Chapter 1
History and Current Status of the Allegheny Woodrat

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Introduction

In early 2007, the announcement of a new species of clouded leopard (*Neofelis diardi*) received international press coverage. In fact, this animal, the largest predator in Borneo, was already well known to biologists. The actual news was that DNA analysis showed it to be a species distinct from its close mainland Asian relative, a result that researchers said should "increase the urgency of clouded leopard conservation efforts" (Buckley-Beason et al. 2006). At the same time, another research group was reporting that the population size of clouded leopards in Borneo was considerably lower than previously estimated (Wilting et al. 2006).

The case of the clouded leopard illustrates twin problems that bedevil our understanding of species of conservation concern—identifying what the species is and recognizing its level of distress. However, most threatened animals have considerably less public visibility and research support than the clouded leopard. The Allegheny woodrat (*Neotoma magister*) may be a more realistic model for illustrating the significance of these problems, and how we can confront them for better conservation.

In this chapter, I first trace the convoluted taxonomic history of the Allegheny woodrat. While the case has some unusual twists and turns, similar confusion has occurred for many other species. I then review how the Allegheny woodrat came to be perceived as a species in decline, and why this perception has been hard to validate with data. Where baseline data are lacking, as is often the case, documenting a decline may require creative reconstruction of history by a variety of means. Our experience with the Allegheny woodrat is an object lesson in what basic information needs to be gathered before proceeding to management plans. This information includes an understanding of genetics and geography, attention to the primary literature (however old), use of the best baseline data available, establishment of clear
goals and criteria for meeting those goals, and development of a framework for coordination and communication.

As background for this review, and to aid in understanding the basis for the literature related to woodrat taxonomy, I compiled a database of existing museum specimen records for what is now designated *N. magister*. These records, from standard museums (Hafner et al. 1997), but also from additional sources cited in the literature or suggested by colleagues, typically included specimen identification number, collection date and locality, and often the collector’s name. To select records for the database, I did not examine most of the specimens, but used recorded collecting locality as the primary guide. I first included all *Neotoma* specimens whose collection county appeared to fall within the geographic range mapped in Hall (1981) for *Neotoma floridana magister* (as it was then designated). I then examined records along the ambiguous southeastern border of that mapped range (through North and South Carolina, Georgia, and Alabama) and followed the determinations by Ray (2000) for geographic range of *N. magister* versus *N. floridana*.

The total museum specimen database (available on request) comprised over 950 records. From these, I produced maps of collecting localities, using geographic coordinates listed with the record or that I estimated according to Mammal Networked Information System (2007) guidelines. Specimens whose collecting locality was described only to the county level were excluded from the geographic data, except for two records that were the exclusive ones for that county (Chester County, PA and Buckingham County, VA); for these I estimated coordinates near the center of the county. I created time-series maps of the specimen localities using ARC GIS 9.2 (Environmental Systems Research Institute, Inc.) to illustrate the extent of documented geographic range of this species at different points in time.

The records in the museum specimen database, with their dates of collection, imply how much was known to biologists about *N. magister*’s morphology and distribution at various points in the past. In comparing these records with the historic literature, I have made the simplifying assumption that the collection date of each specimen is when it became “known to science” and available to researchers. While this may not be true of all specimens, it is probably true of the considerable majority.

**Early Recognition: Extant or Extinct?**

The Allegheny woodrat was first described as *Neotoma magister*, with a later name *Neotoma pennsylvanica* being discarded as invalid. It was then reclassified as a subspecies of *Neotoma floridana* (*N. floridana magister*), but more recently has been recognized as a distinct entity under the original name, *Neotoma magister* (Castleberry et al. 2006). Such a bald account, however, falls short of conveying how this confusing history evolved as a result of a gradually accumulating base of specimen material, beginning with a few fossil jaws.

Initially, the species was introduced to science by biologist Spencer Fullerton Baird. As Assistant Secretary to the Smithsonian Institution, Baird contracted
biological teams to accompany the railroad survey crews in the American west, shipping specimens back to Washington, and forming the core of what is now the United States National Museum of Natural History. In 1857, on the basis of these specimens, Baird published a synopsis of known and newly described American mammals, including seven living species in the woodrat genus *Neotoma*, five of them new to science (Baird 1857).

Baird’s geographically extensive North American collections allowed him to put into context some curious cave fossils he had brought with him to the Smithsonian from his years as a student and professor at Dickinson College in Carlisle, Pennsylvania (Miller 1940). Although they were incomplete jaw fragments, he recognized them as *Neotoma*. The only other eastern U.S. woodrat specimens Baird had for direct comparison were six skulls of *N. floridana* from South Carolina, Georgia, and Arkansas. Baird asserted that the Carlisle specimens were much bigger, and speculated that the animal they represented “could not have been less than 12 inches in length.” He named the large species ‘*Neotoma magister*’ and declared it extinct (Baird 1857).

Baird also commented on a woodrat collected in New York, along the Hudson River, which he had as a taxidermy specimen without a skull. Despite being impressed with its “unusually large size,” Baird (1857) grouped it with the smaller *N. floridana* from the Gulf Coast, “although I have not heard of any intermediate localities.” Why Baird chose to make this convoluted determination instead of the more parsimonious one of assigning the New York specimen to *Neotoma magister* is unknown.

Knowledge of the geographic range of North American woodrats accumulated slowly. Ironically, the next discovery in the northeastern U.S. was only 30 km from where Baird had done his early fieldwork. In 1893, two woodrats were collected on a rocky ridge south of Carlisle, Pennsylvania, and sent to the Academy of Natural Sciences at Philadelphia, where Wittmer Stone, primarily known as an ornithologist, described them as a new species, *Neotoma pennsylvanica* (Stone 1893). Stone gave no indication he was aware of Baird’s fossil *N. magister*. He differentiated his Pennsylvania woodrats from two Florida specimens of *N. floridana*, citing *pennsylvanica*’s hairier tail, larger size, and several cranial characters (Stone 1893).

The following year, Samuel Rhoads (1894) attempted to resolve whether Baird’s fossils and Stone’s *N. pennsylvanica* were really different species, and whether they were distinct from *N. floridana*. Again, the investigation was constrained by limited specimen material. To represent *N. pennsylvanica*, Rhoads used Stone’s two skins and skulls. For comparison, he did not have Baird’s *N. magister* type specimens, but substituted “fossil” bones from two eastern Pennsylvania caves, which he assumed were equivalent to Baird’s *N. magister*. Rhoads also used two woodrats that had been trapped in a cave in western Virginia, far from the known range of any woodrat to that date. Surprisingly, he included these as *N. magister* without comment, despite Baird’s claim that *magister* was an extinct species and despite the fact that their collector, Philadelphia biologist E. D. Cope, had called them “*Neotoma floridanum*” [sic], a logical choice given the Mississippi drainage from which they were taken (Cope 1869). From this small sample Rhoads (1894) concluded that the
"N. pennsylvanica" specimens were indistinguishable from N. magister, and Baird's original name magister should take precedence for both living and fossil forms.

The "unusually large" Hudson River woodrat that had been grouped by Baird with southern N. floridana also got Rhoads's attention. It would have been logical to include this specimen with his other living N. magister, but Rhoads did not do so. He noted that all his northern (i.e., N. magister) specimens had been collected in caves or cave-like fissures, whereas the Gulf Coast N. floridana were not cave animals. In fact, he consistently referred to the northern species as "cave rat" and the southern as "woodrat." Apparently, this habitat distinction convinced him that Baird's Hudson River, New York, specimen had to be a "large Neotoma floridana ... probably imported in a cargo of southern lumber" (Rhoads 1894).

Rhoads's speculation about the anomalous Hudson River woodrat came under immediate challenge when Allen (1894) reported a specimen caught live along the Hudson, a few miles upstream from Piermont, New York. Allen described features showing his specimen was not N. floridana and claimed that his animal, as well as the Hudson River one seen by Baird, was "doubtless" Stone's N. pennsylvanica. The woodrat was caught along a "cliff, full of deep crevices" (Allen 1894), an observation consistent with Rhoads's claim that the northern species was a cave and fissure specialist.

In the same year, C. H. Merriam (1894) proposed a systematic arrangement of species of the genus Neotoma. He did not say what northeastern woodrat specimens he examined, but he was probably aware of those held in the Academy of Natural Sciences of Philadelphia and the U.S. National Museum. This would have included 17 specimens (from two localities in Pennsylvania and one each in Virginia, Kentucky, and New York) plus "fossil" bone deposits from several Pennsylvania caves (Fig. 1.1).

Merriam, like Rhoads, was a strong subscriber to the theory that each species was associated with a particular habitat. He completed a detailed study in Arizona (Merriam 1890) that led to the development of his enormously influential Life Zones concept, in which flora and fauna were arranged in discrete elevational bands from base to summit of western mountains. In the Neotoma review, he applied his Life Zone approach to the eastern woodrats, separating them into N. pennsylvanica, with a geographic range he estimated (from no more than five localities) as "Allegheny Mountain region of Pennsylvania and probably the whole of the southern Alleghenies; north to southern New York" and N. floridana, belonging to the "austropirarian fauna of South Atlantic and Gulf Coasts and upper Mississippi Valley" (Merriam 1894). Merriam's range designations thus emphasized a montane habitat for the northern species and a valley habitat for the southern one. As to what he termed the "subfossil" N. magister, Merriam noted that Baird had collected it in a Pennsylvania valley, which would make it difficult to reconcile with his supposedly montane N. pennsylvanica. He elected to keep magister as a separate (extinct) species, speculating that the cave N. magister of Pennsylvania were the same as Pleistocene bones from Missouri caves (Merriam 1894).

As new material accumulated, E. A. Goldman (1910) undertook a new revision of the entire genus Neotoma. To address the magister/pennsylvanica split, he
took pains to obtain Baird’s original type specimens. He devised skull metrics to compare them with *N. pennsylvanica*, using five new specimens from West Virginia, Kentucky, and the Potomac River near Washington. In a comparative table, the Baird mandibles were generally larger in all metrics than the "*pennsylvanica*" jaws, and Goldman concluded that *N. pennsylvanica* and *N. magister* should be separately recognized, but only after taking the questionable step of omitting two of Baird’s mandibles because they were “probably *N. pennsylvanica*.”
Goldman (1910) also published the first range map for "N. pennsylvanica." It was based on much more material than had previously been available—94 specimens from 18 localities. The map depicted a range extending from northern Alabama up the Tennessee River Valley in a narrow band northward along the Appalachians to the Hudson River in New York, and included a branch across Kentucky but excluded Ohio and Indiana (Fig. 1.1). Goldman did not comment specifically on this animal's relationship to N. floridana; but as he placed the two species far apart in his text and said that N. pennsylvanica required "no close comparison with any known living form," apparently he regarded it as easily distinguishable.

Goldman’s scheme, with N. pennsylvanica and fossil N. magister as separate species, was not seriously challenged for three decades, but Poole (1940) eventually raised the question, once again from an expanding specimen base. Poole was particularly impressed with woodrat remains he had found alongside pre-Colonial human artifacts. His investigations convinced him that the woodrats present in Pennsylvania and Maryland, from the earliest postglacial deposits through the archaeological material to current-day populations, were all one continuous species. Poole re-examined Baird’s type specimens and seven museum skulls of "N. pennsylvanica," concluding that they overlapped entirely and that the name pennsylvanica was invalid. Although Poole used only a few specimens in his measurements, his arguments carried the day, perhaps because the typological thinking of Goldman's day was being replaced by the modern synthesis of paleontology, population genetics, and Darwinian evolution that emphasized variation within a species. Poole’s (1940) paper apparently settled the magister/pennsylvanica question, as the synonymy of the two forms has not seriously been questioned since, and the designation "N. pennsylvanica" has dropped out of use.

**Mid-1900s: The Sinking of N. magister**

While increasing numbers of specimens had done away with a false distinction between fossil and extant woodrats, the same trend soon threatened to eliminate N. magister as a species entirely. In the early years, woodrat taxonomists had compared Allegheny woodrats from the northern Appalachians with woodrats from the distant Gulf Coast and readily concluded that they were different. Goldman’s (1910) mapped range for N. floridana was separated by hundreds of kilometers from the Allegheny woodrat's range. But as museum collections grew, closing the geographic gaps between the two, cline-minded biologists began proposing that the Allegheny woodrat was just a subspecies of the earlier described and very variable N. floridana.

The logic and techniques brought to bear on this question were new. Taxonomic works were beginning to be supported by more sophisticated statistical analysis of entire series of specimens. Rhoads’ (1894) simplistic dichotomy of "cave rat" (N. magister) versus "wood rat" (N. floridana) would not accommodate a growing awareness of the variety of habitats used by eastern woodrats. Merriam’s (1894) distinction of upland versus valley zones had similarly been eroded, as specimens
were collected in intermediate localities. By the mid-1950s, museums held more than 700 Allegheny woodrat specimens collected from nearly 80 U.S. counties (Fig. 1.2).

Schwartz and Odum (1957) used these newer approaches to analyze taxonomic relationships among woodrats of the eastern United States. They examined variation in 12 morphological metrics taken from 224 specimens that they grouped by subspecies. Presenting their results in what at that time was a relatively novel graphic—a box-whisker plot showing means, standard errors, and ranges—they compared *N. magister* specimens with *N. floridana*, but divided the *N. magister*
specimens into northern and southern samples. They argued that “northern” *N. magister* were indeed significantly larger than all *N. floridana*, but “southern” *magister* specimens (from Kentucky, Virginia, and southward) were intermediate in size and not significantly different from *N. floridana*. Schwartz and Odum (1957) claimed that earlier studies had exaggerated the size of *N. magister* by using a biased sample of primarily northern specimens. Clinal variation in size, a newly recognized phenomenon, could explain the bigger woodrats in the northern United States, they suggested, and it would be “more fitting to regard *magister* as a subspecies of *floridana*.” They then reinforced this somewhat guarded wording with a new range map depicting just one eastern woodrat, *N. floridana*, with a continuous range from the Gulf Coast to Massachusetts. Within this range, the subspecies “*N. f. magister*” was represented from northern Alabama and central Tennessee northward (Schwartz and Odum 1957).

This revision received a boost when Hall and Kelson (1959) accepted their arrangement in the monumental work *The Mammals of North America*, the first comprehensive systematic and geographic listing of the American mammal fauna. Hall and Kelson’s (1959) range map, like that of Schwartz and Odum (1957), showed *N. f. magister* as one arm of a continuous distribution for *N. floridana*. This map depicted a much larger range for *N. magister* than Goldman’s (1910), citing museum specimens as the basis for doubling the territory in Tennessee and Kentucky and adding southern Indiana and Ohio (Fig. 1.2).

Relegating *N. magister* to subspecies status had a ripple effect through the secondary literature that strongly influenced conservation biology. Through the period of the 1960s–1980s, while conservation awareness for other species was growing, the Allegheny woodrat was almost universally treated as a subspecies of the “eastern woodrat” *N. floridana*. An important review of the biology of *N. floridana* (Wiley 1980) incorporated literature on the Allegheny woodrat into a composite description of biology that would make it difficult for subsequent researchers to tease them apart. State and regional mammal guides for the northeastern states written by mammalogists during this era listed the woodrat of the northeastern United States as *N. floridana* (Paradiso 1969, Gottschang 1981, Mumford and Whitaker 1982, Merritt 1987). The second edition of *The Mammals of North America* retained the subspecies designation (Hall 1981), while expanding the range further into Indiana and the mountains of Georgia. The most widely used popular mammal field guide (Burt and Grossenheider 1952) also used a range map that referred to all woodrats east of the Mississippi as “eastern woodrat.” Although Birney (1976) did note that he was unable to hybridize “*N. f. magister*” in the laboratory with other *N. floridana* and suspected they were a separate species, his finding had little impact. Overall, the sources most readily available to management agencies, educators, and the general public during this period consistently presented the cave-and-fissure woodrat of the U.S. northeast as being a somewhat peripheral variant of the very common and widespread “eastern woodrat.” In a context of competing issues and limited resources, there was little chance that the Allegheny woodrat would command much attention for conservation.
Molecular Approaches and the Re-establishment of *N. magister*

The development of new molecular methods in the early 1990s created an opportunity to re-examine the taxonomic identity of the Allegheny woodrat. Hayes and Harrison (1992) conducted mitochondrial DNA analyses of 114 woodrats from 33 localities, including 49 *N. f. magister* woodrats from seven states, 50 individuals representing other subspecies of *N. floridana*, and 15 individuals of other *Neotoma* species. Analyses of mtDNA data produced cladograms that grouped all putative *magister* samples together, and demonstrated that *N. magister* was as divergent from *N. floridana* as other woodrat species were from each other (Hayes and Harrison 1992).

Conclusions based on molecular genetics were supported by morphological analyses. Hayes and Richmond (1993) studied skull and other morphological characteristics of 917 specimens representing 418 *N. f. magister* as well as the other six *N. floridana* subspecies. A principal components analysis based on morphological characteristics demonstrated almost complete separation of *magister* from *floridana* (Hayes and Richmond 1993). In fact, one cranial characteristic, the presence of a maxillovomerine notch, was virtually foolproof in distinguishing the two groups. Collecting localities of notch-bearing woodrats closely conformed to the previous descriptions of *magister* range, with “the single exception” of three woodrats collected at Muscle Shoals, Alabama, “just south of the Tennessee River” and outside *magister*’s range. However, historic maps of that locality before river impoundment indicate that Hayes and Richmond (1993) were probably mistaken in this “exception” and that the specimens in question were more likely collected on the north shore of the Tennessee, consistent with Hall’s (1981) *magister* boundary (C. Ludwig pers. comm.).

The compelling combination of molecular and morphological evidence from the largest and most geographically comprehensive samples studied to that time prompted Hayes and Richmond (1993) to propose resurrection of *N. magister* as a species. Subsequent genetic analyses by Planz et al. (1996) supported this distinction in a context of the entire *N. floridana* species group. As further confirmation, Ray (2000) found a distinct karyotypic form and a trustworthy mitochondrial DNA marker to differentiate *N. magister* from *N. floridana haematoreia* in the southern Appalachians, with preliminary evidence that the same character could be used to distinguish *N. magister* from *N. floridana illinoensis* on the western border. The only evidence of introgression between *magister* and *floridana* was in two ambiguous specimens from Burke County, North Carolina (Ray 2000).

In light of the mounting evidence, *N. magister* was listed as a separate species in the Revised Checklist of North American Mammals (Jones et al. 1997, Baker et al. 2003). Also, it has been recognized in a world list of species (Wilson and Reeder 2005), profiled in a review of its biology (Castleberry et al. 2006), and was recently recognized in the Natural Heritage database NatureServe (2006). However, more than a decade after publication of the first molecular studies, many museums and websites still list this species as *N. floridana* (or even *N. pennsylvanica*), and much
of the older literature is still in use. This lack of consistency makes it difficult to coordinate information and effort, as nonspecialists may not be aware that they are dealing with the same species under different names.

**Determining Current Status**

This volume characterizes the Allegheny woodrat as a species in decline, but we do not know, nor are we ever likely to determine, when and where its populations began to diminish. It is possible, however, and perhaps more instructive, to review the history of how the decline of this species was detected and perceived by biologists and the public. Documenting the decline of a species is complicated. The World Conservation Union (IUCN 2006) specifies criteria to determine conservation status of species worldwide. For example, the IUCN asks evaluators to quantify the geographic range of occupied habitat, estimate population size, and calculate the rate of decline over the past decade. In other words, it matters not just that a species has disappeared from places it once occupied, but also that it has such a trajectory of decline or has reached such a reduced condition that it appears doomed within a short period without intervention. All of the IUCN criteria are at least semiquantitative and demand supporting data.

Species status determination among the various U.S. states is considerably less standardized. The procedures always involve scientific data, but may also rely on expert opinion and political concerns. Supporting data may range from detailed long-term demographic studies to occasional questionnaires sent to conservation officers. In the absence of real data, newsletter or word-of-mouth accounts of what is happening in other states may have an influence. All of these methods have figured in the case of the Allegheny woodrat.

Several features of Allegheny woodrat biology make perceiving and documenting a population decline difficult (Mengak et al. Chapter 7). Because *N. magister* inhabits rock outcrops, cliffs, and caves that are often inaccessible, the habitat is patchily distributed and poorly mapped. Furthermore, woodrats are seldom observed directly, and trapping is laborious, expensive, and potentially disruptive. The lack of historic baseline data is also a problem. State-specific and regional mammal guides have often depicted distributional ranges in vague terms, especially for species perceived as common. Museum records and some published literature show historic woodrat sites, but location of many sites was not recorded precisely, so resurveying them involves guesswork. Even those museum records that are potentially valuable are frequently inaccessible. In addition, there is virtually no record of appropriate habitat that was searched in the past but found vacant. It is thus difficult to determine what fraction of appropriate habitat was historically occupied, or whether some current populations might even represent a range expansion.

A particularly complex issue that applies to the Allegheny woodrat is detecting a population decline in a metapopulation complex—a set of subpopulations that are linked by dispersal. The very nature of a metapopulation implies that even in a self-maintaining complex, individual sites will “wink out” from time to time and
later be recolonized from nearby sites (Krohne 1997). Simply noting that woodrats are absent from a site previously populated is therefore not definite evidence of decline. Ideally, the entire metapopulation area needs to be surveyed repeatedly, and this has seldom been done or even considered.

Biologists have, however, been able to take advantage of one fortunate aspect of woodrat biology in detecting decline. Even if not directly observed, woodrats leave conspicuous, lasting sign of their occupation. Fecal piles ("latrines") are characteristic, winter food caches may be visible at rock surface, and plant-fiber nests may be seen in caves (Poole 1940). Experienced observers can distinguish fresh sign from sign produced in a previous season, so old sign can be used to detect former occupation. Using the evidence from woodrat sign, an observer can, in a single survey visit, determine with reasonable accuracy that a site was formerly occupied (old sign) but is now vacant (no fresh sign).

With these considerations in mind, we can examine how the Allegheny woodrat came to be recognized as a species of concern early on in some places, and only much later, if at all, in others:

Pre-Colonial range contraction—As early as 1940, Poole used woodrat bones from archaeological excavations in Pennsylvania to argue that the species' range before European settlement must have been considerably broader (Poole 1940). Similarly, Richards (1972, 1987) catalogued woodrat bones in numerous Indiana caves north of the species' current range. However, noting no "European materials" associated with these woodrat middens, Richards (1987) interpreted the range contraction as occurring prior to European settlement. Newcombe (1930) did claim that in pioneer days, woodrats "frequently came into the houses of settlers" and so must have been more common then, but until the 1970s, most authorities considered woodrats abundant in the northeastern United States. For example, in Pennsylvania's statewide mammal survey in the late 1940s, surveyors did not bother to trap for woodrats in some regions but merely noted that "every mountain talus slope and block area examined by us held woodrats" (Gifford and Whitebread 1951). The idea of a prehistoric larger range for the woodrat was consistent with findings for fossil bison, tapir, horse, and ground sloth, and did not draw the attention of conservationists.

New York—Various records through the 1970s showed woodrats to be found in most of the available habitat in the Hudson Highlands and Shawagunk Ridge in counties west of the Hudson River. No alarm was raised until their disappearance was noted at the Mohonk Preserve in Ulster County around 1977. This report led to new surveys of historic habitat, in which only five sites were found to be occupied (Hicks 2005). The last known New York woodrats were removed in 1987 for captive propagation. At that time, the Allegheny woodrat was thought extirpated in New York. More recent sightings may represent migrants from New Jersey rather than a breeding population, but the species is now officially categorized as endangered in New York (Hicks 2005).

Connecticut and Massachusetts—Only one confirmed Allegheny woodrat record exists from Connecticut, a specimen collected prior to 1932 along the New York border (Goodwin 1932). The lone record from Massachusetts is a specimen in the
museum of the University of Kansas that was collected in Berkshire County (N. Slade pers. comm.). The existence of actual populations has never been established in either state. Connecticut lists the woodrat as a species of concern, “believed extirpated,” with no plan for reintroduction (Connecticut Department of Environmental Protection 2004).

New Jersey—Prior to 1960, woodrats had been collected from several locations in the four northernmost New Jersey counties. In the early 1980s, concerned by reports of decline in New York, the New Jersey Division of Fish and Wildlife surveyed three historic woodrat sites but found no woodrats or recent sign there (Valent 2003). Searches of other appropriate habitat eventually located two previously unknown populations, one of which subsequently became extirpated. New Jersey designated the Allegheny woodrat an endangered species in 1991 based on these results (Valent 2003). The sole remaining woodrat population, along the Hudson Palisades, has been monitored with live-trapping periodically since 1987, and it has maintained a stable population size in recent years between about 20 and 30 (New Jersey Department of Environmental Protection 2005).

Pennsylvania—Biologists conducting bat surveys in the 1970s noted old, but not fresh, woodrat sign in a number of Pennsylvania caves. This observation led to a systematic live-trapping investigation by Hall (1988) at sites where museum specimens of woodrats had been collected in statewide mammal surveys conducted around 1950. Of 54 historic sites trapped, 21 no longer supported woodrat populations by the late 1980s (Hall 1988). Hall’s alert led to the nomination of the Allegheny woodrat as a threatened species in Pennsylvania in 1981 (C. Butchkoski pers. comm.). Since that time, the Pennsylvania Game Commission has allocated annual effort to building a database of occurrence reports and field surveys to determine the distribution and abundance of woodrats in the state (Butchkoski 2006). These studies have documented recent disappearance of woodrats from much of the northern and eastern extent of the species’ distribution in Pennsylvania, and some more central areas as well (Butchkoski 2006).

Maryland—Although the first Maryland woodrat specimens were taken on the Potomac River just outside the District of Columbia in 1921, Paradiso (1969) interpreted this part of the range as a quite recent expansion from Virginia. He implied that the mountains of western Maryland were the species’ native range, and deemed woodrats “abundant” in Allegany County in western Maryland in 1961 (Paradiso 1969). There was little systematic effort to determine distribution or abundance of the species through the mid-1980s, but Feldhamer et al. (1984) recommended that the woodrat be designated threatened in Maryland “because of its affinity for rocky areas, especially caves” which were considered at risk from frequent disturbance. After woodrat declines were reported in northern states, surveys and monitoring in Maryland in the 1990s showed woodrats disappearing or already gone from many of the sites containing signs of previous occupation, and the species was designated endangered in the state in 1994 on the basis of this decline (D. Fellér pers. comm.).

West Virginia—From the results of a statewide mammal survey and other records, McKeever (1954) showed the range of the Allegheny woodrat as covering nearly all of montane West Virginia (the southern and eastern portions of the state).
A considerable amount of ecological and genetic research has been done in the core region of Allegheny woodrat distribution in West Virginia (Castleberry et al. 2006), where woodrats have been presumed common and secure. In response to declines noted elsewhere, some sites that were trapped in the 1990s were trapped again in 2004, with no pattern of decline evident (Stihler 2004). However, in a detailed demographic study, Manjerovic (2004) and Wood (Chapter 3) documented a population decline at their study site. The state’s Wildlife Conservation Plan portrays West Virginia as the species’ “stronghold” (West Virginia Division of Natural Resources 2005), yet the woodrat is noted in that plan as a species of greatest concern in a number of habitats, and it is singled out for special attention with plans for monitoring, surveying, mapping, and assessment of threats.

**Virginia**—Before 1950, Bailey (1946) and Handley and Patton (1947) compiled specimen and other records for the Allegheny woodrat to determine its distribution in Virginia. They reported woodrats in some 18 counties through the Appalachian chain and along the Potomac River. No measures of abundance were reported, but woodrats were described as “common from the Blue Ridge westward wherever suitable habitat occurs” (Handley and Patton 1947). Trapping studies through the 1990s have showed no remaining populations along the Potomac River border with Maryland (Mengak 1999). Elsewhere in Virginia, many historical collecting sites are now vacant of woodrats, but other active sites have been discovered, so no overall trend is clear (Mengak 1999). The state has awarded the Allegheny woodrat no special concern status, and mentions it only as Tier IV (relatively low priority) for attention in Virginia’s Wildlife Conservation Strategy (Virginia Department of Game and Inland Fisheries 2005).

**North Carolina**—Only one record of the Allegheny woodrat was noted in North Carolina by Hall and Kelso (1959), and only two by Clark (1987), who emphasized the lack of knowledge of this species in the western mountains of North Carolina and gave its status only as “undetermined.” Ray (2000) trapped specimens at additional localities in six counties, and suggested that the Allegheny woodrat was more abundant in North Carolina than previously recognized. The strong similarity between *N. magister* and *N. f. haematoreia* of the mountains farther southwest has contributed to the confusion about this species. However, Ray (2000) developed methods to distinguish them karyotypically (Ray and Webster 2002) and using multiplex PCR analysis of mitochondrial DNA (Ray et al. 2002). The status of North Carolina woodrat populations is currently unknown (S. Bosworth pers. comm.), but North Carolina’s Wildlife Conservation Strategy lists *N. magister* as a “priority species” for periodic monitoring (North Carolina Wildlife Resources Commission 2005).

**Georgia**—Although Cross (1955) and Golley (1962) stated that the Allegheny woodrat could be found on the Lookout Plateau of northwestern Georgia, Hayes and Richmond (1993) and Ray (2000) classified specimens from this region as *N. f. haematoreia* without comment, and state agency publications do not appear to recognize *N. magister* as a member of the fauna of Georgia.

**Alabama**—Howell (1921) depicted the Allegheny woodrat’s range as that part of the state north of the Tennessee River, which would include the northernmost tier of counties. This distribution is consistent with trapping results by Zambarnardi
(1956). Although there appears to have been little if any population-level analysis on this species in Alabama, it has been given a Priority 2 status ("high" but not "highest" conservation concern) with a recommendation to survey bluff habitats to better determine its distribution and status (Alabama Department of Conservation and Natural Resources 2005).

Tennessee—Some range maps for the Allegheny woodrat show it spreads over most of the state of Tennessee (e.g., Hall 1981), but museum records indicate a more limited historical distribution in two roughly parallel north–south bands, corresponding to the elevated Cumberland Plateau in the east and the Highland Rim in the west. There is a dearth of field data to determine possible decline, but based on expert opinion by state mammalogists, Tennessee has designated the Allegheny woodrat a Tier 1 species for high-priority attention in its Wildlife Action Plan (Tennessee Wildlife Resources Agency 2005). A recent study found active woodrat populations at 11 of 15 reported or suspected sites in the Cumberland Plateau (Parker 2006). These will be useful monitoring sites for future analysis.

Kentucky—The range of the Allegheny woodrat in Kentucky was only poorly known by 1974, when Barbour and Davis (1974) showed it spottily distributed in 11 central and eastern counties. No statewide field surveys have been done since then, but a database of "all historical data" has been assembled for use by the Kentucky Department of Fish and Wildlife Resources. This database shows a much broader distribution—42 counties had records within the last 70 years, and four more had only historic records before 1930 (Thomas 2003). Woodrat distribution in Kentucky falls into two regions, the Cumberland Plateau in the east and a Highland Rim karst band west of the center of the state. Whether populations statewide have increased, decreased, or remained stable is not yet known. A five-year study in Mammoth Cave National Park showed no trend (Thomas 2003). Krupa et al. (2004) found active woodrat populations in Breathitt County but not in adjacent Knott County, despite similar habitat and old sign: They hypothesized either that the vacancies in Knott County might be a normal part of the dynamics of a metapopulation, or alternatively that a genuine extirpation had resulted from fragmented habitat. At this point there is no clear indication of decline, but Kentucky has designated the Allegheny woodrat as a priority species for some local monitoring in its Wildlife Conservation Strategy (Kentucky Department of Fish and Wildlife 2005).

Ohio—By 1930, woodrats had been collected in five counties in Ohio (Peneston et al. 1999). The Allegheny woodrat was on Ohio's original endangered species list created in 1974 (A. LeCount pers. comm.). A 1976 survey located active populations only in Adams County, along the Ohio River, but not in other historic sites (Peneston et al. 1999). Another statewide assessment of all historic sites in 1998 found only a remnant few of the Adams County sites active and concluded that the species had "declined dramatically since its presence was first documented in the 1920's" (Peneston et al. 1999). A more intense survey of Adams County showed little change in the number of sites between 1986 and 2004, but suggested a probable overall decrease in woodrat abundance (Mollohan and LeCount 2004). Analysis of raccoon scats collected from extirpated woodrat sites in Hocking and Fairfield
Counties showed 26% of samples infected with potentially lethal raccoon roundworm, whereas none from Adams County were infected (Mollohan and LeCount 2004).

**Indiana**—Indiana declared the Allegheny woodrat a threatened species as early as 1984 (Cudmore 1985), apparently not on the basis of a known decline but because available records showed a very limited distribution in the state. An extensive live-trapping study was then conducted to gain an accurate picture of the species’ distribution. Woodrats were found at 20 sites in three southern counties along the Ohio River, with old but recent sign at four more sites. From these findings, Cudmore (1985) estimated the statewide population as 781 and recommended that the woodrat be listed as endangered. Again, this recommendation was apparently based on the potential vulnerability of a species with restricted habitat and low total numbers, rather than on evidence of precipitous recent decline. Since 1990, however, intensive efforts in Indiana have documented a clear decline to critical population levels (Johnson 2002).

**Overall pattern**—In the late 1980s a coalition of biologists, concerned by indications of woodrat decline in the northeast, attempted to determine the status of the Allegheny woodrat. To supplement the scanty literature, they enlisted expert opinion in each state of the species’ range, and summarized the results in a petition to the U.S. Fish and Wildlife Service to list the Allegheny woodrat under the Endangered Species Act (A. Linzey pers. comm.). The petition was denied (A. Linzey pers. comm.) on the grounds that the populations of concern, from Connecticut to Maryland and Ohio, were not “isolated” from those farther south where no decline was claimed. Indeed, the decline of the Allegheny woodrat has frequently been characterized as proceeding from the northern and eastern range perimeters. However, this apparent pattern may be an artifact of higher vigilance in northern states, with less scrutiny farther south. It is becoming increasingly clear that population declines have occurred through central Pennsylvania, western Maryland, and parts of Virginia and West Virginia, so it appears that central areas are not invulnerable. Indeed, it is not at all certain that the Allegheny woodrat is secure in its southern range through North Carolina, Alabama, and Tennessee, as very little recent survey work has been done in those states.

**Conservation and Management of Declining Species**

Conservation biologists considering the Allegheny woodrat, like those concerned with the clouded leopard, have had to grapple simultaneously with two slippery questions. On the one hand, is the species declining, and how can we tell? And on the other, just what is a clouded leopard, or an Allegheny woodrat? The answer to the taxonomic question is crucial for interpreting the demographic one.

This review has been written as if the designation of the Allegheny woodrat as *N. magister*, and its distribution as mapped here, are the final word on this species, but this may not be the case. As genetic analyses become more refined, previously inclusive taxonomic entities are being divided into several species. Cryptic species of woodrats in western North America have recently been recognized this way.
(Edwards et al. 2001). If the Allegheny woodrat is really declining in some parts of its range yet secure in others, the difference in status may be due to varying severity of threats to this species, but there also may be genetic differences in resistance to those threats that could matter to conservation. Attention to the species’ genetic identity will also help in drawing appropriate stock for reintroductions. It will be important for managers to keep abreast of genetic studies and for researchers to help managers understand the implications of their findings.

The knotty taxonomic history of the Allegheny woodrat has hampered efforts to understand not only its conservation status but also its overall biology. Much of the secondary literature of the last decades has combined data for *N. magister* and *N. floridana*, which have very different habitat requirements and behavior, and likely have different demography and relationships with predators, parasites, diseases, and mast food supply. Understanding the Allegheny woodrat requires disentangling the information for this species and identifying the gaps in knowledge. Attempts to accomplish this are underway (Castleberry et al. 2006). To succeed, attention to geography and taxonomy will be crucial. As future studies are conducted, it will be important, for this and other species of concern, to specify clearly the geographic sites of field studies and monitoring efforts. GPS and GIS tools should be universally used to accomplish and communicate this information with precision. The simple shaded range maps of the past will not be adequate to define a species’ range if that range is patchy and subject to change.

The new technologies of genetics and digital mapping will be the essential tools. At the same time, we need to remember that our historic understanding of the taxonomic identity of most species is still based on studies of morphology, especially of museum specimens. Moreover, museum collections have been a unique resource for setting the baseline to detect Allegheny woodrat decline; for many other species, specimen-based records from the past are the only reliable geographic history that is available. Museum collections and their records are an irreplaceable resource that must be guarded for the future, and these data must be made more accessible.

As our understanding of population dynamics becomes more sophisticated, we need to define more carefully the criteria that we use to measure population changes. Spot checks of presence or absence will not be adequate. Where wildlife species contend with increasingly fragmented and disturbed habitat, we will need better definitions of “population” and “decline” to detect what is really taking place.

Finally, the disjointed state-by-state attention (or lack of it) that has been paid to the Allegheny woodrat is, unfortunately, not an isolated case. In preparing this review, I found repeatedly that experts in one state are often completely uninformed about what efforts or findings are taking place elsewhere. The federally mandated state Comprehensive Wildlife Conservation Strategy reports (also called Wildlife Action Plans), first produced in 2005, offer the first relatively standardized effort to communicate the status and projected future of wildlife in each state. These reports should be a first-stop for an overview of any species of concern throughout its range, and future versions of these reports should be written with better inter-state coordination of knowledge and resources in mind.
References


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