Chapter 5
Den Use Behavior of Allegheny Woodrats Inhabiting Rock Outcrops in Pennsylvania

John D. Peles and Janet Wright

Introduction

Since the decline of the Allegheny woodrat (*Neotoma magister*) was first noticed in the late 1970s, most information concerning the ecology of this species has been acquired from studies focusing on its association with rocky habitats (Newcombe 1930, Poole 1940, Hall 1985, Wright and Butchkoski 2005, Castleberry et al. 2006). This habitat specialization has been implicated in microhabitat selection during foraging (Castleberry et al. 2001), home range movements (Castleberry et al. 2002, Hornsby et al. 2005), and persistence of woodrat populations (Balcom and Yahner 1996, Ford et al. 2006).

Less attention has been given to understanding how behavioral characteristics of *N. magister* may render this species vulnerable to decline and present a challenge for conservation and management. The importance of integrating behavioral ecology with conservation biology has received increased attention in recent years (Caro 1998, Morris 2001) and has been applied to conservation questions involving small mammals such as the Stephens' kangaroo rat (*Dipodomys stephensi*; Brock and Kelt 2004) and the riparian woodrat (*N. fuscipes riparia*; Gerber et al. 2003).

There are indications that behavioral characteristics are relevant to the conservation ecology of *N. magister* as well. For example, Castleberry et al. (2001) showed that Allegheny woodrats willingly forage in timber clearcuts adjoining the rock patches they inhabit. While this may have been a benign or even advantageous behavior in former times when occasional fires or blowdowns created temporary clearings, the same tendency may now expose foraging woodrats to increased predation when large expanses of the forest matrix are routinely removed (Castleberry Chapter 4). LoGiudice (2001) demonstrated that *N. magister* harvest dried, seed-loaded scats such as those of raccoons, retrieving them intact to a food cache rather than consuming them when found. While an appropriate behavior in terms of nutrition, this tendency maximizes exposure of woodrats using the cache to the

J.D. Peles
Pennsylvania State University-Greater Allegheny, McKeesport, PA 15132

lethal roundworm *Baylisascaris procyonis* harbored in raccoon feces (LoGiudice 2001).

In this chapter, we examine how a particular set of behaviors—those that determine the use and spacing of dens in rock habitat—influences Allegheny woodrat ecology. Individual woodrats construct nests of plant fibers in caves or large crevices within rocks (Newcombe 1930, Wright and Butchkoski 2005). Nests are also likely to be constructed beneath the surface of rock outcrops or other rocky habitats that are not accessible to observers. Similar habits of nest construction within rocky habitats are exhibited by the bushy-tailed woodrat (*N. cinerea*; Escherich 1981, Hickling 1987), and several studies point to availability of suitable den sites as a limiting factor for local population size of this species (Escherich 1981, Hickling 1987, Moses and Millar 1992, Topping and Millar 1996a,b).

To complicate the picture, Moses and Millar (1992) have suggested that agonistic behavior by *N. cinerea* influences population size at rock outcrops because not all potential den sites are used. Similar observations for Allegheny woodrats indicate that intraspecific behaviors or individual preferences could be influencing den use. For example, Allegheny woodrats are known to be aggressive toward nonkin (Kinsey 1976, 1977) and this might limit proximity of simultaneously occupied den sites. Wright (1998) observed that woodrats change den sites frequently and suggested that they preferentially use certain den sites when available. Thus, behavioral characteristics of woodrats could potentially further limit the size of a local population within an area that already has a finite number of den sites.

Knowledge of specific ecological requirements of *N. magister* is critical to the development of a long-term strategy for the conservation and management of this species. In this chapter, we describe results from an intensive four-month radiotelemetry study of den use behavior by adult Allegheny woodrats inhabiting rock outcrops in southwestern and central Pennsylvania. Specifically, the purpose of the investigation was to determine: (1) frequency of den relocations and proportion of time spent at den sites by individual woodrats; (2) frequency of occupation for individual dens; and (3) spatial distribution of simultaneously occupied dens during a four-month period. Results of this investigation, along with findings from our long-term studies of den use in woodrats, are used to develop a conceptual model of the influence of den selection and den use behaviors of woodrats on the dynamics of local populations and metapopulations. We then apply our findings to the conservation and management of the Allegheny woodrat as well as other declining species.

**Short-Term Study of Den Use**

**Study Sites**

Woodrats were studied over a period of four months at three sites—two (Strangford Cave and Strangford Mountain) in southwestern Pennsylvania and one (Cove Mountain) in the central portion of the state. Strangford Cave (Indiana County, 40°25' N,
79°12' W) is an abandoned quarry along the Conemaugh River and is characterized by rock highwall with numerous large openings ("caves") and crevices with a series of sandstone boulders along the base of the highwall. Strangford Mountain (Indiana County, 40°25' N, 79°10' W) and Cove Mountain (Perry County, 40°21' N, 76°56' W) consist of sandstone boulder outcrops along ridgetops.

**Methods**

Den fidelity and den selection behavior of woodrats were monitored by radiotelemetry at each site during an early summer period (P-I) and a late summer/early fall period (P-II) in 2002. At Strangford Cave and Strangford Mountain, P-I covered 21 June–26 July, and P-II was 19 August–11 September. At Cove Mountain, P-I covered 17 June–24 July, and P-II was 18 August–12 September. The end of P-I and the beginning of P-II were separated by a hiatus of three or four weeks at each site. Following the end of P-II, woodrats at Cove Mountain were monitored 1–2 times per week until 6 November 2002.

Live-trapping was conducted prior to P-I, between monitoring periods, and following P-II. During each live-trapping period, Tomahawk live traps baited with sliced apples were used, and traps were set for two nights at each site (n = 40 traps per night). This trapping protocol was based on experience demonstrating two nights of live-trapping was sufficient to capture virtually all woodrats present. For example, during studies between 1994 and 2006 at these sites, we conducted 16 sessions with multiple-night trapping (three or four nights within a week). Of 97 captures in these sessions, only two woodrats were first caught after the second night of trapping.

Upon first capture, body mass, sex, and reproductive condition were determined, and each individual was given an identifying mark with an ear tattoo. Woodrats used for radiotelemetry were fitted with a 3.5 g temperature-sensitive radiotransmitter (PD-2CT; Holohil Systems, Ltd., Carp, Ontario) and released at the point of capture. All adults (>225 g; Mengak 2002) captured prior to P-I and between monitoring periods were fitted with radiotransmitters. Thus, the total number and sex ratio of woodrats monitored at each location and during each period varied based on the number of adult woodrats present. For analysis, individuals present for the entire study period (P-I through P-II) were classified as residents and those present during only P-I or P-II were classified as nonresidents.

Radiotelemetry was used to track woodrats to their den locations by homing (White and Garrott 1990) during daylight hours, and geographic coordinates, determined by GPS, were recorded for each location. Study sites were visited three times per week during each of the monitoring periods with no more than two days between visits. The location of all radio-collared individuals was recorded for each visit to a study site. Because the location of individuals was determined during daylight hours when woodrats are not active, these locations were presumed to represent den sites. Dens located within the main rock outcrop were classified as central dens and those associated with isolated rock formations separated from the main rock outcrop by >25 m were classified as peripheral dens.
Whenever a woodrat was tracked to a new location, the date of movement was estimated as the midpoint between the last known date of occupancy in the previous den and the first date that it was tracked to the new den. Maximum percentage of time spent at any given den was determined for each woodrat. This value was calculated by expressing the greatest number of days for which an animal was estimated to have occupied a den without moving as a percentage of the total days the animal was known to be present at the rock outcrop.

Multi-Year Studies of Den Use

In order to better understand the use of den sites and its associated behavior, we also examined data from several long-term studies of den use conducted by one of us (J. Wright) at other locations in central Pennsylvania. Study sites included Stoney Mountain (40°25' N, 76°48' W) in Dauphin County, Waggoners Gap (40°16' N, 77°16' W) in Cumberland/Perry Counties, and Bowers Mountain (40°16' N, 77°30' W) in Perry County. Each site is a sandstone boulder outcrop located along a ridgetop.

Radiotelemetry was conducted over extended periods of time and was used to determine the location of woodrat dens during the following time periods: Stoney Mountain: May–September 1995 (n = 5 woodrats), April–October 1996 (n = 4); Waggoners Gap: July 1996–June 1998 (n = 1); May–December 1997 (n = 6); Bowers Mountain: July–November 2002 (n = 7), June–November 2003 (n = 4), October 2004–March 2005 (n = 4). The frequency at which den locations were determined varied among study sites (three times per week to once per month), and not all woodrats were present for the entire time period. Because of differences in the frequency of tracking and the length of study periods for the multi-year studies, statistical analyses were not performed for these data. However, results from these studies are presented, where appropriate, to provide additional insight into the den use behavior of woodrats.

For one aspect of the analysis—the influence of season on the tendency of woodrats to change dens—the den location data from the short-term (Cove Mountain) and multi-year studies in central Pennsylvania were combined. Each change of den from the previous tracking session for an individual was categorized by month. An index of den-changing frequency for each month of the year was then developed by expressing the total number of den changes during each month as a fraction of the total number of tracking observations for that month.

Results and Discussion

Live-Trapping

Results of live-trapping at Strangford Cave and Strangford Mountain (Fig. 5.1) reflect the presence of several juveniles prior to P-I (body mass \( \bar{X} = 174 \text{ g} \);
range = 105–210 g). Two juveniles (200 g each) remained at these sites at the end of P-I and only one (X = 220 g) remained at the end of P-II. No juvenile woodrats were trapped at Cove Mountain during the study.

Conclusions regarding den use and selection behavior of radio-collared individuals are valid only if these behaviors are not influenced by the presence of other adult woodrats whose movements were not monitored. No additional adults were captured at Strangford Cave and Cove Mountain at the end of P-I or P-II, and none were captured at Strangford Mountain at the end of P-II (Fig. 5.1). However, three previously unknown adults were present at Strangford Mountain following P-I. Although it is unknown when these individuals arrived at the site, any influence that they might have had on movements appears to be minimal given that the radio-collared adults at the site did not change dens during P-I.

**Den Locations**

Den locations (n = 286) were determined for 12 adult woodrats (5 males, 7 females) during the investigation, and 7 (3 males, 4 females) individuals were present during both P-I and P-II. Twenty-seven different dens were used by the 12 woodrats monitored at Strangford Cave, Strangford Mountain, and Cove Mountain (Table 5.1). Approximately one-fourth (25–29%) of dens at each site were classified as
Table 5.1 Summary of dens used by Allegheny woodrats (*N. magister*) at study sites in Indiana County (Strangford Cave, Strangford Mountain) and Perry County (Cove Mountain), Pennsylvania during 2002. Number of reused dens refers to dens used by more than one woodrat, but at different times.

<table>
<thead>
<tr>
<th>Site</th>
<th>Total known dens</th>
<th>Central dens</th>
<th>Peripheral dens</th>
<th>Maximum percent of known dens occupied (%)</th>
<th>Number of reused dens</th>
</tr>
</thead>
<tbody>
<tr>
<td>Strangford Cave</td>
<td>12</td>
<td>9</td>
<td>3</td>
<td>33</td>
<td>2</td>
</tr>
<tr>
<td>Strangford Mountain</td>
<td>8</td>
<td>6</td>
<td>2</td>
<td>63</td>
<td>2</td>
</tr>
<tr>
<td>Cove Mountain</td>
<td>7</td>
<td>5</td>
<td>2</td>
<td>43</td>
<td>1</td>
</tr>
<tr>
<td>All Sites</td>
<td>27</td>
<td>20</td>
<td>7</td>
<td>44</td>
<td>5</td>
</tr>
</tbody>
</table>

Peripheral. The proportion of total observations occurring at peripheral dens did not differ significantly between time periods ($\chi^2 = 2.84, p > 0.05$) or between residents and nonresidents ($\chi^2 = 3.74, p > 0.05$). The percentage of peripheral dens at Stoney Mountain (22% of 9 den sites) was similar to the three short-term sites, whereas peripheral dens represented a much higher percentage of den sites at Bowers Mountain (59% of 17 dens) and Waggoners Gap (69% of 13 dens).

Male woodrats (49%) were located for a significantly ($\chi^2 = 36.15, p < 0.001$) greater proportion of the time at peripheral dens compared to females (23%). Occupancy of central dens by males was limited to those that were a minimum of 40 m from the nearest female-occupied den. We also observed two cases where a female woodrat apparently displaced a male from a central den. Female territoriality has been documented in the southern plains woodrat (*N. cinerea*; Conditt and Ribble 1997) and eastern woodrat (*N. floridana*; Goertz 1970). Although territoriality has not been studied in *N. magister*, territorial behavior by females is suggested by the fact that this sex occupies smaller home ranges than males (Castleberry et al. 2002, Castleberry Chapter 4) and are aggressive toward nonkin (Kinsey 1976, 1977). Thus, our results suggest the restriction of males to peripheral habitats by female territoriality.

There was little visual evidence (i.e., presence of scat or caches) of woodrats in the small, isolated rock formations that contained peripheral dens, and these sites are typically not the focus of live-trapping efforts. However, peripheral den sites represent landscape features that should not be overlooked in the development of management plans for this species. At the very least, the availability of peripheral dens around one or more large rock outcrops would maximize the size of a local woodrat population. This is especially relevant for areas such as Waggoners Gap and Stoney Mountain where a high percentage of dens are peripheral. Furthermore, if males are restricted to peripheral den sites by female territoriality, these areas would be necessary for males to remain near rock outcrops and have access to females during periods of reproduction. Peripheral den sites also represent landscape elements that could increase connectivity and facilitate the movement of
individuals between rock outcrops in a local population or between two local populations in a metapopulation (Fahrig and Merriam 1985).

**Quantity and Quality of Den Sites**

Results indicate that the number of individuals inhabiting a rock outcrop and its associated peripheral areas was not limited by the number of den sites. Of the total number of dens documented at Strangford Cave, Strangford Mountain, and Cove Mountain, the maximum percent of dens occupied during any given time was 63% (Table 5.1). Similarly, maximum percent occupancy at the multi-year study sites ranged from 24 to 56%.

Species of North American *Neotoma* exhibit both a den-centered ecology and habitat specificity that creates the potential for the availability of den sites to limit the density of breeding adults within local populations (Toppling and Millar 1996a, Dial 1988). The influence of number of den sites on local population size has been documented in several studies of *N. cinerea* inhabiting rock outcrops in western Canada (Escherich 1981, Hickling 1987, Moses and Millar 1992, Toppling and Millar 1996b). Support for this notion also is provided by results of studies involving other species of *Neotoma*, such as the eastern woodrat (*N. floridana*; HaySmith 1995) and white-throated woodrat (*N. albicula*; Newton 1990) that have very different habitat requirements from *N. magister*. Thus, the habitat-specific nature of *N. magister* (Newcombe 1930, Poole 1940, Hall 1985, Castleberry et al. 2006) makes it likely that the maximum size of local populations of this species also is limited by the availability of den sites. However, total quantity of den sites alone is probably no longer a limiting factor in regions such as southwestern and central Pennsylvania where woodrat populations have declined (Hall 1985; Wright and Butchkoski 2005, Castleberry et al. 2006).

At least one den at each study site was used by more than one woodrat during the investigation (Table 5.1). All five of the dens occupied by more than one woodrat were central dens and four were occupied by different woodrats in successive tracking sessions. The high level of use for some specific dens suggests the existence of preferred den sites. McGowan (1993) also observed occupancy of certain dens in succession by more than one individual in a study of translocated Allegheny woodrats in New York. Similar observations have been made in studies of *N. f. floridana* (HaySmith 1995) and *N. micropus* (Merkelz and Kerr 2002).

The existence of preferred den sites in this and other investigations suggests differences in den quality (McGowan 1993, HaySmith 1995, Merkelz and Kerr 2002). Woodrats use dens for a number of reasons including shelter, protection from predation, rearing of young, and storing of food caches (Hickling 1987, Kelly 1989, Newton 1990). Variation in the suitability of individual den sites for these and other functions likely results in differential preference for certain dens. Although the quality of a den site might be enhanced by the presence of a nest or food cache left by the previous occupant (Poole 1940), there are a variety of other physical (e.g., microclimate) and biological (e.g., access to foraging sites) factors that could affect
the suitability of a den for meeting specific needs. The availability of high-quality den sites would be especially important for female woodrats occupying centrally located dens on the main rock outcrop during periods of reproduction. Dens of poor quality also could limit the amount of time that an individual may occupy the den or may even lead to increased mortality. Mortality of *N. lepida* has been shown to be correlated with decreasing den quality (Brown et al. 1972).

**Den Fidelity and Behavior**

Although the mean maximum percentage of time spent by an individual at any given den was relatively high (68%), nearly all woodrats at Strangford Cave, Strangford Mountain, and Cove Mountain changed dens at least once (Table 5.2). In fact, only two individuals remained in the same den for the entire four-month period, and the mean number of dens used per woodrat was greater than 1.0 at each of the study sites. Similarly, in the multi-year studies, 50% of all individuals moved at least once, and the mean number of dens used per woodrat was greater than 1.0 at all sites.

At the three short-term sites, number of den relocations did not differ significantly between males and females \((t = 0.54, p > 0.05)\) or between P-I and P-II \((t = 0.43, p > 0.05)\). These results are in contrast with those from a similar study of den relocation in *N. cinerea* (Holmes 1995). In that investigation, Holmes (1995) used radiotelemetry to track den locations of 11 adult *N. cinerea* from July through November. All females except one each maintained a single den throughout the study period. In contrast, all males changed dens during the study and averaged nearly three den relocations per individual (Holmes 1995).

Although number of relocations was not significantly different for residents compared to nonresidents \((t = 1.92, p > 0.05)\), nonresidents \((\bar{X} = 2.8 \pm 1.6 \text{ SD})\) changed dens more than twice as often as residents \((1.1 \pm 1.3)\). Mean maximum percent time spent at any given den differed significantly \((t = 4.11, p = 0.003)\) between nonresidents \((47.1 \pm 8.2)\) and residents \((83.3 \pm 20.9)\). It is not known whether individuals that disappeared by the end of P-I represented over-wintering adults or those that immigrated to the sites during the early spring. However, differences in den fidelity and movements between residents and nonresidents suggest that at

| Table 5.2 Summary of den use behavior by Allegheny woodrats (*N. magister*) at study sites in Indiana County (Strangford Cave, \(n = 4\); Strangford Mountain, \(n = 5\)) and Perry County (Cove Mountain, \(n = 3\)), Pennsylvania during 2002 |
|-----------------|-----------------|-----------------|-----------------|-----------------|
| Site            | Mean number of different dens used | Mean number of relocations | Mean maximum percent time at a den (%) | Mean distance moved (m) | Percent using multiple dens (%) |
| Strangford Cave | 3.0              | 2.0              | 72              | 61.6             | 50                           |
| Strangford Mt.  | 1.8              | 1.2              | 70              | 24.5             | 80                           |
| Cove Mountain   | 2.3              | 2.7              | 61              | 50.0             | 100                          |
| All Sites       | 2.3              | 1.8              | 68              | 47.3             | 83                           |
least some adults could be forced to leave the rock outcrop or experience mortality because of difficulty in becoming established at a den site. Similarly, adults entering the rock outcrop prior to P-II exhibited much greater movement among dens than those present during the entire study period. These increased movements by some individuals could reflect a lack of unoccupied quality den sites and/or exclusion from quality sites on the main rock outcrop as a result of agonistic behavior.

Female aggression toward nonkin individuals is exhibited by *N. magister* (Poole 1940, Kinsey 1976, 1977; Castleberry et al. 2002) and other species of *Neotoma* (Dial 1988, Moses and Millar 1992, Conditt and Ribble 1997). In fact, *N. magister* has been shown to form dominance hierarchies in confined populations and both males and females exhibit agonistic behavior toward all conspecifics (Kinsey 1976, 1977). Thus, agonistic behavior could account for the apparent difficulty of nonresidents in becoming established within an occupied den site. This behavior would also contribute to the low rate of juvenile persistence in rock outcrops that we have observed in this and other investigations (Fig. 5.1; J. Peles and J. Wright pers. obs.).

The mean nearest-neighbor distance between simultaneously occupied dens at the three study sites was 89 m, and nearest-neighbor distances for some dens were greater than 150 m (Fig. 5.2). Mean nearest-neighbor distance between dens simultaneously occupied by two females ($\bar{X} = 81$ m) did not differ significantly ($t = 0.12, p > 0.05$) from those occupied by a male and female (78 m). Because there were relatively few pairs of simultaneously occupied dens for males ($\bar{X} = 66$ m), these were not compared statistically to male/female or female/female pairs. In contrast, mean nearest-neighbor distance between dens occupied by a resident and

![Distance Between Den Sites (m) vs. Percent of Observations](image-url)

**Fig. 5.2** Summary of nearest-neighbor distances between pairs of dens simultaneously occupied by Allegheny woodrats (*Neotoma magister*) at three locations (Strangford Cave, Strangford Mountain, and Cove Mountain) in Pennsylvania during June through September 2002. Results are summarized as the percent of all observations represented within each of six distance categories.
nonresident (\( \bar{X} = 61 \) m) differed significantly (\( t = 2.96, p = 0.02 \)) from the distance between two residents (\( \bar{X} = 143 \) m). Mean distance between nonresident dens (\( \bar{X} = 41 \) m) was significantly (\( t = 2.89, p = 0.03 \)) lower compared to resident dens but did not differ significantly (\( t = 0.90, p > 0.5 \)) from the distance between nonresident/resident dens.

In the context of agonistic behavior, it might be expected that there exists some minimum distance tolerated between two simultaneously occupied dens. Evidence to support this expectation is provided by the fact that the mean nearest-neighbor distance between dens occupied by residents was more than 2.5 times greater than the distance between resident/nonresident dens. Dens occupied by two residents represent sites that the occupants are less likely to vacate (i.e., residents change dens less often) whereas resident/nonresident pairs represent a situation where one of the dens is likely to be vacated (i.e., nonresidents change dens more frequently). In fact, occupancy of dens separated by less than 30 m accounted for only 11% of our observations (Fig. 5.2) and, in all cases, one of the dens was occupied by a resident and the other by a nonresident that eventually left the den. In contrast, the greater distance between resident dens apparently minimizes the probability of agonistic interactions.

Our findings suggest that behavioral interactions could have a significant influence on the population ecology of Allegheny woodrats. Specifically, agonistic behaviors among woodrats could limit the long-term residence of breeding adults at a rock outcrop by influencing the use of quality of den sites. Similar conclusions have been drawn from an investigation of *N. cinerea* (Moses and Millar 1992). More recently, Gerber et al. (2003) has determined that the spatial arrangement of artificial den sites—reflecting behavioral interactions among individuals—was an important factor in the success of translocation experiments for *N. fuscipes riparia*.

Despite the fact that a relatively high degree of den fidelity was exhibited by residents compared to nonresidents, even most of these individuals changed dens at least once. In three cases, an individual changed dens, and eventually moved back to a den that it had previously occupied. Similar behavior also has been documented for other species of woodrats (HaySmith 1995, Conditt and Ribble 1997, Merkelz and Kerr 2002). Although the reason for this behavior is uncertain, adult woodrats exhibit an apparent need to occupy more than one den over a relatively short period of time. It is even possible that woodrats defend more than one den site at a time, something we cannot determine by conducting radiotelemetry during daylight hours. This behavior might further limit the number of breeding adults that could occupy a rock outcrop at any given time.

The tendency to shift dens appeared to have a distinct seasonal component. Nearly all (92%) of the den shifts that we observed in the multi-year studies and in the extended monitoring period at Cove Mountain took place in the late spring to summer months (May–August). In contrast, only 59% of our total observations took place during these months (Fig. 5.3). No woodrats shifted den locations between mid September and late January. Although our data did not meet assumptions of independence necessary for statistical analysis, the striking seasonal pattern we observed suggests that this is an important aspect of woodrat behavior that
Fig. 5.3 Seasonal pattern of den shifting for Allegheny woodrats (*Neotoma magister*) at four sites in central Pennsylvania. Den shifting (Y-axis) is the proportion of total radiotracking observations for each month in which a woodrat changed den location since the previous observation. Number of radiotracking points for each month is shown above bar.

Deserves further study. In Pennsylvania and West Virginia, Allegheny woodrats begin storing winter food caches in late summer (Castleberry 2000). During winter they do not hibernate but remain active, consuming their stored food cache, and reproduction typically commences in early spring (Poole 1940). A litter is nursed for about a month, after which juveniles may remain with their mother for sometime but do their own foraging (Poole 1940). As far as is known, young do not remain at the maternal den through their first winter, but probably must find and provision their own winter den site. The summer den shifting we observed in adult woodrats may represent exploration or competition for position to establish both a secure winter refuge, and for females, an appropriate site for rearing the next spring’s litter. After mid-September, a shift to a new den would leave little time to establish a winter food cache, and the safest strategy may be to hold on to the current den through winter.

**Influence of Behavior on Population Dynamics**

**A Proposed Model**

Although historical data are not available from all study sites, as many as 50 woodrats were captured during three-night trapping periods at Strangford Cave in the mid-1970s (A. Linzey pers. comm.). Thus, the number of woodrats (3–13) we documented at any given time at our study sites was likely much less than existed prior to the decline of this species in Pennsylvania. Numbers that are far below the expected capacity of a rock outcrop make it difficult to draw definitive conclusions about the influence of behavior on ecological processes. However, our findings, considered with known aspects of woodrat behavior, strongly suggest that den
Fig. 5.4 Conceptual model of the possible influence of den characteristics and behaviors on the size of local and regional populations of the Allegheny woodrat (*Neotoma magister*).

Use and den selection could have a significant influence on population dynamics of Allegheny woodrats.

We propose an empirically testable model for understanding the influence of behavior on local population size that distinguishes between maximum occupancy and sustainable population size (Fig. 5.4). Maximum occupancy reflects the potential number of woodrats present at a rock outcrop at any given time and includes resident adults, transients, and juveniles. Because Allegheny woodrats are habitat-specific (Newcombe 1930, Poole 1940, Hall 1985, Wright and Butchkoski 2005, Castleberry et al. 2006), the maximum number of individuals present is expected to depend on the quantity of den sites.

In contrast to maximum occupancy, sustainable local population size reflects the number of breeding adults residing at a rock outcrop over an extended period of time. Although we clearly did not observe maximum occupancy at any study site, support for the notion of a dichotomy between maximum number and sustainable population size is provided by the observation that nearly all juveniles had disappeared from the sites by mid-August (Fig. 5.1). In addition, results indicated
that some adults (i.e., nonresidents) had difficulty in becoming established at any given den site for an extended period of time and at least some disappeared from the rock outcrop.

Whereas quantity of dens determines maximum occupancy, three characteristics of dens and behaviors associated with their use would limit the sustainable size of a population at a rock outcrop (Fig. 5.4):

1. **Quality of den sites**—Differences in the quality of dens might influence behavior in several ways. For example, woodrats would be expected to select dens preferentially based on quality and to exhibit aggressive defensive behavior at these sites. In addition, the frequency of den relocations by an individual woodrat would be increased if poor quality dens are unable to support a woodrat for an extended period of time or if den quality decreases over time. Therefore, even if many dens are available, various aspects of quality and behaviors related to the use of these dens would reduce the number of woodrats that could be supported at a rock outcrop.

2. **Spatial arrangement of dens**—The observation that the minimum distance between den sites of resident woodrats averaged 103 m likely reflects agonistic behavior of woodrats toward conspecifics (Kinsey 1976, 1977). If there exists a minimum distance between den sites, then local population size would be maximized by a spatial arrangement that maximizes distances between sites. Thus, even in a rock outcrop with many high quality den sites, sustainable population size would be limited by agonistic behavior.

3. **Availability of peripheral dens**—In addition to the need for a minimum distance, results suggest that male woodrats may be restricted to peripheral den sites that are not located on the main rock outcrop. In this scenario, sustainable population size is limited by the availability of peripheral sites that allow male woodrats to establish permanent residence and permit access to females during the breeding season.

The concept of a metapopulation reflects the existence of local populations in a given area that are connected by dispersal (Hanski 1996). This concept fits well with our current knowledge of the Allegheny woodrat in Pennsylvania and elsewhere. In this case, behavioral processes that influence local populations would also influence the dynamics of the metapopulation (Batzli et al. 1999). For example, increased sustainable population size at individual outcrops would increase the probability that other outcrops in the metapopulation would be colonized when local extinctions occur (Fig. 5.4).

**Testing the Model**

The small size of *N. magister* populations in southwestern and central Pennsylvania make it difficult to distinguish normal population and behavioral processes from stochastic events (Hanski 1996). Consequently, empirical tests of predictions concerning the influence of den selection and den use behaviors on the size of
local populations of *N. magister* will require data collected from healthy populations where maximum occupancy of rock outcrops might be expected at certain times of the year (e.g., late spring). Ideally, these investigations would be conducted in conjunction with studies from areas where the species has declined to permit comparison of woodrat behavior between rock outcrops that differ with respect to population density.

Relatively little is known concerning changes in woodrat population size and demographic composition during a single year or over the course of several years (Wood Chapter 3). The seasonal changes in den use we observed, with little or no moving to new dens in fall or winter, suggests that there may be a seasonal bottleneck in high-quality dens that can affect over-winter survival and spring reproduction. Therefore, live-trapping data collected over a time span including the early part of the breeding season through the early fall during several years are needed. These data would permit us to determine if there is consistency in woodrat population dynamics at a rock outcrop over time and if our dichotomy between maximum occupancy and sustainable population size is valid. Furthermore, information concerning demographic composition would permit us to determine if there exists a consistent ratio of breeding adults from one year to the next.

The patterns we observed, and on which our model is based, need to be confirmed with radiotelemetry studies in areas where woodrats have not experienced recent decline. Within these populations, our model predicts: (1) the existence of a minimum distance between den sites; (2) the existence of preferred den sites that are used disproportionately; (3) differences in den use behavior between sexes including predominant use of peripheral dens by males; (4) differences in the frequency of den relocation between residents and nonresidents; (5) periodic changing of dens by all woodrats; and (6) seasonal variation in den shifting. It is important that these predictions be addressed in conjunction with data concerning population dynamics and demographic characteristics.

Although not specifically required to test our model, information concerning various aspects of woodrat ecology and genetics would greatly enhance our understanding of the influence of behavior on population dynamics. For example, information concerning genetic relatedness among individuals, considered in conjunction with distances between individual den sites, would provide insight into the influence of social relationships on den selection. Data concerning the fate of juveniles and adults that disappear from the outcrop would be important to determine if these individuals disperse, suggesting that they are forced to leave the outcrop, or suffer mortality. Lastly, information concerning the relationship between survivorship and various aspects of den quality would provide support for the significance of preferred den sites.

**Conservation and Management of Declining Species**

In this chapter, we have proposed a model of how behaviors related to the selection and use of dens by Allegheny woodrats could influence the dynamics of populations at individual rock outcrops as well as the dynamics of metapopulations.
Consequently, the behavior of *N. magister,* deserves consideration in the context of conservation and management of this species. We further suggest that behavior may be an important factor for many other species in decline. For example, our model is clearly applicable to other species of *Neotoma.* This is particularly relevant given the fact that regional populations or subspecies of several species of North American *Neotoma* have experienced declines in the past 50 years (Feldhamer and Poole Chapter 11).

Like *N. magister,* most species of *Neotoma* are habitat specialists and exhibit den-centered ecology within selected habitats (Dial 1988, Topping and Millar 1996a). Habitat specificity is considered a characteristic that is correlated with susceptibility to extinction processes (Terborgh 1974) and the need for appropriate den sites within selected habitats further limits the size of a local population (Dial 1988, Topping and Millar 1996a). Behaviors such as agonistic defense of den sites, selection for den quality, and frequent den relocation would further limit the number of individuals inhabiting a local population. In this regard, behavior further limits the use of an already limiting resource and makes regional populations more susceptible to decline.

Behaviors that could make a species susceptible to decline also could complicate conservation efforts for that species. For example, re-establishment of woodrats at sites that have been subjected to local extinction would require consideration of the spatial arrangement of den sites to minimize the likelihood of agonistic interactions among individuals. In their evaluation of the potential for the translocation of a population of the endangered riparian woodrat (*N. fuscipes riparia*), Gerber et al. (2003) concluded that the distribution of potential dens and configuration of habitat structures was an important consideration based on the behavior of the species. Closer study of the determinants of a high-quality den site is needed for an informed choice of reintroduction sites, and especially to open the possibility of den-site enhancement. In the case of *N. magister* in southwestern and central Pennsylvania, this consideration is further complicated by the fact that many outcrops are linear in nature. Efforts to conserve declining local populations or reintroduce woodrats to extirpated populations should also consider that a main rock outcrop alone may not be sufficient but that associated peripheral sites for males might be necessary to support a breeding population (Serfass Chapter 10).

Our studies of den selection and den use in *N. magister* and our subsequent model of the influence of behavior on population dynamics (Fig. 5.4) address behaviors that apply specifically to *N. magister* and, in more general terms, to other species of *Neotoma.* However, findings from our study of *N. magister* suggest general principles that are applicable to the conservation and management of many declining species. For example, behaviors related to habitat use may limit local population size and make these populations more susceptible to stochastic processes and local/regional extinctions. This is especially true for species that are highly habitat-specific (Terborgh 1974) and exhibit a patchy distribution throughout the landscape. Furthermore, many behavioral processes (i.e., sociality, habitat selection, habitat use) may represent important considerations for management or reintroduction efforts. Similar conclusions have been drawn in a recent study of the Stephens’
kangaroo rat (Brock and Kelt 2004). Thus, the opportunity to study both declining and healthy populations of Neotoma magister will provide us further insight into the relationships between behavior and conservation of declining species.

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