Chapter 4
Home Range, Movements, and Habitat Selection

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Introduction

Home range, movements, and habitat selection are commonly used metrics to examine the response of vertebrates to habitat change. Localized habitat disturbance from land management activities, such as forest management, have been proposed as a threat to Allegheny woodrat (Neotoma magister) populations (Castleberry et al. 2001). Dependence upon rock outcrops makes Allegheny woodrats especially vulnerable to disturbance in habitat surrounding the outcrop. Local disturbances can change vegetative structure and resource distribution, and these have been shown to influence demographics, home range size, and microhabitat use of rodents (Yahner 1986, Bowers et al. 1990, Jones 1990, Lacher and Mares 1996, Taulman et al. 1998).

Few data are available on home range, movements, and habitat selection by the Allegheny woodrat. Furthermore, few studies have examined the effects of local disturbances on these aspects of woodrat ecology. In this chapter, I summarize the existing knowledge on home range, movements, and habitat use in general and how these variables are influenced by local disturbance, such as timber harvesting.

Home Range Size and Foraging Movements

Three published studies have examined home range size and movements of the Allegheny woodrat (Castleberry et al. 2001, Mengak 2002, Hornsby et al. 2005). When considered together, these three studies provide estimates of home range size and movements throughout the year from the east-central portion of the species’ range (Table 4.1). Published home range estimates are not available from other areas within the distribution.

Castleberry et al. (2001) used radiotelemetry to examine home range size and foraging movements in the Allegheny Mountains and Plateau region of east-central
### Table 4.1 Comparison of mean (±SE) home range and foraging movements of male (M) and female (F) Allegheny woodrats (*Neotoma magister*) among seasons reported in three published studies. Methods for each study are described in the text.

<table>
<thead>
<tr>
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<th>Summer¹</th>
<th>Fall²</th>
<th>Winter³</th>
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<tr>
<td></td>
<td>M</td>
<td>F</td>
<td>M/F</td>
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<tr>
<td>Home range (ha)</td>
<td>6.5</td>
<td>2.2</td>
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<td></td>
<td>(1.8)</td>
<td>(1.3)</td>
<td>-</td>
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<tr>
<td>Foraging rate (m/hr)</td>
<td>-</td>
<td>-</td>
<td>202.6</td>
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<tr>
<td></td>
<td>(9.2)</td>
<td>(23.1)</td>
<td>(22.6)</td>
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<tr>
<td>Maximum distance (m)</td>
<td>-</td>
<td>-</td>
<td>151.0</td>
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<td></td>
<td>(7.3)</td>
<td>(8.7)</td>
<td>(25.0)</td>
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<tr>
<td>Linear distance (m)</td>
<td>-</td>
<td>-</td>
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<td>(Site 1)</td>
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<tr>
<td>Linear distance (m)</td>
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<td>(Site 2)</td>
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¹ Summarized from Castleberry et al. (2001); home range data pooled across sexes, years, and timber harvest methods; movement data pooled across years and timber harvest methods.

² Summarized from Hornsby et al. (2005); data pooled across timber harvest methods.

³ Summarized from Mengak (2002).

West Virginia. They reported mean (±SE) home range estimates of Allegheny woodrats during summer (May–August) in east-central West Virginia as 6.5 (±1.8) ha and 2.2 (±0.3) ha for males (n = 19) and females (n = 18); respectively, and 4.4 (±1.0) ha for males and females combined. These home range estimates during summer were considerably larger than reported estimates from fall (Hornsby et al. 2005) and winter (Mengak 2002). On the same West Virginia study area using similar methods as Castleberry et al. (2001), Hornsby et al. (2005) reported mean home range size in fall (October–December) as 0.65 (±0.20) ha for males and females combined, and 0.49 (±0.13) ha and 0.78 (±0.35) ha for males (n = 3) and females (n = 4), respectively. Mengak (2002) used radiotelemetry and live-trapping to estimate mean home range size during winter in Virginia. Based on radiotelemetry, he reported mean home range size of four females at 0.18 (±0.003) ha and the home range of one male at 0.11 ha. Mean home ranges derived from trapping at two Virginia study sites were estimated at 0.19 (±0.14) and 0.23 (±0.20) for females (n = 14) and males (n = 15), respectively, and 0.07 (±0.08) and 0.06 (±0.05) ha for females (n = 10) and males (n = 9), respectively.

The larger home ranges in summer as compared to fall and winter are most likely explained by variation in movements of woodrats in response to seasonal variation in food availability. In spring and summer, woodrats forage primarily on fungi, green vegetation, and various fruits (Castleberry et al. 2002a, Castleberry and Castleberry Chapter 6) that may be located away from the rock outcrops. In late fall and winter, woodrats are relying primarily on cached foods and seldom move > 50 m from the
den (Hornsby et al. 2005). Although annual home range estimates are not available, they would likely be intermediate as the larger summer home range sizes are averaged with the smaller fall/winter home ranges.

Estimates of Allegheny woodrat home range, especially in summer, generally are larger than estimates reported for most other Neotoma species (Goertz 1970, Cranford 1977, Vaughan and Schwartz 1980, Lynch et al. 1994, Conditt and Ribble 1997). This disparity may be explained by N. magister's dependence on rocky habitats. Topping and Millar (1996a) reported home range size estimates for the bushy-tailed woodrat (N. cinerea), a species also associated with rock outcrops, obtained in spring and summer in Canadian Rockies. Their home range sizes were similar to those reported by Castleberry et al. (2001). Home ranges of bushy-tailed woodrats over a three-year period ranged from 5.10 (±0.84) ha to 7.27 (±0.70) for males and 3.13 (±0.65) to 4.44 (±0.33) for females. Topping and Millar (1996a) speculated that the relatively large home ranges they observed in the bushy-tailed woodrat were a consequence of dependence on rock outcrops for den sites. Outcrops may not be close to necessary food resources, so that individuals may need to forage at farther distances. Outcrops probably provide better protection from weather and predators and a more stable microclimate than exposed stick nests. Thus, the benefits of occupying a rock outcrop probably outweigh the energetic costs and possible predation risk associated with a large home range (Topping and Millar 1996a).

Movement patterns with regard to season appear to follow trends similar to home range size. Castleberry et al. (2001) and Hornsby et al. (2005) collected foraging movement data on the same study area using similar methods, with the primary difference between the studies being the season of data collection. In both studies, two indices of foraging movements were calculated from telemetry locations. Castleberry et al. (2001) reported mean foraging rate (defined as the sum of the linear distances between successive telemetry locations for each night, divided by the time elapsed between the first and last locations) of Allegheny woodrats in summer as 202.6 (+9.2) m/hr over all individuals combined. Maximum nightly distance traveled from the den (defined as the linear distance from the den to the farthest telemetry location for each night) averaged 151.0 (+7.3) m. In fall, Hornsby et al. (2005) reported estimates of mean foraging rate and maximum nightly distance traveled as 86.2 (+15.5) m/hr and 54.2 (+13.0) m, respectively, for all individuals. Mengak (2002) used trapping data to examine winter movements on two study sites in Virginia. He reported mean linear movement distances (calculated as the distance between the farthest two trap stations at which an animal was captured) as 169.7 m (+108.3) and 190.6 m (+92.3), and 102.1 (+68.8) and 104.0 (+68.1) for males and females, respectively.

The greater foraging movement distances in summer likely reflect the lack of food availability and reliance on cached food in fall and winter. Restricted movement away from the den due to the reliance on cached foods has similar effect on foraging movements as on home range. However, breeding in Allegheny woodrats begins in winter (Castleberry et al. 2006) and may influence movement patterns and rates. Mengak (2002) observed that movements determined through radiotelemetry appeared to increase in February with the onset of the breeding season.
There are limitations in using data from multiple studies for comparing seasonal home range size and movement distances among seasons. Differences in the data collection and analysis methods used in the three investigations may affect seasonal comparisons. Furthermore, to date, only one study from each season has been published. Nonetheless, results seem consistent with expectations based on woodrat life history. For example, home range size and movement distances obtained through trapping by Mengak (2002) in winter generally were consistent with those obtained by Hornsby et al. (2005) in fall using radiotelemetry. Similar home range and movements in fall and winter would be expected as woodrats rely on cached food throughout both the seasons. Castleberry et al. (2001) and Hornsby et al. (2005) used similar methods on the same study area to obtain home range sizes and movement distances in summer and fall, respectively. Thus, the differences observed likely are representative of actual seasonal differences rather than artifacts of methodological differences. However, additional studies of seasonal home range and movements are needed to validate previous results. Additional studies also are needed to investigate differences between sex and age classes, particularly as related to energetic requirements of breeding adult females (Cranford 1977, Topping and Millar 1996b).

Habitat Selection

Several investigations have provided a quantitative examination of characteristics of rock outcrops and surrounding areas associated with woodrat presence (Balcom and Yahner 1996, Myers 1997, Bommarito 1999, Krupa et al. 2004). Proportional use of available habitats within the home range (Castleberry et al. 2001) and characteristics of habitat at known foraging locations (Castleberry et al. 2002b) also have been studied. Other studies have noted use of various habitats by the species (Ivanovich et al. 2001, Wood 2001, Chamblin et al. 2004). In the following discussion I provide an overall synthesis of Allegheny woodrat habitat selection.

Several generalities regarding the association of habitat characteristics with Allegheny woodrat presence at rock habitats may be drawn from previous studies. The physical characteristics and size of the rock habitat are critical for woodrat presence. Myers (1997) and Krupa et al. (2004) concurred that larger rock outcrops with a moderate to high number of crevices are considerably more likely to be occupied. In both studies, > 84% of all occupied sites exhibited these two basic characteristics. Myers (1997) suggested that larger outcrops with numerous crevices provide increased rock surface largely devoid of leaf litter that provide foraging pathways on which woodrats are less likely to be detected by predators. Chamblin et al. (2004) also noted the importance of rock surface to woodrat presence, suggesting that the area of rock surface reflected the complexity of rock crevices and the ability of a site to provide adequate protection from predators. A complex network of crevices is important in providing denning areas that are inaccessible to many predators (Newcombe 1930, Poole 1940). Although most studies have examined emergent rock outcrops as woodrat habitat, Ivanovich et al. (2001) examined the potential importance of caves as Allegheny woodrat habitat in Kentucky and found that
susceptibility of the underlying geology to karstification (erosion of limestone to form caves) was an important variable in predicting occurrence.

Results of previous studies strongly suggest that increased probability of outcrop occupancy by woodrats is associated with increasing slope (Balcom and Yahner 1996, Myers 1997, Bommarito 1999, Ivanovich et al. 2001). Myers (1997) suggested that slope and important physical characteristics of outcrops are related. Outcrops on steep slopes are exposed to greater rates of erosion resulting in larger portions of the outcrop being exposed, increasing the rate of weathering. Increased weathering causes the rocks to break, crack, and fall. Breaking and cracking, along with the resulting accumulated fallen rock, produces numerous caves and crevices at the base of the outcrop that are important for woodrat presence. Bommarito (1999) suggested that the importance of steep slopes reflected the presence of cliffline habitats which were the only occupied rock formations on her Kentucky study area.

Most habitat studies have concluded that human disturbance in the proximity (generally <1000 m) of occupied outcrops does not influence Allegheny-woodrat occupancy. Balcom and Yahner (1996) and Myers (1997) found no evidence to suggest that disturbance in the proximity of rock outcrops affected woodrat presence. Common types of disturbance in these studies were major roads, railroad grades, and right-of-way clearings. Wood (2001) found that disturbance at the site was the single best predictor of woodrat abundance at New River Gorge National River in south-central West Virginia. However, counter to the expected outcome, woodrats were more abundant where disturbance levels from recreational rock climbing were greater. While it is likely that characteristics making rock habitats suitable for recreational rock climbing also make them suitable for woodrat presence, these results suggest that Allegheny woodrats are somewhat tolerant of human presence. Castleberry et al. (2001) found that clearcutting directly adjacent to outcrops had little effect on woodrat movements and that woodrats commonly foraged in one- to three-year-old clearcuts. In Kentucky, Ivanovich et al. (2001) found that occupied outcrops were farther from human disturbance, especially large (100-ha) disturbance patches, than random locations. However, their data suggest that woodrat presence is most likely influenced by human disturbance at the landscape scale (i.e., farther distances from the outcrop), as suggested by Balcom and Yahner (1996) and Ford et al. (2006), rather than local-scale disturbance.

Although Balcom and Yahner (1996) and Myers (1997) speculated that disturbance near colonies may increase predation from edge-related predators, such as great-horned owls (Bubo virginianus), neither study demonstrated any influence of local disturbance on woodrat presence. Mengak (2002) captured Allegheny woodrats in an old field as well as in the adjacent intact forest, concluding that there were no negative effects of the habitat disturbance on movement patterns. The types of disturbances most commonly found in the proximity of rock outcrops in previous studies, such as right-of-ways and clearcuts, may contain adequate vegetative cover to provide protection from avian predators. Other types of disturbance that result in greater reductions in vegetative cover (e.g., urban development or agricultural development) may have negative consequences.
Studies examining the influence of overstory stand condition have demonstrated variable results. The apparently lack of congruency in results may be in part due to lack of standardization in methods used to quantify overstory condition. Wood (2001) examined tree density in stem size classes and found evidence of a positive relationship between 3.0 and 8.0 cm DBH tree density and woodrat abundance. Using similar methods, Myers (1997) found a negative relationship between woodrat presence and density of trees in the 0.0–15.0 cm DBH size class, but larger diameter trees were present at occupied as well as unoccupied sites. Bommarito (1999) found a positive relationship between woodrat presence and tree density, but did not examine stem size classes separately. Balcom and Yahner (1996) found a positive relationship between overstory basal area and woodrat presence, but did not examine tree density. The lack of standardization in describing overstory condition among the studies makes drawing definite conclusions difficult. Nonetheless, all studies indicate that some level of overstory cover at the rock outcrop is necessary for woodrat presence.

Although overstory tree cover appears to be an important factor influencing presence, woodrats appear to tolerate a wide range of canopy cover. Chamblin et al. (2004) found that woodrats occupying drainage channels associated with reclaimed coal mines in southern West Virginia were associated with lower levels of overstory tree cover (~50%) than most other studies. Although Castleberry et al. (2001) found no effect of canopy removal adjacent to outcrops from clearcutting on woodrat foraging movements, they noted that woodrats were not found in rock outcrops where the canopy directly over the outcrop had been removed. The increase in solar radiation resulting from complete canopy removal may create unsuitable thermal conditions in the exposed outcrop.

Castleberry et al. (2001) examined proportional use of clearcut and intact forest at clearcut sites where woodrats had access to the harvested area on one side of the outcrop and intact forest on the other. Selection of the two habitats did not differ from random, indicating that woodrats used clearcuts and adjacent forested areas in proportion to their availability. The authors suggested that use of clearcut areas in summer is facilitated by dense growth of ground-level vegetation and an increase in food resources following canopy removal. Previous studies on other small mammal species have demonstrated increases in abundance following clearcutting, presumably in response to increases in ground cover and food availability (Kirkland 1977, Monthey and Soutiere 1985, Clough 1987). Succulent growth from hardwood stump sprouts in clearcuts represents a more abundant and palatable food for woodrats than vegetation under the forest canopy. Although Castleberry et al. (2001) recommend harvest planning that retains intact forest immediately covering rock outcrops on one adjacent side, they suggest that resource availability can be sufficiently maintained, or possibly improved, by timber harvests in the proximity of occupied outcrops.

In the only study to examine foraging habitat selection, Castleberry et al. (2002b) examined microhabitat characteristics of Allegheny woodrat foraging locations in relation to timber harvesting practices. Individuals at clearcut, diameter-limited, and intact forest stands were radio-collared and located during nocturnal foraging bouts. Physical and vegetative characteristics were measured at the foraging locations
and were compared to random locations within each individual’s foraging range. Interestingly, the type of harvest method did not influence selection of foraging sites by woodrats. However, when foraging and random locations were compared across harvesting methods, it became apparent that woodrats selected foraging sites with more diverse understory vegetation, regardless of overstory stand condition. The authors concluded that Allegheny woodrats are capable of tolerating a broad range of macrohabitats created through anthropogenic disturbance, as evidenced by presence at clearcut, diameter-limit, and intact forest stands, but habitat selection is largely determined by microhabitat factors. They further suggested that selection at the microhabitat scale is likely explained by the high mobility of the species and its generalist herbivore diet. Allegheny woodrats are capable of searching larger areas to locate suitable foraging microhabitats than other small mammals.

Local Habitat Disturbance and Conservation of the Species

In general, Allegheny woodrats appear tolerant of local (generally defined as <1000 m from a site) disturbance as long as overstory tree cover is retained at the rock outcrop on at least one adjacent side (Castleberry et al. 2001). Several studies have examined the influence of local disturbance on presence or abundance, and all concluded that disturbance had little or no influence (Balcom and Yahner 1996, Myers 1997, Ford et al. 2006). In fact, one study noted a positive relationship between woodrat abundance and anthropogenic disturbance (Wood 2001). The few studies that examined woodrat home range and movements have suggested little influence of local disturbance. However, there are several factors to be considered regarding the relationship between Allegheny woodrats and local disturbance.

The influence of local disturbance on home range and movements appears to be variable, depending on seasonal and annual differences in food resources. Castleberry et al. (2001) noted that patterns in home range size and foraging movements were larger and more variable in the first year of their study and largest in stands that had been harvested using a diameter-limit approach. They speculated that the patterns were related to differences in hard mast, primarily acorn, abundance. They only observed differences in home range and foraging movements in the year following a poor mast crop, and observed the greatest increase at the diameter-limit harvest sites where mast producing trees were scarce and widely scattered and where understory vegetation was limited. Low mast abundance and low understory diversity may have required woodrats to travel farther distances while foraging, subsequently increasing home range size. In fall, Hornsby et al. (2005) reported no differences in home range and movements between harvested and unharvested stands. The authors suggested that woodrats are affected less by timber harvesting in fall and winter when movements away from the outcrop are restricted.

Studies that have examined canopy cover in relation to the presence of woodrats have documented that a minimum level of canopy cover directly over the rock outcrop site is critical for woodrat presence. Most have found that occupied sites
have canopy cover >71.5% (Myers 1997, Bommarito 1999). However, Chamblin et al. (2004) found that woodrats occupied rocky drainage channels with a mean canopy cover of 47.9%, ranging from 10% to 100%. Castleberry et al. (2001) noted that woodrats were not found in rock outcrops where the canopy directly over the outcrop had been removed. Interestingly, no studies that have quantitatively examined overstory condition relative to woodrat presence have found canopy cover to be an important variable in predicting presence, suggesting that above a minimum threshold level woodrats tolerate a broad range of canopy cover.

Although canopy cover at the rock outcrop is important for woodrat presence, canopy cover in foraging areas appears less important. Several studies noted disturbances such as roads, railroad and utility right-of-ways, and clearcuts adjacent to colony sites (Balcom and Yahner 1996, Myers 1997, Castleberry et al. 2001, 2002b). It is likely that these types of disturbances provide foraging opportunities as well as adequate cover for protection from predators (Castleberry et al. 2001). Similarly, Sakai and Noon (1997) concluded that dusky-footed woodrats (N. fuscipes) in northwestern California apparently were less susceptible to predation by northern spotted owls (Strix occidentalis caurina) when foraging in young, dense habitats than in more open, older-aged forests.

The influence of local habitat disturbance on gene flow among colonies, and subsequently on population structure, is unknown. Studies on movements and habitat use (Castleberry et al. 2001, 2002b) have shown that Allegheny woodrats commonly cross roads, right-of-ways, and harvested stands, suggesting that these types of disturbances do not severely impede dispersal among geographically proximate colonies. Larger scale disturbances and habitat modifications, such as intensive agriculture and residential development, appear to have a greater influence on population structure (Balcom and Yahner 1996, Ford et al. 2006). These disturbance types result in large-scale habitat fragmentation that may isolate rock outcrops and reduce recolonization probabilities (Ford et al. 2006, LoGiudice 2006). LoGiudice (2006) speculated that impeded dispersal as a result of habitat fragmentation was responsible for extirpation of the species in New York.

Although the body of literature suggests that local disturbance is not a major factor contributing to the decline of the species, most of the available data have been gathered from within the core of the distribution where populations appear relatively stable. The influence of local disturbance is not well studied in the northern periphery of the distribution where population declines are most pronounced. LoGiudice (2006) suggested that habitat disturbance has played a role, acting in concert with several other factors, in the observed population declines in those areas.

Conservation and Management of Declining Species

In this chapter, I have provided an overview of home range, movements, and habitat use by Allegheny woodrats. Additionally, I have summarized the available literature on the response of the species to local habitat disturbance. Using home range and movements as metrics for examining the response of a species to habitat change
has general applicability to other declining species. However, some factors should be taken into consideration when relating inferences drawn from the Allegheny woodrat to other species.

The foraging strategy of the Allegheny woodrat may make inferences particularly pertinent to other central-place foraging species. The typical assumption in habitat use studies is that an individual’s selection of a habitat is only influenced by the habitat type (Rosenberg and McKelvey 1999). Central-place foraging species leave from and return to a central location during foraging bouts (e.g., a nest; Orians and Pearson 1979). In this case, distance from the central location may influence an individual’s use of a particular habitat type. Rosenberg and McKelvey (1999) found that traditional methods of assessing habitat selection were biased when applied to central-place foraging species, potentially leading to erroneous conclusions. Similarly, the degree to which a species is influenced by local disturbance may differ for central-place foragers. Allegheny woodrats are less sensitive to disturbance in the proximity of the rock outcrop, possibly because, as central place foragers, proportionally more of their movements occur closer to the outcrop. Whether other central-place foraging species exhibit a similar relationship with local disturbance is unknown, but foraging strategy of the species in question should be considered when applying conclusions herein to other species.

Although the literature suggests that local habitat disturbance has little effect on Allegheny woodrats, most of the information come from areas within distribution where population numbers are apparently stable. How those results relate to areas where populations are less stable, or how the results relate to other species, is unknown. LoGiudice (2006) suggested that multiple factors acting in concert have caused Allegheny woodrat declines in the northern portions of the distribution. For example, local habitat disturbance has little or no effect in areas where agricultural and urban development is limited. However, habitat disturbance where agricultural and urban development is high may result in an increase in raccoon abundance (Prange et al. 2005) which can facilitate transmission of raccoon roundworm (Baylisascaris procyonis; LoGiudice 2003). Although conducting research in more stable areas may be more conducive to obtaining adequate sample sizes from which to make inferences regarding declining populations, caution must be taken when applying those results to areas where other factors may be at work.

References


