Toward a Synthetic View of Extinction: A History Lesson from a North American Rodent

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Although it is recognized that many factors interact to cause extinctions, it is difficult to consider multiple factors when investigating species declines. I conducted a post hoc exploration of the major hypotheses for the decline of the Allegheny woodrat (Neotoma magister), incorporated the historical environmental changes that accompanied and preceded the decline, and considered how these events may have affected the species. What emerges is a complicated picture involving multiple, relatively minor stressors, all attributable to human activities. The temporal pattern of the decline is most coherent when considered from a historical perspective. Among the factors that are likely to have affected Allegheny woodrats are two exotic tree pathogens, a native parasite, the proliferation of human-adapted competitors, and habitat fragmentation. In addition, changes in competitive and predatory regimes appear to have influenced the timing of the collapse. Although the historic record cannot give definitive answers, taking a synthetic, historical–ecological approach can enhance understanding of species declines.

Keywords: Allegheny woodrat, raccoon roundworm, American chestnut, extinction, historical–ecological context

The circumstances that are at the root of modern extinctions were famously enumerated in 1989 by Jared Diamond. He described the "Evil Quartet" of overkill, habitat destruction and fragmentation, introduced species, and secondary extinctions, all of which can be directly attributed to human activities. Pimm (1996) examined this with regard to Hawaiian extinctions, and concluded that most extinctions were caused by synergistic interactions between multiple factors rather than being attributable to a single cause; nevertheless, a search of the literature since 1996 shows that most investigations of declines and extinctions focus on a single factor. Certainly, in a few cases, extinctions can be traced directly to a simple human action, such as the introduction of the brown tree snake to Guam (Fritts and Rodda 1998). But more often, a suite of unrelated, human-induced adverse effects combine to drive a species or population to extinction. When this occurs, the mechanism may not be immediately obvious, since each factor, in itself, appears too slight to precipitate a population collapse. Our understanding of the problem can be further confounded by ecological changes of a compensatory nature that can temporarily ameliorate the impact of the adverse effects, and by the many indirect effects that accompany any environmental perturbation. To fully understand the causes of extinction, it is necessary not only to consider multiple factors but also to consider them in their historical context.

The relevance of history to the study of endangered species has been recognized (Alagona 2004), but is rarely taken into account in management plans. In this article, I discuss the decline and local extirpation of the Allegheny woodrat (*Neotoma magister*), using a multifaceted approach that considers all reasonable hypotheses and includes an examination of the historical–ecological context. This 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). It has been less commonly used to investigate changes in wildlife populations. This is perhaps because of the inherent difficulty of measuring population dynamics of animals, their relatively short lives, and the absence of long-term records of their abundance, such as can be obtained in the pollen deposits of trees. Given the difficulty in estimating the size of current populations, estimating past population trends and inferring their causes must by definition be a somewhat speculative endeavor. Despite these difficulties, Foster and colleagues (2002) succeeded in using various scientific and cultural sources to trace the dynamics of many highly visible animal species in New England, documenting trends that had previously existed only as general impressions in the minds of ecologists and natural historians. Similarly, others have used trapping records to track long-term trends in economically important species (McDonald and Harris 1999, Zielinski et al. 2001, Gompper and Hackett 2005).

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These works paint a backdrop against which the dynamics of other, lesser-known species can be studied, allowing us to take into account the changing competitive and predatory regimes to which they have been exposed. In this context, I will examine the puzzling 30-year decline of the Allegheny woodrat (Balcom and Yahner 1996). An examination of the ecological history implies that this decline may have been set in motion much earlier, and that a series of adverse and compensatory effects combined to draw out the demise of the species until it finally succumbed in the northernmost parts of its range. The story of the Allegheny woodrat provides a lesson in the importance of considering multiple hypotheses when investigating the decline of a species; of examining the possibility of additive, synergistic, and threshold effects; and of taking a long-term perspective in contemplating how historical fluctuations in the biotic environment may have influenced the timing and pattern of decline.

The Allegheny woodrat is a small mammal native to the Appalachian mountain range of the eastern United States, with a recent range extending from southern New York to northern Alabama (figure 1). Archaeologists from the New York State Museum have documented the presence of the woodrat at the northern extremes of its range for at least 7000 years (Hicks 1989). The woodrat is not a well-studied species, being neither a nuisance nor economically important to humans. Thus, there is limited historical evidence (e.g., popular accounts, newspapers, town histories, and bounty records; Foster et al. 2002) about its abundance beyond the similarly limited scientific and museum accounts. Nevertheless, it is possible to critically combine these scientific resources with an understanding of concurrent ecological changes to reconstruct a hypothetical scenario for the species' decline.
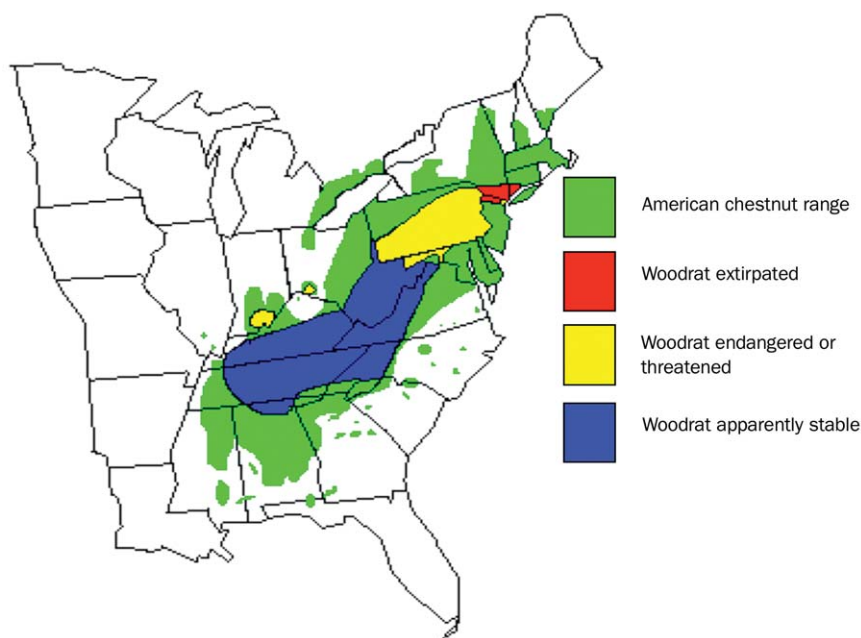
The disappearance of the Allegheny woodrat was first noticed in the late 1970s in New York and Pennsylvania (Hicks 1989). Within a decade, the species was extirpated from New York, Connecticut, and much of New Jersey; endangered in Maryland and Ohio; and threatened in Pennsylvania and Indiana. The loss of woodrat populations, which was first noticed in the northern parts of the species' range, appears to have spread southward in a wave of extinction (figure 1). The causes for the woodrat decline are unclear, and no single member of the "evil quartet" appears to be wholly responsible. As mentioned, overexploitation is not a candidate, nor is simple destruction of habitat, as the rocky talus slope habitat preferred by woodrats is largely intact throughout the affected area. There is no known introduced predator or competitor; and although secondary extinction is possible because of the loss of a food source, the American chestnut (*Castanea dentata*), woodrats survived this event by more than 50 years.

Some evidence suggests that the woodrat decline was set in motion long before it came to the attention of wildlife professionals. As early as 1759, Kalm (cited in Rhoads 1894) noted that woodrats appear to be intolerant of coexistence with humans, as did Rhoads in 1903. Several early 20th-century accounts of the Allegheny woodrat also mention a decline in its numbers (Newcombe 1930, Poole 1940). Nevertheless, the records of the New York State Museum show that the Allegheny woodrat survived, even in the northernmost part of its range, at least until the 1960s (Hicks 1989).

In the absence of a smoking gun, three hypotheses have been suggested to explain the demise of the Allegheny woodrat: (1) habitat fragmentation or disturbance (Balcom and Yahner 1996), (2) a decrease in food availability (Balcom and Yahner 1996), and (3) parasite mortality (McGowan 1993). A brief examination of the evidence for these hypotheses suggests that each is likely to have been a contributor, but the timing is best understood by considering them in concert and in their historical–ecological context. This means considering a fourth factor—the varying pressures exerted by changing animal and plant communities. By considering multiple impacts in their historical context, we can better understand the phenomena leading to the decline of this species.

Habitat fragmentation hypothesis

In their northern range, Allegheny woodrats are habitat specialists, found in small groups on rocky outcrops, talus slopes, and associated areas. This patchily distributed habitat lends them a classic metapopulation structure, and there is evidence of the natural blinking on and off of subpopulations, as is expected in a metapopulation (Daniel Feller, Maryland Department of

Figure 1. Historical range of the Allegheny woodrat superimposed on the former range of the American chestnut (green).

American chestnut range

Woodrat extirpated

Woodrat endangered or threatened

Woodrat apparently stable

Natural Resources, Swanton, MD, personal communication, 2 September 2005). Although there has not been broadscale destruction of the talus habitats themselves, the forests surrounding the talus, on which the animals depend for food, have been widely disturbed. Several authors have examined landscape and microhabitat characteristics of extant and extirpated woodrat sites in Pennsylvania. They found that colonies were more likely to be extirpated in smaller forest patches, and that the probability of colony occupancy increased with distance from the forest edge (Balcom and Yahner 1996, Hassinger et al. 1996).

Since the metapopulation structure of woodrats is pronounced, fragmentation may be the ultimate cause of decline. The long-distance dispersal abilities of Allegheny woodrats are not well known, but translocated animals have moved more than 1.5 kilometers (km) upon release, so they could be sensitive to any human development that would block dispersal routes. If various human impacts have increased the frequency of local extirpations, and fragmentation has reduced dispersal probabilities, then there may be a threshold proportion of extant subpopulations, below which recolonization becomes so unlikely that rapid collapse of the entire metapopulation follows. This may explain the swift disappearance of the New York populations, which appeared to be robust in the 1960s but were nearly extinct within a decade.

Food decline hypothesis

The food decline hypothesis, first proposed by Hall in the late 1980s (Balcom and Yahner 1996), was based on the coincidence of woodrat population disappearances and intense gypsy moth (*Lymantria dispar*) infestations in the 1970s. Repeated defoliations of oak trees by gypsy moths caused widespread mast failure and oak mortality during this period (McManus and McIntyre 1981). Woodrats are known for the large, varied food caches from which they feed in the winter. A decline in the availability of acorns, a high-quality and long-lasting winter food, could have a negative impact on population dynamics by increasing mortality from exposure and predation as animals are forced to forage farther during the winter and by reducing recruitment as animals enter the breeding season in poor condition.

Subsequent to the first serious gypsy moth outbreaks, changing forest conditions have continued to challenge the dominance of oak species in eastern forests. The suppression of fire has created conditions favorable to faster-growing species such as birch and maples, at the expense of the slower-growing but fire-tolerant oaks (Spurr and Barnes 1980), and overgrazing by white-tailed deer (*Odocoileus virginianus*) is also thought to have reduced oak abundance (Healy 1997).

Many woodrat researchers believe that the food decline hypothesis should include the effects of the virtual extermination of the American chestnut by the chestnut blight (*Cryphonectria parasitica*; Wright and Kirkland 2000), which occurred in woodrat range from approximately 1910 through 1930 (Campbell and Madden 1990). The chestnut and the Allegheny woodrat were sympatric, with the range of the woodrat being completely contained within the range of the American chestnut (figure 1). Before its destruction, the American chestnut was a prodigious mast producer and a dominant tree in the Appalachian forests, accounting for more than 25 percent of stems and growing to massive size (Brewer 1995).

The relatively few studies available fail to establish definitively that hard mast is necessary for Allegheny woodrat survival, but they do indicate that mast has a prominent place in the woodrat diet (LoGiudice 2000, Wright and Kirkland 2000) and that seeds and fruits are preferred over leaves and twigs (Rhoads 1903, Newcombe 1930, Poole 1940, Post et al. 1993). It is possible that a lower-quality, fibrous diet allows Allegheny woodrats to survive a poor mast winter, but that a higher-quality diet of nuts and seeds is necessary for successful reproduction, as has been found in several western woodrat species (Justice and Smith 1992). If so, the replacement of the American chestnut, a species that produced consistently large annual seed crops (Christisen 1965, Brewer 1995), by oaks, whose crops are variable (McShea and Schwede 1992), may have resulted in high interannual variation in reproductive output by Allegheny woodrats, making extinctions of subpopulations more likely. The slow reproductive rate and late sexual maturity of woodrats relative to many other North American rodents (Whitaker and Hamilton 1998) further support this hypothesis, as does the species' heavier reliance on stored fat reserves, indicating that maternal prebreeding condition has a proportionately greater influence on reproductive success (McClure 1987).

In general, wildlife responses to the loss of the chestnut are very poorly documented, and no quantitative data exist to indicate the effect of the chestnut blight on woodrats. It has been reported that populations of grey squirrels (*Sciurus carolinensis*), which rely heavily on hard mast, declined sharply during the period from 1910 to 1920, rebounding strongly in the 1930s (Foster et al. 2002). This suggests that the loss of the chestnut could have precipitated a decline in woodrats as well (Wright and Kirkland 2000). That there was no rebound in woodrat populations, and that the woodrat survived the loss of the chestnut in most of its range by more than 50 years, suggests that other forces were also in play, however.

Parasite mortality

The third hypothesis for the decline of the Allegheny woodrat implicates *Baylisascaris procyonis*, or raccoon roundworm (McGowan 1993, Birch et al. 1994, Balcom and Yahner 1996, LoGiudice 2003). Raccoon roundworm is an intestinal nematode capable of passing through a broad array of intermediate hosts on its way to the gut of a raccoon, where it matures and reproduces. The eggs are passed in raccoon feces, and intermediate hosts ingest the eggs directly, by foraging among these feces (which often contain seeds and other edible material), or indirectly, by grooming eggs off their fur or feathers (Page et al. 1999). Ingested larvae undergo a somatic migration, with some reaching the central nervous

system, where they virtually always cause the death of the host (Kazacos 2001).

The parasite mortality hypothesis was developed from a diagnostic study conducted by the New York State Department of Environmental Conservation (McGowan 1993) and tested experimentally in New York and New Jersey (LoGiudice 2003). Both of these studies consisted of experimental reintroductions, and in all cases woodrats survived longer in areas of low raccoon use than in areas heavily used by raccoons (figure 2). It is thought that urbanization, changes in hunting and trapping practices, and changes to the predator community (i.e., mesopredator release) allowed an increase in

those receiving supplemental food (Page et al. 2001, LoGiudice and Ostfeld 2002). If woodrats respond similarly, then increased reliance on the boom–bust cycle of oaks may cause elevations in roundworm-induced mortality during mast failures that are far beyond what would otherwise be caused by either factor independently. The infection of Allegheny woodrats with raccoon roundworm has been confirmed sporadically in Pennsylvania (Janet Wright, Biology Department, Dickinson College, Carlisle, PA, personal communication, 24 August 2005) and Indiana (Scott Johnson, Indiana Department of Natural Resources, Indianapolis, personal communication, 1 September 2005), but there is

Pre-European settlement

Habitat loss
Large-scale deforestation and conversion to agriculture

Lack of competitors. 1900–1960s
White-tailed deer and wild turkeys were extirpated from much of the woodrat's range by the mid-19th century, reducing competition.

1900

Intolerant of human disturbance
"… any permanent inroads of civilization into their territory results in their speedy extermination" (Rhoads 1903)

1920

Loss of the American chestnut. 1910–1930
This dominant tree of the Appalachian forests was a consistent nut producer and was undoubtedly an important winter food source for the woodrat. It was wiped out by an introduced fungus.

Chestnuts replaced by oaks. 1920s–1960s
Acorns may have partially compensated for the loss of chestnuts as winter forage.

1940

Going . . .
"Less common than in past"
(Newcombe 1930, Poole 1940).

Color Key:
Red: Adverse effects
Blue: Compensatory effects

Photo by A. Hicks

Figure 2. Hypothetical population trajectory of Allegheny woodrat populations in northeastern North America, from a pre-European settlement high in the upper left to the current low in the lower right. Adverse effects that may have precipitated population decline are shown in red. Compensatory effects that may have allowed periods of population stability are shown in blue. Actual effects on population size and the precise timing of the decline are unknown and are not implied by the graphics.

raccoon populations during the second half of the 20th century (Balcom and Yahner 1996, LoGiudice 2003, Prange and Gehrt 2004), making woodrat–raccoon interactions more common.

Peculiarities in woodrat behavior conspire to magnify the effects of this parasite. For example, woodrats collect raccoon feces and store it in food caches (LoGiudice 2001). Since raccoon roundworm eggs are extremely long-lived and woodrat den sites are used sequentially, both current and subsequent occupants of a den may be exposed to the parasite, causing a chain of roundworm-induced mortality, as was documented in the New York State study (McGowan 1993). There may be a synergy between raccoon roundworm and food availability. White-footed mice in unmanipulated populations are more likely to forage in raccoon latrines than are

little evidence that it is a widespread problem for woodrats in these states or in other parts of the species' range (Owen et al. 2004). Parasite prevalence appears to decline with latitude (Kazacos 2001, Owen et al. 2004; but see Eberhard et al. 2003), a possible explanation for the apparent stability of southern woodrat populations.

Historic fluctuations in competitor and predator communities

When considering the downward trajectory of an endangered species, it is easy to forget how much the wildlife community of the 19th and early 20th centuries differed from that present in forests today (Foster et al. 2002). By 1800, Americans had successfully exterminated most large predators and herbivores from eastern North America. Major consumers of

hard mast, browse, and forbs, such as white-tailed deer and wild turkeys (*Meleagris gallopavo*), were largely absent from the range of the Allegheny woodrat from the mid- to late 19th century through at least the mid-20th century (Rhoads 1903, Spurr and Barnes 1980, Eaton 1992, McCabe and McCabe 1997). It is possible that woodrats were able to persist after the loss of the chestnut in part because of the lack of competition for mast. The reintroduction and proliferation of deer and turkeys—large, highly mobile competitors—would have further reduced the amounts of mast and other plant foods available to woodrats (Feldhamer et al. 1989, Eaton 1992, McShea and Schwede 1992).

The impacts of changes to the predator community are less clear, as little is known about woodrat enemies. Nevertheless, the virtual elimination of most predatory mammal species by the mid-19th century (Foster et al. 2002) is likely to have reduced mortality from this source until populations of mesopredators rebounded in the 20th century. The elimination of larger predators may have positively affected the smaller predatory species likely to prey on woodrats.

Hypothetical chronology

Although none of the hypotheses considered emerges as the clear cause of the extirpation of northern Allegheny woodrat

populations, there is evidence that each may be a contributor. Rather than being mutually exclusive, the effects of these factors appear to have been working in concert. Some of these changes may have silently diminished woodrat populations from the mid-19th century or earlier, finally precipitating population collapses that drew human attention in the late 1970s. What follows is a hypothetical timeline of the decline of the Allegheny woodrat in its northeastern range, based on the dates of the influencing factors and on published observations of naturalists and scientists (figure 2). Rather than tracing a steady downward trajectory, it suggests a stepwise progression to extinction, including periods of decline followed by periods of stability at smaller population sizes, with compensatory effects softening the blows dealt by adverse events until the final, seemingly sudden collapse.

It is likely that deforestation in the 18th and 19th centuries negatively influenced woodrats before 1900, as noted by Rhoads (1894, 1903). At the same time, elimination of predators and competitors may have ameliorated these losses. Populations may have stabilized by the mid-19th century, once most forested land had been cleared (Foster et al. 2002). The loss of the reliable annual chestnut crop most likely set another decline in motion, reducing the carrying capacity of the woodrat's environment, decreasing reproductive rates, and
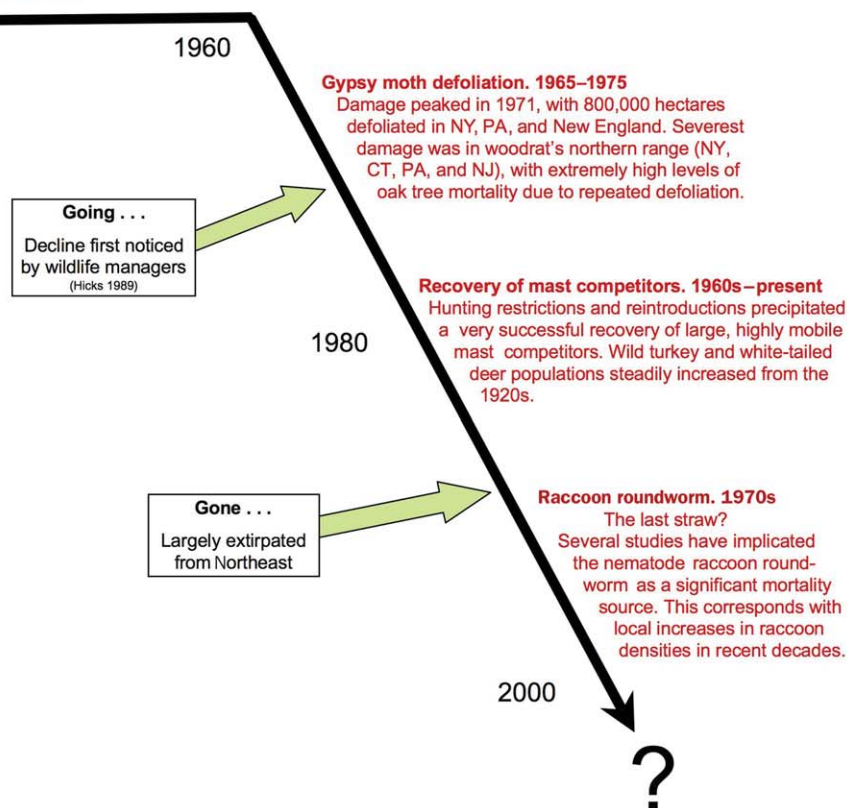
Habitat fragmentation. 1940s–present
Extensive human development of northern range since WWII blocked dispersal routes. Human use of forests has been associated with decline.
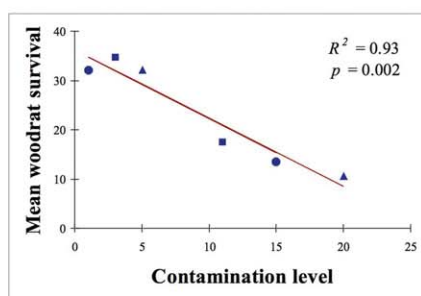
Survival (in weeks) of reintroduced populations of Allegheny woodrats as a function of roundworm contamination (raccoon latrines found per hour of search time) of reintroduction site (redrawn from LoGiudice 2003).
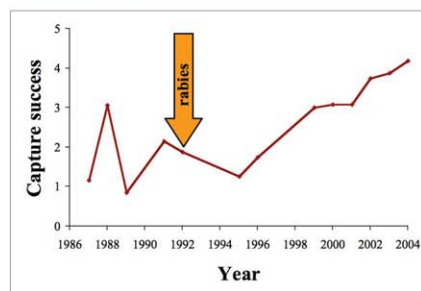
Capture success (individuals per 10 trap nights) of Allegheny woodrats before and after rabies reduced raccoon populations in the only remaining woodrat site in New Jersey. Data courtesy of James C. Sciascia and Michael Valent, NJ Division of Fish and Wildlife.

1960

Gypsy moth defoliation. 1965–1975
Damage peaked in 1971, with 800,000 hectares defoliated in NY, PA, and New England. Severest damage was in woodrat's northern range (NY, CT, PA, and NJ), with extremely high levels of oak tree mortality due to repeated defoliation.

Going . . .
Decline first noticed by wildlife managers
(Hicks 1989)

1980

Recovery of mast competitors. 1960s–present
Hunting restrictions and reintroductions precipitated a very successful recovery of large, highly mobile mast competitors. Wild turkey and white-tailed deer populations steadily increased from the 1920s.

Gone . . .
Largely extirpated from Northeast

Raccoon roundworm. 1970s
The last straw? Several studies have implicated the nematode raccoon roundworm as a significant mortality source. This corresponds with local increases in raccoon densities in recent decades.

2000

?

increasing the frequency of local extinctions. The destruction of the chestnut was complete by about 1920 in Connecticut, New York, and Pennsylvania, and by 1930 in Ohio, Maryland, and Indiana (Campbell and Madden 1990). Marginal habitat that previously supported small woodrat populations may have been abandoned, which would serve to isolate remaining populations. This timing corresponds with the published observations of decline (Newcombe 1930, Poole 1940) and may have been followed by another period of stability during which, in the absence of large mast competitors, Allegheny woodrats could exploit periodic acorn crops and sustain their numbers, albeit at lower levels.

Enactment of strict hunting regulations early in the century, together with deer and turkey reintroductions, precipitated a rapid recovery in the densities of these two mast competitors. US populations of wild turkeys increased from about 130,000 in the late 1940s to 1.25 million in 1970 and had reached 4 million by the early 1990s (Eaton 1992). Similarly, deer populations have dramatically increased from the 1920s to the present, with the recovery well under way by the 1960s (McCabe and McCabe 1997). Deer densities frequently exceed 10 deer per km², a level at which they have been found to prevent forest regeneration and succession and to reduce the densities of small mammals (McShea and Schwede 1992, Healy 1997). The heightened competition from these two species would have increased the stress on Allegheny woodrat populations. In addition, rebounds in the populations of great horned and barred owls and mammalian mesopredators (Foster et al. 2002) may have increased predation pressures to near, or even above, presettlement levels.

Throughout this entire period, the fragmentation of Allegheny woodrat habitat by human development blocked dispersal routes, making the recolonization of extirpated sites less frequent and less likely. Many extirpated populations are in the southern reaches of the Hudson River valley, one of the most densely developed parts of the woodrat's range, where highways and human development dominate the landscape.

In the 1970s, concurrent with the surging of the turkey and white-tailed deer populations, there was another threat to the woodrat's share of the food supply. The gypsy moth, introduced into the United States near Boston in the late 1860s, was sweeping through the Northeast, consuming all the forests in its wake. The damage peaked in 1971, with 800,000 hectares defoliated in New York, Pennsylvania, and New England. Connecticut, New York, Pennsylvania, and New Jersey incurred the most damage, experiencing extremely high levels of oak mortality due to repeated defoliations (McManus and McIntyre 1981). It is in these states that the woodrat decline was first noted.

At this time, raccoon populations also appear to have been increasing. The suburbanization of rural landscapes and the corresponding relaxation of hunting pressure in the decades following World War II are likely to have increased the densities of this adaptable species (Riley et al. 1998). Qualitative observations recorded by Dan Smiley, a prominent naturalist in southern New York State, suggest such an increase, with raccoons being a noted rarity in the 1920s and 1930s and a common nuisance by the 1970s. Allegheny woodrat populations, fragmented, depleted, and isolated by the early 1970s, would have been vulnerable to stochastic mortality sources that could have driven whole metapopulations to extinction. In New York and New Jersey, at least, this stochastic force appears to have been the raccoon roundworm, which may have interacted synergistically with food shortage caused by gypsy moth defoliation.

All these factors appear to have converged in the 1970s, tipping the balance and causing collapses of entire metapopulations. More recently, woodrats have stabilized or recovered somewhat in New Jersey, with the last remaining population appearing to grow and reinvade extreme southern New York (figure 2). This may be a result of the spread of raccoon rabies in the early 1990s, which reduced raccoon densities at least temporarily (Riley et al. 1998). The reasons for the apparent stability of more southerly Allegheny woodrat populations remain unknown. Reduced winter metabolic demands, lower raccoon roundworm exposure (Owen et al. 2004), and diminished forest impact are all possibilities, but at present there is no answer to this question.

The plight of the Allegheny woodrat is undoubtedly typical of many endangered species. As humans manipulate nature in increasingly complex ways, we set off ecological chain reactions that may be largely invisible for many decades, until it suddenly becomes clear that something has gone wrong. What can this exercise teach us about the management of endangered species? First, we should not ignore factors that cause seemingly small increases in mortality or reductions in fitness. Although they may be insignificant individually, the cumulative effects of these insults may be enough to tip a population over the edge. It is necessary, although challenging, to take a synthetic approach, considering all reasonable hypotheses for the decline of a species and anticipating that their impacts may interact in complex ways. Second, we should not underestimate the importance of dispersal. Blocked dispersal routes may quickly destabilize a metapopulation if other factors cause local extinctions. Finally, we should recognize the importance of historical contingencies and realize that forces important in the past may be inconsequential now, and vice versa. We must train ourselves to look broadly (in the ecological sense) and deeply (in the historical sense) when investigating the causes of species declines.

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