midland Naturalist 110(2):276–285.

Holbrook, S.J. 1979. Habitat utilization, competitive interactions, and coexistence of three species of cricetine rodents in east-central Arizona. Ecology 60(4):758–769.

Hornsby, B.S., A.M. Ruiz, S.B. Castleberry, A.L. Castleberry, P.B. Wood, W.M. Ford. 2005. Fall movement of Allegheny Woodrats in harvested and intact stands in West Virginia. Northern Journal of Applied Forestry 22:281–284.

Howe, R.J. 1978. Agonistic behavior of three sympatric species of woodrats (*Neotoma mexicana*, *N. albigula*, and *N. stephensi*). Journal of Mammalogy 59(4):780–786.

Kanine, J.M., E.M. Kierepka, S.B. Castleberry, M.T. Mengak, N.P. Nibbelink, and T.C. Glenn. 2018. Influence of landscape heterogeneity on the functional connectivity of Allegheny Woodrats (*Neotoma magister*) in Virginia. Conservation Genetics 19:1259–1268.

Kniowski, A.B., and W.M. Ford. 2018. Spatial patterns of White-tailed Deer herbivory in the central Appalachian Mountains. Environmental Monitoring and Assessment 190:248. https://doi.org/10.1007/s10661-018-6627-1

Lashley, M.A., M.V. Cove, M.C. Chitwood, G. Penido, B. Gardner, C.S. DePerno, and C.E. Moorman. 2018. Estimating wildlife activity curves: Comparison of methods and sample size. Scientific Reports 8:4173. https://doi.org/10.1038/s41598-018-22638-6

Linkie, M., and M.S. Ridout. 2011. Assessing tiger–prey interactions in Sumatran rainforests. Journal of Zoology 284(3):224–229.

LoGiudice, K. 2003. Trophically transmitted parasites and the conservation of small populations: Raccoon Roundworm and the imperiled Allegheny Woodrat. Conservation Biology 17(1):258–266.

LoGiudice, K. 2006. Toward a synthetic view of extinction: A history lesson from a North American rodent. BioScience 56(8):687–693.

LoGiudice, K. 2008. Multiple causes of the Allegheny Woodrat decline: A historical–ecological examination. Pp. 23–41, *In* J.D. Peles and J. Wright (Eds.). The Allegheny Woodrat: Ecology, Conservation, and Management of a Declining Species. Springer-Verlag Publishers, New York, NY. 234 pp.

Lombardi, J.V., M.T. Mengak, and S.B. Castleberry. 2022. Allegheny Woodrat occupancy across western Virginia, United States. Wildlife Biology 2022:e01023. https://doi.org/10.1002/wlb3.01023

McCarthy, J.L., K.P. McCarthy, T.K. Fuller, and T.M. McCarthy. 2010. Assessing variation in wildlife biodiversity in the Tien Shan Mountains of Kyrgyzstan using ancillary camera-trap photos. Mountain Research and Development 30(3):295–301.

Meek, P.D., F. Zewe, and G. Falzon. 2012. Temporal activity patterns of the Swamp Rat *(Rattus leutreolus*) and other rodents in northeastern New South Wales, Australia. Australian Mammalogy 34:223–233.

Mengak, M.T. 2002. Analysis and summary of eleven years of Allegheny Woodrat trapping data in southwest Virginia, 1990–2000. Report to the Virginia Department of Game and Inland Fisheries, Richmond, VA, Contract No. 2002-04796. 52 pp.

Meredith, M., and M. Ridout. 2014. Overlap: Estimates of coefficient of overlapping for animal activity patterns. R package. Version 0.2.3. Available onlin at http://CRAN.R-project.org/package=overlap.

Morris, D.W., and D.L. Davidson. 2000. Optimally foraging mice patch use with habitat differences in fitness. Ecology 81:2061–2066.

Nouvellete, P., G.S.A. Rasmussen, D.W. McDonald, and F. Courchamp. 2011. Noisy clocks and silent sunrises: Measurement methods of daily activity patterns. Journal of Zoology 286:179–184.

Page, L.K., S.A. Johnson, R.K. Swihart, and K.R. Kazacos. 2012. Prevalence of *Baylisascaris procyonis* in habitat associated with Allegheny Woodrat (*Neotoma magister*) populations in Indiana. Journal of Wildlife Diseases 48(2):503–507.

Poole, E. 1940. A life-history sketch of the Allegheny Woodrat. Journal of Mammalogy 21(3):249–270.

Poulson, T.L., and W.B. White. 1969. The cave environment. Science 165(3897):971–981.

Powers, K.E., M.S. Dimas, A.I. Leon, and L.M. Vanmeter. 2020a. Observed predation of *Neotoma magister* (Allegheny Woodrat) by *Strix varia* (Barred Owl) in Virginia. Northeastern Naturalist 27(1):N1–N5.

Powers, K.E., M.T. Mengak, R.R. Sheehy, W.M. Ford, and R.J. Reynolds. 2020b. Bot fly parasitism of Allegheny Woodrats (*Neotoma magister*) in Virginia. American Midland Naturalist 184(1):62–72.

R Core Team. 2022. R: A language and environment for statistical computing.Version 4.2.2. R Foundation for Statistical Computing, Vienna, Austria. Available online at https://www.R-project.org/.

Randolph, J. 1980. Daily energy metabolism of two rodents (*Peromyscus leucopus* and *Tamias striatus*) in their natural environment. Physiological Zoology 53(1):70–81.

Ridout, M.S., and M. Linkie. 2009. Estimating overlap of daily activity patterns from camera-trap data. Journal of Agricultural, Biological, and Environmental Statistics 14(3):322–337.

Romero, A. 2009. Cave Biology: Life in Darkness. Cambridge University Press, New York, NY. 291 pp.

Rowcliffe, J., J. Field, S. Turvey, and C. Carbone. 2008. Estimating animal density using camera traps without the need for individual recognition. Journal of Applied Ecology 45(4):1228–1236.

Rowcliffe, J.M., R. Kays, B. Kranstauber, C. Carbone, and P.A. Jansen. 2014. Quantifying levels of animal activity using camera-trap data. Methods in Ecology and Evolution 5(11):1170–1179.

Sasso, C.R., and M.S. Gaines. 2002. Competition between *Neotoma floridana* and *Peromyscus gossypinus* on Key Largo, Florida. Florida Scientist 65(4):267–272.

Schmid, F., and A.Schmidt. 2006. Nonparametric estimation of the coefficient of overlapping theory and empirical application. Computational Statistics and Data Analysis 50(6):1583–1596.

Smyser, T.J., S.A. Johnson, L.K. Page, and O.E. Rhodes Jr. 2012. Synergistic stressors and the dilemma of conservation in a multivariate world: A case study in Allegheny Woodrats. Animal Conservation 15:205–213.

Stovall, E.A., and S.E. Hayslette. 2013. Activity patterns of Allegheny Woodrats in Tennessee. Southeastern Naturalist 12(4):748–756.

Thorne, E.D., K.E. Powers, R. Reynolds, M.E. Beckner, K.A. Ellis, and W.M. Ford. 2022. Comparison of survey methods to maximize detection of a declining rodent, the Allegheny Woodrat (*Neotoma magister*), in Virginia. Journal of Fish and Wildlife Management 13(2):396–406.

Timm, R.M., G.S. Jones, T.W. French, J.E. Cardoza. 2019. Historical documentation of the Allegheny Woodrat (*Neotoma magister*) in Massachusetts. Northeastern Naturalist 26(4):N46–N51.

Venarsky, M.P., B.M. Huntsman, A.D. Huryn, J.P. Benstead, and B.R. Kuhajda. 2014. Quantitative food-web analysis supports the energy-limitation hypothesis in cave stream ecosystems. Oecologia 176:859–869.

Virginia Department of Game and Inland Fisheries (VDGIF). 2015. Virginia's 2015 wildlife action plan. Virginia Department of Game and Inland Fisheries, Henrico, VA. 1135 pp.

Watson, G.G. 1962. Goodness-of-fit tests on a circle. II. Biometrica 49:57–63.

Webster, A.B., M.E. Pretprius, and M.J. Somers. 2021. The determinants of mesocarnivore activity patterns in highveld grassland and riparian habitats. African Journal of Wildlife Research 51:178–192.

Wiley, R.L. 1971. Activity patterns and movements of the Eastern Woodrat. Southwestern Naturalist 16:43–54.

Wolff, J., R. Dueser, and K. Berry. 1985. Food habits of sympatric *Peromyscus leucopus* and *Peromyscus maniculatus*. Journal of Mammalogy 66(4):795–798.

Wright, J. 2008. History and current status of the Allegheny Woodrat. Pp. 3–22, *In* J.D. Peles and J. Wright (Eds.). The Allegheny Woodrat: Ecology, Conservation, and Management of a Declining Species. Springer-Verlag Publishers, New York, NY. 234 pp.

**Appendix 1.** Summary of mammalian species with >50 documented remote camera events during surveys for *Neotoma magister* (Allegheny Woodrat; NEMA) across 83 sites in western Virginia and 2 in eastern West Virginia, 2017–2022. Presented are total number of species-specific detections across 13,002 camera events, as well as subset of events (no. in parentheses) at locations in which Allegheny Woodrats also were documented.

| Order/Family | Scientific name | Common name | No. events (with NEMA) |
|---|---|---|---|
| Order Artiodactyla | | | |
| Family Cervidae | | | |
| | *Odocoileus virginianus* | White-tailed Deer | 67 (24) |
| Order Carnivora | | | |
| Family Procyonidae | | | |
| | *Procyon lotor* | Raccoon | 433 (216) |
| Family Ursidae | | | |
| | *Ursus americanus* | American Black Bear | 148 (80) |
| Order Didelphimorphia | | | |
| Family Didelphidae | | | |
| | *Didelphis virginiana* | Virginia Opossum | 199 (105) |
| Order Lagomorpha | | | |
| Family Leporidae | | | |
| | *Sylvilagus obscurus* | Appalachian Cottontail | 65 (15) |
| Order Rodentia | | | |
| Family Cricetidae | | | |
| | *Myodes gapperi* | Southern Red-backed Vole | 71 (30) |
| | *Neotoma magister* | Allegheny Woodrat | 3833 |
| | *Peromyscus* spp. | Mouse - White-footed or Deer | 6521 (3330) |
| Family Sciuridae | | | |
| | *Marmota monax* | Woodchuck | 288 (155) |
| | *Sciurus carolinensis* | Gray Squirrel | 224 (175) |
| | *Tamias striatus* | Eastern Chipmunk | 1088 (559) |