Chapter 2
Multiple Causes of the Allegheny Woodrat Decline: A Historical–Ecological Examination

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Introduction

Wandering through the former haunts of the Allegheny woodrat (*Neotoma magister*) in the Shawangunk Mountains of New York State, one might easily imagine that this landscape is largely unchanged from what it was hundreds of years ago. Massive chestnut oaks (*Quercus prinus*) protrude from rocky hillsides and steep talus slopes conceal complex systems of fissures and galleries beneath. However, one need not look far to see signs of changing land uses all around this beautiful region. Even in areas seemingly untouched by human hands, the plant and animal communities of northeastern North America have undergone profound changes in the past 400 years—a fact not often considered when pondering the causes for a species’ decline. And yet, a short moment of reflection brings to mind a plethora of important species that no longer exist in our landscape. The American chestnut (*Castanea dentata*) and the American elm (*Ulmus americana*) are no longer found in our forests. The eastern hemlock (*Tsuga canadensis*), American beech (*Fagus grandifolia*), and eastern dogwood (*Cornus florida*) are fast disappearing. The list of animal species once found in the northeast but now absent is also quite impressive, including wolves (*Canis lupus*), cougars (*Felis concolor*), passenger pigeons (*Ectopistes migratorius*), wolverines (*Gulo gulo*), bison (*Bison bison*), and lynx (*Lynx canadensis*).

Equally noteworthy is the reversal of devastating trends that once appeared unidirectional; deforestation gave way to reforestation which has given way to suburbanization. Some species appear to have disappeared from the northeast forever. Others, like white-tailed deer (*Odocoileus virginianus*), American turkeys (*Meleagris gallopavo*), black bears (*Ursus americanus*), and American beavers (*Castor canadensis*) declined only to rebound to levels once thought impossible. From a nadir in the 1850s, when Henry David Thoreau noted that the muskrat
(Ondatra zibethicus) was the largest animal in the Massachusetts countryside (Foster 2000), we have seen a steady rise in the numbers of increasingly bold, human-adapted species. Deer feast on our shrubbery, turkeys strut in our backyards, and countless other species benefit from the changes we have made to the landscape. In addition, non-native species have proliferated in our forests and cities. Both through natural range expansions and deliberate or accidental introductions, many species that were unknown in eastern North America even 50 years ago are now well established.

Historical changes in the plant and animal communities must form the backdrop when we consider the changing population dynamics of the Allegheny woodrat (Neotoma magister). Woodrats have experienced repeated changes in food resources, competitors, predators, parasites, and landscape characteristics. Thus, impacts of adverse factors like the loss of an important food resource might be compounded or even ameliorated by other concurrent changes in the competitive or predatory regime to which the woodrat was exposed, causing a temporal disconnect between the onset of the stressor and the population response.

This mosaic of interacting factors might explain why the reasons for the decline of the Allegheny woodrat remain enigmatic. None of the factors most commonly believed to cause extinction—overharvesting, habitat destruction, impacts of introduced species, or secondary extinction (Diamond 1989)—seem capable of explaining the widespread disappearance of the species. Woodrats are economically unimportant either as a resource or as a pest, so overkill cannot explain their demise. The talus and cliff faces that form woodrat habitat proper are generally intact and no introduced predator or competitor has directly threatened the species. The introduction of the chestnut blight (Cryphonectria parasitica) and subsequent elimination of the American chestnut has been suggested as a case of secondary extinction but the woodrat survived this loss, even in the extremes of its range, by at least 50 years (Campbell and Madden 1990). Nevertheless, the possible factors that explain the species’ demise are all related to human actions. In this chapter, I will examine the decline of the Allegheny woodrat by focusing on the three hypotheses that have been suggested to explain it. I also propose a fourth hypothesis that incorporates the first three, but places them in their “historical-ecological” context (Foster 2002) and considers whether concurrent ecological changes may help to explain the strength of the response. I then present a hypothetical chronology of the events leading to the decline of the Allegheny woodrat.

Decline of the Allegheny Woodrat

As outlined in Chapter 1, the former range of the Allegheny woodrat extended from southern New York and Connecticut to northern Alabama. The current decline was first noticed in the late 1970s in Pennsylvania and New York, but there is some evidence of a long-term constriction of its range, particularly in the northern
extremes. Fossil remains several thousand years old have been found in caves near Albany, NY, approximately 80 km north of the recently known range (Hicks 1989, Whitaker and Hamilton 1998). There is evidence that the range also has constricted since the Pleistocene in Ohio and Indiana (Cudmore 1983, Whitaker and Hamilton 1998). Thus, it is possible that the observed decline is a continuation and acceleration of a long-term trend occurring for thousands of years.

The older scientific literature contains some suggestions that woodrats are intolerant of coexistence with humans. This was first mentioned by Peter Kalm in 1759 (cited in Rhoads 1894). In this early account, the woodrat was described as living “far from mankind among the stones and caverns in the Blue Mountains.” Rhoads (1903) stated that “any permanent inroads of civilization into their territory result in their speedy extermination.” Several early 20th century accounts of the Allegheny woodrat mention a perceived decline in its numbers: Newcombe (1930) described the Allegheny woodrat as being far less common than it was in “former years” and, in contrast to earlier intimations that they avoid humans, reported that “in the early days it frequently came into the houses of settlers” and carried away dried fruits and other small objects. Poole (1940) commented that, despite being well adapted to predator avoidance, “the animal seems to have narrowed its range in recent times to the immediate vicinity of rock ledges, boulder tumbles, and caves.” Nevertheless, the records of the New York State Museum show that the Allegheny woodrat survived, even in the northern-most part of its recent range, at least until the 1960s (Hicks 1989).

The historical-ecological approach has been extremely successful in interpreting forest vegetation patterns, exposing the highly dynamic nature of natural systems and helping to frame conservation issues (Eberhardt et al. 2003), but it has been less commonly used to investigate changes in wildlife populations. This may be due to the inherent difficulty in measuring population dynamics of animals. It is difficult enough to estimate the size of any animal population today, and to do this retroactively is even more challenging and speculative. However, some authors have succeeded in combining historical, scientific, and cultural sources with trapping records and fur prices to trace the dynamics of many highly visible and economically important animal species (McDonald and Harris 1999, Zielinski et al. 2001, Foster et al. 2002, Gompper and Hackett 2005).

No such historical records exist for the Allegheny woodrat, but these works provide the context in which the dynamics of less studied species can be examined. By taking into account the changing competitive and predatory regimes that might have magnified or minimized the impacts of other relevant perturbations, the important causative factors might be more easily identified and possibly remedied. Although it is not clear that we can save the Allegheny woodrat, its story teaches us to consider multiple hypotheses when investigating the decline of a species, to examine the possibility of additive, compensatory, synergistic and/or threshold effects, and to take the long-term perspective by being cognizant of how historical fluctuations in the biotic environment may have influenced the timing and pattern of decline.
Hypotheses to Explain the Decline

The three most common hypotheses to explain the decline of the Allegheny woodrat are: (1) decrease in food availability; (2) habitat fragmentation/disturbance; and (3) parasite mortality (Balcom and Yahner 1996).

Food Decline Hypothesis

The food decline hypothesis was suggested by Hall (1987), based upon his observation that the disappearance of Allegheny woodrat populations in Pennsylvania during the late 1970s was concurrent with intense gypsy moth (Lymantria dispar) infestations that had been affecting these regions since early in the decade (McManus and McIntyre 1981). Repeated defoliations can cause mast failure and oak mortality (Liebhold et al. 1994). The food decline hypothesis suggests that woodrat populations were responding to a decline in the availability of winter food in the form of acorns, an important component of the Allegheny woodrat diet (Castleberry et al. 2002). Hall posited that the reduction in acorn availability was affecting woodrats in two ways: (1) by forcing increased movements during winter, thereby increasing exposure to weather and predation; and (2) by reducing reproductive output as animals entered the breeding season with depleted fat reserves (Hall 1987, Balcom and Yahner 1996).

There are two lines of evidence to suggest that woodrats need good winter nutrition to launch a successful reproductive effort. The first involves correlative data from various woodrat species in the field; secondly, evidence from reproductive physiology experiments on eastern woodrats (N. floridana). Several investigators have observed that woodrat populations have increased after the production of an abundant acorn crop or collapsed after a complete mast failure. Murphy (1952) observed a large increase in an eastern woodrat population during two years of abundant acorn crops (1949 and 1950). Anecdotally, a record high population of Allegheny woodrats was recorded in New Jersey in the year following an exceptional mast year (J. Sciascia and K. LoGiudice unpublished data), and a precipitous crash of a thriving Allegheny woodrat population occurred immediately after a mast failure in Maryland (D. Feller pers. comm.).

A comparison of two experimental reintroductions of Allegheny woodrats also indicates that good winter nutrition results in a strong reproductive effort. In both studies, animals were introduced in the late summer after the breeding season had ended. The first reintroduction (McGowan 1993) was conducted in an exceptional oak mast year, whereas the second reintroduction (LoGiudice 2003) was carried out during a year with a moderate acorn crop. In the following breeding season, average recruitment in the first study (4.8 young weaned per female) was more than twice as great as the second study (2.3). This difference would perhaps have been more extreme if females in the second study had not been provided with supplemental food (LoGiudice 2003). In that study, two females survived the winter and the entire breeding season—one supplementally fed, and the other a control. In this small
sample, the difference in reproductive success was striking. The food-supplemented animal weaned at least five young in three litters and the control animal weaned only one offspring. In both reintroductions, there appears to have been enough food because all animals gained weight throughout the fall (K. LoGiudice unpublished data, E. McGowan and A. Hicks unpublished data). However, it is possible that the smaller acorn crop prevented animals from caching enough food to last through the winter, resulting in females entering the breeding season with less than optimal fat reserves.

Although little has been published on the reproductive physiology of the Allegheny woodrat, the reproductive energetics of the eastern woodrat have been well studied. Both species share similar reproductive cycles, which include small litters, slow postnatal development, and an unusually long lactation period (Poole 1940, McClure and Randolph 1980, Mengak 2002). In a series of experiments, McClure and colleagues compared reproductive energetics of the eastern woodrat to the hispid cotton rat (Sigmodon hispidus; McClure and Randolph 1980, McClure 1987). They found that eastern woodrats (a “slow” reproducer) require a larger energetic output per pup than do cotton rats (a “fast” reproducer), in part because of the slow development of the pups (McClure and Randolph 1980). When food was severely restricted during lactation (McClure 1987), cotton rats were able to successfully wean 75% of their young, whereas only 47% of the woodrat young survived to weaning. The author noted that many more woodrat pups would have died if she had not removed woodrat mothers from the experiment when their weight decreased below a certain threshold. When these experiments were repeated (Sikes 1995), somewhat better woodrat pup survival was reported (68%), but there was still a high cost to maternal malnutrition. In addition, under conditions of food restriction, woodrats depend on stored fat more heavily than cotton rats, indicating that reproductive success in woodrats is more heavily influenced by maternal prebreeding condition (McClure 1987). McClure hypothesized that the slow reproductive cycle of woodrats is an adaptive response to limited food resources and a stable, predictable food supply. It is possible that, in the case of the Allegheny woodrat, this stable food supply was the American chestnut (E. McGowan pers. comm.), with which it shares its entire range.

Many authors (Balcom and Yahnner 1996, Wright and Kirkland 2000, LoGiudice 2003, 2006, Ford et al. 2006) have expanded the food decline hypothesis to include the impact of loss of the American chestnut by the chestnut blight. This parasitic fungus eliminated chestnuts from the range of the woodrat beginning in about 1910 and continuing through the 1930s (Woods and Shanks 1959, Day and Monk 1974, Campbell and Madden 1990). Before its destruction, the American chestnut was the dominant tree in the Appalachian forests, both in abundance (comprising about 25% of all woody stems) and in size (growing to nearly 4 m in diameter; Elias 1980, Brewer 1995). It is likely that the loss of the food resources provided by the American chestnut had a significant impact on Allegheny woodrat populations.

Unfortunately, the historical importance of American chestnuts in the Allegheny woodrat diet can only be inferred since chestnuts are rarely mentioned by early
authors. As most woodrat research was done after the destruction of mature American chestnuts, this is not necessarily indicative of the former importance of chestnuts in the woodrat diet. Only Poole (1940) reported direct evidence of chestnuts in the diet—chestnut meat in analyses of stomach contents conducted over a number of years starting in 1922. The blight had killed more than 50% of the mature chestnut trees in Poole’s study site in Berks County, Pennsylvania by 1922 and probably quite a bit earlier since more than 50% of the trees in the county were reported to be infected by 1912 (Pennsylvania Chestnut Blight Conference 1912, Campbell and Madden 1990). Thus, evidence of chestnuts in the diet may imply that chestnut meat was a particularly important resource. Today the populations studied by Poole in Berks County are extirpated (Pennsylvania Game Commission 1995).

It is well established that populations of other North American rodents, such as the white-footed mouse (*Peromyscus leucopus*), cycle with oak masting events. Populations reach its peak during summer after a heavy mast year and crash after a mast failure (Wolff 1996, Jones et al. 1998). However, mice, voles, and other cricetids can produce multiple large litters of young per year (Whitaker and Hamilton 1998), whereas woodrats rarely produce more than two litters of two to four young annually (Whitaker and Hamilton 1998, Mengak 2002). Furthermore, other cricetids reach sexual maturity quickly, producing several generations per year, whereas woodrats do not breed during their first year (McClure and Randolph 1980). The comparatively slow reproductive rate of woodrats would appear to make it more crucial to maintain steady, predictable reproductive output from year-to-year.

Stable interannual reproductive rates may not have been possible given the changes to food resources experienced by Allegheny woodrats in the past 80 years. Woodrats can apparently sustain themselves on a high fiber diet of foliage and browse when necessary. However, seeds and fruits are preferred when available (Rhoads 1903, Newcombe 1930, Poole 1940, Castleberry et al. 2002, Castleberry and Castleberry Chapter 6). It is possible that the Allegheny woodrat can survive during the winter on a poor quality fibrous diet, but requires a higher quality diet supplemented with nuts and seeds for successful reproduction, as has been demonstrated for several western *Neotoma* species (Justice and Smith 1992). If so, interannual reproductive output may have become more erratic as woodrats adapted to the boom and bust masting cycle of oaks (McShea and Schwede 1992) from the reliable annual crops of the American chestnut (Brewer 1995, Anagnostakis 2000). This could result in large fluctuation in the size of populations and exaggerate the effects of stochastic mortality sources.

Beyond the loss of the chestnut and the invasion of the gypsy moth, changing forest conditions have converged to challenge the dominance of oak species in the eastern forests and reduce the availability of hard mast. Altered forest management regimes—and suppression of fire have favored faster growing species such as maples (*Acer* spp.) and birch (*Betula* spp.) at the expense of the fire tolerant oaks (Spurr and Barnes, 1980, Shtota et al. 1992, Healy et al. 1997). Overabundant white-tailed deer populations consume acorns and young oak trees, further suppressing oak recovery (McCabe and McCabe 1997). All these forces have likely reduced the share of nutritious nuts available to Allegheny woodrats.
Habitat Fragmentation/Destruction Hypothesis

A second hypothesis states that habitat destruction and/or fragmentation has caused the extirpation of Allegheny woodrat populations (Balcom and Yahnner 1996, Ford et al. 2006). Allegheny woodrats are habitat specialists, found primarily in rocky outcrops, caves, cliff faces and talus slopes (Whitaker and Hamilton 1998). There is little evidence for wide-scale destruction of these habitats in the northern portions of the woodrat range where the species decline is most pronounced. Most, if not all, historic woodrat sites in New York, New Jersey, Pennsylvania, and Maryland have been visited in the past 20 years by state conservation agencies and there have been very few reports of loss of rocky habitat (D. Feller pers. comm., Hassinger and Butchkoiski 1999, A. Hicks pers. comm., J. Sciascia pers. comm.). Woodrat habitat in the southern part of the range where veins of coal underlie the cliffs may have undergone more direct disturbance. Coal mining completely destroys habitat, but as this occurs primarily on private lands, the extent to which mining has impacted woodrat populations is largely unknown (Chamblin et al. 2004, Ford et al. 2006). Chamblin et al. (2004) found that there was some use of reclaimed mining lands by woodrats, although the extent to which these habitats can be permanently occupied is still an open question. However, throughout the range of the Allegheny woodrat, forests surrounding the talus have had varying degrees of disturbance and there is some evidence that fragmentation may be adversely affecting this species. The patchy distribution of Allegheny woodrat populations could magnify the effects of fragmentation if major dispersal routes were blocked.

Several authors have examined sets of extant and extirpated woodrat habitat sites and compared the probability of occupation by woodrats with multiscale habitat and landscape variables: In Pennsylvania, Balcom and Yahnner (1996) found that the probability of colony occupancy increased with distance from the forest edge, with the detrimental effects of the edge evident for up to 2 km. They went on to suggest that woodrats might be impacted by the larger populations of predators such as great horned owls (Bubo virginianus) that are often associated with agricultural development adjacent to the sites.

Ford et al. (2006), working in Maryland, Virginia, and West Virginia, used a spatially explicit model selection approach to compare the fit of several multiple logistic regression models to woodrat presence–absence data. Independent variables included distance to water, roads and railways, percent forest, agricultural, mining and pastoral cover, and most presciently, distance to nearest occupied rock outcrop. By far, the most important predictor of site occupancy was distance to the next nearest occupied site. Occupied sites were an average of 5 km from the next nearest active site; extirpated sites were more than twice as far on average (11.1 km). The most parsimonious model included the nearest neighbor distance, physiographic subprovince (Allegheny Plateau in WV, Ridge and Valley in WV/VA, and the Blue Ridge/Piedmont in VA/MD), and position relative to the Potomac River (north or south). Once distance to nearest occupied site was incorporated, probability of extirpation increased from west to east and was higher north of the Potomac. Also, there was some support for a second model that added percent forest area within 1 km
of the colony site. This pattern of north to south and east to west extinction seems consistent with patterns in the more northern parts of the range. Ford et al. (2006) posited that a longer history of human development in the north and east may explain at least part of the pattern.

**Parasite Hypothesis**

Increased mortality caused by the parasitic raccoon roundworm (*Baylisascaris procyonis*; McGowan 1993, Birch et al. 1994, Balcom and Yahnert 1996, LoGiudice 2003, 2006) is the third hypothesis for the decline of the Allegheny woodrat. The raccoon (*Procyon lotor*) serves as the definitive host for this intestinal nematode, but the parasite can also invade many species of intermediate hosts during its complex life cycle. The mature worms inhabit the small intestine of a raccoon and the eggs are passed in its feces. The sticky eggs are ingested by birds and mammals as they forage for seeds and undigested material in raccoon latrines, or are picked up passively and groomed off the feathers or fur (Page et al. 1999). Once ingested, larvae embark on an extended migration through the host tissues with some reaching the central nervous system where they almost always result in the death of the host, either directly or by causing behavioral changes that make the animal more vulnerable to predation (ataxia, circling, etc.). The cycle of transmission is completed when the intermediate host is consumed by a raccoon. Raccoon roundworm has been shown to cause pathology in more than 50 species of avian and mammalian intermediate hosts infected naturally or experimentally (Kazacos 2001).

Developed from a study conducted by the New York Department of Environmental Conservation (DEC), in 1991 (McGowan 1993), the parasite hypothesis is supported by an experimental trial conducted in New York and New Jersey (LoGiudice 2003). Both were translocation studies and in each case, woodrats introduced into sites heavily contaminated with raccoon roundworm eggs survived for significantly less time than those introduced into less contaminated sites. The DEC study was aimed at determining causes of mortality and attempted to recover dead and moribund animals from the talus. Ten of the 11 animals recovered for necropsy had *B. procyonis* larvae in the brain, and an examination of the release sites revealed extensive contamination with infected raccoon feces (McGowan 1993).

In a subsequent investigation conducted in 1996–1997, LoGiudice (2003) tested the parasite hypothesis by releasing woodrats into four historical sites in New York, and New Jersey. Two of the release sites were heavily used by raccoons and contained many infected feces (high exposure sites) and two had lower levels of contamination (low exposure sites). LoGiudice found that animals survived significantly longer in the low exposure sites than in the high exposure sites (33.6 vs 15.5 weeks, respectively), supporting the parasite hypothesis. Allegheny woodrat mortality caused by *B. procyonis* also has been confirmed in Pennsylvania (J. Wright pers. comm.) and Indiana (Hudson et al. 2006), and infected raccoon feces have been found in rock outcrops occupied by woodrats in Maryland (D. Feller pers. comm.).
The behavior of collecting and storing a broad array of items, both edible and nonedible, seems to put woodrats at higher risk to raccoon roundworm than other small mammals. They appear to be attracted to the feces of raccoons and other animals (Rhoads 1894, Poole 1940, McGowan 1993, LoGiudice 2001, 2003, Hudson et al. 2006), collecting and caching whole feces regardless of seed content. In contrast, white-footed mice show some aversion to feces and remove seeds from scat immediately (LoGiudice 2001). Since roundworm eggs are harmless until embryonated, a process that takes up to 30 days, the caching of feces by woodrats puts them at a considerably higher risk to roundworm mortality than mice. Under the conditions in caves and talus passages, the eggs can remain infective for years (Kazacos 2001), prolonging the period of possible fatal infection. Furthermore, woodrats sequentially use dens for many generations (Newcombe 1930). Thus, a contaminated den could become a “parasite trap” that could kill many successive residents, as was observed by both McGowan (1993) and LoGiudice (2003). Allegheny woodrats have little or no resistance to B. procyonis infection. When infected with a standard dose of infective B. procyonis eggs, woodrats were significantly more likely than white-footed mice to develop fatal neurological disease (K. Kazacos pers. comm.).

Racoon roundworm seems certain to have played a role in the disappearance of the Allegheny woodrat from New York, New Jersey, and probably Connecticut. There is evidence that raccoon population densities increased dramatically during the mid-20th century due to loss of predators, changes in land use, and relaxation of hunting and trapping pressures (Balcom and Yahner 1996, LoGiudice 2003, Prange and Gehrt 2004). This is likely to have increased woodrat exposure to raccoon roundworm. How common this mortality source is in other parts of the species’ range is not clear. Owen et al. (2004) performed fecal analyses on raccoons trapped in woodrat habitat in West Virginia and found that B. procyonis was completely absent. Although the sample size was somewhat low (n = 9) for animals collected during the fall period of highest egg shedding and the detection technique is not the most effective (fecal analysis is the least effective method of detecting infection compared to latrine analysis and necropsy; Page et al. 2005), it is likely that if B. procyonis was present even at low prevalence, it would have been detected in at least one of the animals. In general, although raccoon activity is commonly detected in and around woodrat sites in many parts of the range (Owen et al. 2004, Hudson et al. 2006), B. procyonis eggs have only sporadically been found in feces. This may be partly due to the time of sampling. Raccoon roundworm shows strong seasonality, with peaks in egg shedding in fall and winter (Page et al. 2005); so sampling should be conducted with this in mind. In addition, the window of time in which the effects of B. procyonis might be detected in a woodrat population is exceedingly short. Cached feces are infrequently found by investigators, and the parasite appears to be so debilitating in woodrats that the probability of capturing an infected animal is low.

Circumstantial evidence in the woodrat monitoring data from Indiana (Johnson 2002, Hudson et al. 2006) suggests that raccoon roundworm might be an important mortality source in this state. Each of the three monitoring sites with the largest
declines in individuals trapped between 2002 and 2005 was reported to have extensive raccoon sign during the 2005 trapping session. In addition, a fourth site at which a *B. procyonis* infected woodrat was captured in 1996 declined from 20 animals in 1996 to 0 in 2002. In three of the four sites experiencing the smallest declines between 2002 and 2005, the authors noted the absence of raccoon activity. With high roundworm prevalence previously reported in parts of Indiana (Jacobson et al. 1982, Kazacos 2001, Page et al. 2005), it is unlikely that *B. procyonis* is not at least periodically present in woodrat sites. A project currently underway is poised to shed some light on the importance of roundworm in Indiana (T. Smyser pers. comm.) and the regular monitoring suggested by the Indiana Department of Natural Resources (Hudson et al. 2006) is likely to help determine the possible impact of this parasite. One final piece of circumstantial evidence comes from the New Jersey woodrat monitoring project, which has documented a steady increase in the last remaining woodrat population (J. Sciascia, M. Valent and K. LoGiudice unpublished data; Fig. 2.1). This increase began several years after raccoon rabies first appeared in the northeast, presumably reducing what had been extremely high raccoon densities.

The importance of *B. procyonis* in the more southern part of the Allegheny woodrat range is very unclear. It has been long believed that prevalence of the parasite declined dramatically with latitude, but recent studies have revealed medium to high prevalences in Georgia (Eberhard et al. 2003) and Texas (Long et al. 2006). Although there are still unanswered questions about the seeming sudden impact of this native parasite, it appears to be common enough that wildlife managers should investigate raccoon activity in woodrat sites.

![Fig. 2.1](image)  
*Fig. 2.1* Trapping index (number of individuals per 10 trapnights) of annual fall monitoring for the Palisades, New Jersey population of Allegheny woodrats (*Neotoma magister*). The arrow indicates the introduction of raccoon rabies and the assumed reduction of the raccoon population in 1992 (updated from LoGiudice 2006)


Historical–Ecological Hypothesis

The three hypotheses described in the preceding sections might be more coherent if taken in an historical–ecological context. It is often easy to forget how much the wildlife community of the 19th and early 20th centuries differed from that which is present today (Foster 2002, Foster et al. 2002). Most large mammals and birds in the northeastern North America had been hunted to near extirpation by 1800 and did not recover (if at all) until the mid-20th century (Rhoads 1903, Spurr and Barnes 1980, Eaton 1992, McCabe and McCabe 1997, Foster et al. 2002). Thus, during early periods of reduced food resources, the woodrat would have been experiencing relaxed competition from large, highly mobile mast consumers such as white-tailed deer, black bears, and wild turkeys. Subsequently, the recovery of these species would have reduced the share of high quality foods available to woodrats (Eaton 1992, Mc Shea and Schwede 1992).

One can only surmise the impacts of changes in the predator community since the main enemies of woodrats and the influence of predation on woodrat demographics are unknown. Nevertheless, both the elimination of common predators (Foster et al. 2002) and the recovery of many of these species are likely to have had major influences on woodrat populations. The recovery of smaller predators such as mustelids, raccoons, and foxes in the absence of larger predators may mean that woodrats are now subjected to higher predation pressures than any time in their history.

Hypothetical Chronology

It seems unlikely that any one factor could singly be causing the range-wide reductions of the Allegheny woodrat. Rather than being mutually exclusive, the effects of each of these factors may have been working in some sites alone, in some additively, and in some synergistically. It is possible that a concatenation of these changes may have been impacting woodrat populations from the mid-1800s or before, ultimately causing the population collapses that drew human attention in the 1970s and beyond.

The following is a hypothetical timeline (Fig. 2.2) of the decline of the Allegheny woodrat in its northeastern range (NY, NJ, CT) where it is practically extirpated. The events in this timeline are supported by the evidence just discussed and by conjecture. The timeline is based on the dates of the historical–ecological fluctuations that might have affected woodrats and on observations of naturalists and scientists. The chronology suggests that the slope of this decline has not been constant, but rather that woodrat populations have deteriorated in a stepwise fashion, culminating in local extinctions that may have been perceived as sudden to human observers.

The intense deforestation during the 18th and 19th centuries is likely to have had a negative influence on woodrats by removing trees that provided food resources and blocking dispersal routes. This is consistent with the observations of Kalm in 1759 (cited in Rhoads 1894). However, concurrent elimination of predators and competitors may have compensated for such losses. By the time of the maximum forest clearance in the mid-1800s (Foster et al. 2002), large predators and competitors
Fig. 2.2 Hypothetical chronology and population trajectory of Allegheny woodrat (Neotoma magister) populations in northeastern North America, from a pre-European settlement high in the upper left to the current low in the lower right. The impacts of events deleterious to woodrat survival may have been temporarily offset by simultaneous events that enhanced woodrat survival probabilities, causing a temporal disconnect between the onset of deleterious events and the population response. Actual effects of these events on population size and the precise timing of the decline are unknown and are not implied by the graphics (adapted from LoGiudice 2006)

were functionally absent from the Allegheny woodrat’s habitat possibly allowing its populations to stabilize.

The destruction of the American chestnut with its reliable annual chestnut crop almost certainly impacted the woodrat and set another decline in motion. Woodrats appear to respond to food shortages by reduced reproductive output which might have increased the frequency of local extinctions. By 1920, most American chestnuts were eliminated from Connecticut, New York, and Pennsylvania and by 1930 in Ohio, Maryland, and Indiana (Campbell and Madden 1990). In many places, understory oaks filled in the gaps left by dying chestnuts (Woods and Shanks 1959, Day and Monk 1974) allowing woodrats to exploit periodic acorn crops and sustain their numbers in the absence of large mast competitors. Undoubtedly, woodrats were lost from marginal habitats and areas in which nonmasting species filled in the canopy, serving to isolate remaining populations even more. This timing is consistent with observed population declines (Newcombe 1930, Poole 1940) and may have initiated another period of stability, possibly at lower population levels. However, this stability did not last long as the enactment of strict hunting restrictions and deer and turkey reintroductions caused a rapid recovery of these two mast consumers. In
the United States, populations of wild turkeys saw dramatic increases, from about 130,000 in the 1940s to 1.25 million in 1970 to 4 million in 1990 (Eaton 1992). In many places, the recovery of deer populations was even more dramatic, going from complete extirpation to dramatic overpopulation within 50 years. The recovery of the deer herd in New York/New Jersey was well underway by the 1960s (McCabe and McCabe 1997). Current deer densities frequently exceed 10 deer/km² and have been documented at four times that in local areas. Grazing by deer at these densities can prevent oak regeneration (Healy 1997) and reduce small mammal populations (McShea and Schwede 1992). At this time black bear populations were also beginning to recover and direct competition with these three species likely reduced the woodrat’s share of the mast crop. Finally, mortality from recovering populations of great horned (B. virginiensis) and barred (Sistrix varia) owls and mammalian mesopredators (Foster et al. 2002) could have had a large impact on woodrat demographics (Balcom and Yahner 1996).

At the same time that competition and predation were increasing, the woodrat range was being fragmented by human development. This likely blocked dispersal routes and prevented recolonization of extirpated sites, interrupting the metapopulation dynamics. The early disappearance of metapopulations in the lower Hudson River Valley, one of the most densely developed regions in the woodrat range, implies the importance of fragmentation. A similar decline is evident in the central Appalachians north of the Potomac River, also an area of long-term human impact (Ford et al. 2006).

As turkey and white-tailed deer populations surged in the 1970s, another competitor for the oak mast was developing. After a slow start from its introduction near Boston in the late 1860s, the gypsy moth expansion had picked up and was rapidly consuming forests through the northeast. In New York, Pennsylvania, and New England, damage peaked in 1970 with 800,000 ha defoliated. Extremely high levels of oak mortality were reported in New York, Pennsylvania, Connecticut, and New Jersey (McManus and McIntyre 1981). This is consistent with the first discovery of the woodrat decline.

By the 1960s, raccoon populations appear to have reached very high densities in the northern portion of the woodrat’s range. Although quantitative data are scarce, this consummate human-adapted species has benefited from the transition from pastoral to suburban land uses and the resultant reduction in hunting that followed World War II (Riley et al. 1998). Prominent New York naturalist Dan Smiley documented a dramatic increase in raccoons, commenting that they were rare in the 1920s and a nuisance by the 1970s (Smiley 1977). Changes in raccoon habitat use might also have caused more contact between the two species than had been the case during much of their evolutionary history. The loss of large den trees may have pushed raccoons to seek shelter in the talus. The high degree of resistance, to B. procyonis found in the white-footed mouse may imply an evolved response to a long history of exposure (Sheppard and Kazacos 1997). This seems likely since raccoons and white-footed mice typically share woodland habitats. Conversely, lack of evolved resistance to this parasite in the Allegheny woodrat may indicate that, historically, exposure was less common ( Wakelin 1994). To end our timeline, by the
late 1970s woodrat populations appear to have been beleaguered by fragmentation and low recruitment making them highly vulnerable to stochastic mortality sources. Raccoon roundworm is likely to have played this role in New York and New Jersey at least, serving as the final straw and causing the rapid collapses observed in these states.

The forces described in the proposed chronology (Fig. 2.2) need not have acted independently on woodrat populations. Food shortage and increased interspecific competition may have caused death directly by starvation or indirectly, by forcing animals to forage farther for food, exposing them to predation and/or the elements. They may have acted synergistically with parasites by increasing foraging in raccoon latrines and causing chains of mortality as one individual after another occupied a contaminated den site. Increasing intraspecific competition for scarce mast might have caused more agonistic interactions among woodrats. Loss of habitat or dispersal routes could add to these woes. It appears that dispersal in this species is so limited (Wood Chapter 3) that the loss of a single centrally located and productive subpopulation could precipitate the collapse of an entire metapopulation. There may also be undetected threshold effects operating, where recolonization is virtually impossible if metapopulation occupancy drops below a certain limit. More information on the dispersal abilities of woodrats would help to determine the proper spatial scale in which to consider a metapopulation and would facilitate the modeling of metapopulation dynamics.

The small size of individual woodrat subpopulations suggests that they are quite vulnerable to extirpation. Thus, the species has a precarious population structure, with dispersal, mortality, and recruitment delicately balanced to maintain metapopulations. In the past, stability of the metapopulation structure has allowed long-term survival even in the face of stochastic subpopulation extinctions. However, any factor that leads to an increase in mortality or a reduction in dispersal or recruitment could exceed a viability threshold and result in metapopulation collapse. The hypotheses presented here potentially increase mortality (food shortage, increased predation, *B. procyonis*), reduce fecundity (irregular food availability, increased competition), and reduce recolonization frequency (habitat fragmentation and loss of subpopulations), so any combination of these factors could destabilize metapopulations and cause local extinction.

**Conservation and Management of Declining Species**

The Allegheny woodrat is emblematic of many endangered and threatened species. Humans have been changing habitats in complex ways and on multiple levels for centuries. In the process, we set off ecological chain reactions that may be invisible to us until suddenly, and perhaps too late, they attract our attention. Too often, these intricate relationships are all but irreparable without huge commitments of human resources. However, it is useful to examine such cases in the hope that we can learn to recognize the warning signs and avoid making the same mistakes in the future.
What lessons can be learned from studying the decline of the Allegheny woodrat? First, that it is instructive to thoroughly consider multiple hypotheses for a species’ decline before discarding any, regardless of how insignificant they may seem. It is not safe to assume that a single factor is responsible for a decline or that the impact of a given factor is too small to be relevant. In a thorough review of extinctions, Pimm (1996) concluded that most extinctions were caused by synergistic interactions between multiple factors rather than being attributable to a single cause. Synergistic, additive, or compensatory effects may exaggerate the impact of a seemingly mild insult or mask the importance of a major factor, so ignoring a minor factor may be fatal. Threshold effects may also be operating, such that incremental changes have little or no impact until the threshold is exceeded and a large decline ensues. Of course, it is not practical or even possible to thoroughly test and remediate every potential factor. If the collapse of the woodrat range is due to a multitude of factors, how does one identify the “last straw”? This is enormously challenging and requires coordination and collaboration. No one agency, lab, or investigator can adequately explore all possible hypotheses. Thus, it would be helpful to form a working group of state and federal agencies, academics, and other interested parties. This group should work cooperatively to produce and disseminate research “punch lists” of factors that should be investigated in as many places and with as many methods as money and interest allow. Often, small pilot projects can help to identify promising hypotheses. When possible, multiple factors should be investigated simultaneously to test for interactions. And of course, members of the group should share results as promptly as practicable.

Next, we should study the anomalous populations. It is often as instructive to investigate the successes as the failures. Just as we can learn by asking the question: “Why is this population declining?” We can also learn by asking: “Why is this population persisting?” Isolated populations of Allegheny woodrat remain throughout the range, surviving against all the odds as other nearby populations have disappeared. While they exist, they present opportunities to learn about the key factors for population persistence and to discover possible interventions. Comparative studies between these sites would be most instructive. Of course, we should remember the precarious position of these populations which makes manipulative studies quite dangerous, as a small perturbation might be all that is necessary to drive such a population to extinction. Especially with habitat specialists and other vulnerable species, even small population declines may be followed by massive collapse. Close monitoring of representative populations is necessary and a swift reaction should follow if a decline is detected. This means developing an emergency action plan using the best data available.

Finally, it is useful to take the historical–ecological approach and be aware of historical patterns in resource availability, predation, and competition to better understand the varying forces to which endangered species have been subjected. We should keep history in mind and beware of eliminating a potential factor because it does not currently seem important. We must conduct the thought experiment of going back 50, 100 and 200 years to determine as best we can what the species was experiencing at those times. By recognizing the importance of historical patterns
and considering all plausible hypotheses, we can help to expand our understanding of what imperiled species have been through and what they may need to persist.

References


2 Multiple Causes of the Allegheny Woodrat Decline


