The Allegheny Woodrat

John D. Peles · Janet Wright
Editors

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Ecology, Conservation and Management of a Declining Species

Springer

Editors
John D. Peles
Biology Department
Pennsylvania State University-McKeesport
McKeesport, PA, USA
jdp12@psu.edu

Janet Wright
Biology Department
Dickinson College
Carlisle, PA, USA
wright@dicksinson.edu

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To Kim, Joshua, and Mikayla with love and thanks for your patience and support

JDP

To my many students who have trapped, tracked, analyzed, and admired the Allegheny woodrat

JW

In many places throughout these mountains great slides of broken boulders form bare patches on the slopes. Wherever these conditions are sufficiently extensive, one is likely to find signs of Neotoma.

It has strikingly large ears, bright and prominent eyes, and above all, conspicuous long whiskers, the seat of a highly developed tactile sense, which guides the animals in their quick and certain movements among the hazardous ledges and cliffs that they travel, often in total darkness. They are exceedingly agile while traveling over rocks. At Bake Oven Knob they habitually ascend and descend [a] crevice, leaping from one side to the other at top speed.

Passages to the nests are frequently barricaded with a miscellaneous assortment of sticks, stones, leaves, and other objects, doubtless designed to baffle the larger enemies. Frequently, at some distance from the nest, a heap of objects equally miscellaneous and of considerable bulk is stored. I believe that the more desirable storage food is kept in or near the nest, while the large heaps of refuse found at a distance from the nest may be reserve supplies of less desirable food material, or simply objects that have been carried there in fulfillment of the animal's evident desire to store objects in heaps.

E. L. Poole. 1940. A life history sketch of the Allegheny woodrat. Journal of Mammalogy 21:249–270.

Foreword

The Allegheny woodrat (*Neotoma magister*) once ranged from southern Connecticut westward to Indiana and southward to northern Alabama. Now extirpated or declining in over 35% of its range, the species appears to be relatively secure only in Kentucky and in parts of Virginia and West Virginia. Given that until relatively recently the Allegheny woodrat was considered to be a subspecies of the eastern woodrat (*N. floridana*), much of our general knowledge of woodrats in eastern North America is based on research conducted in localities now within the range of *N. floridana*. However, studies over the past 25 years have shown that the Allegheny woodrat differs from its close relative. For example, it is ecologically distinct, preferring caves and other habitats with substantial and structurally complex rock cover. Thus, a volume devoted to the Allegheny woodrat has been critically needed in order to assess our knowledge of this species and determine how this information can be used to develop appropriate strategies to ensure its survival.

Beginning in the 1980s, a group of volunteer mammalogists assisted the Pennsylvania Game Commission in monitoring Allegheny woodrat populations throughout the state. At my assigned site, Strangford Cave in Indiana County, I typically captured 4–6 animals. Yet, a former graduate student in my department, who had worked at Strangford in the 1970s, estimated a population size of 40–50. Unfortunately, the history of this single site has been repeated many times throughout much of the species' range. A decline in populations of *N. magister* was first noted in eastern Pennsylvania by John Hall in the 1980s. With Allegheny woodrats now having disappeared from eastern Pennsylvania and in active decline across the state, it is particularly appropriate that this volume was initiated by two Pennsylvania mammalogists.

The content of this book summarizes what is known about the ecology of the Allegheny woodrat, with an emphasis on reasons for its decline, as well as application of this information to its conservation and management. The initial two chapters provide a framework for the sections that follow. The first reviews information on history and current status throughout the range, while the second presents a synergistic model to explain the species' decline. The second section of the book includes a series of chapters on ecology of the Allegheny woodrat, from landscape and habitat-scale issues to life history characteristics at the local population level. In each case, whether it is population dynamics, microhabitat selection by foraging

woodrats, den selection, or dietary preferences, the authors speculate on how these ecological characteristics might interplay with disturbance to either limit or cause the decline of populations. The third section of the book deals with conservation and management issues, starting with descriptions of long-term monitoring programs in various states. Discussions of genetic diversity patterns and their relevance to management, tailoring of management strategies to biological and ecological characteristics, and review of information bearing on the potential for reintroductions are included here. Another chapter considers how information from *N. magister* can be applied to conservation of other woodrat species. The final section outlines future research needs, as well as summarizing how knowledge gathered during more than two decades of research on Allegheny woodrats can be used to help conserve this species. Although it is hoped that the information compiled in this volume will contribute to actions that will slow or halt the decline of the Allegheny woodrat, conservation biologists may also find this species to be of interest as a general model for analysis of the decline process. Because *N. magister* populations exhibit a continuum from extirpation to apparent health, comparative ecological information gathered on these various populations may help to develop generalizations that can be applied to other species in decline.

Our native small mammals are a beautiful and fascinating component of our terrestrial biodiversity. Unfortunately, rats and mice suffer from a public relations problem, perceived as lacking the charisma, and therefore lacking the enthusiasts associated with some other taxa. A group of Pennsylvania woodrat researchers once made a tongue-in-check proposal that the common name of the Allegheny woodrat should be changed to "long-tailed woods bunny." Fortunately, more and more people are accepting the notion that maintaining biodiversity is a "good thing," even if it is difficult to make a case for the critical importance of any single species.

In asking ourselves what would happen if a particular species disappeared, surely the answer is that "it depends." The loss of the American chestnut sent a shock wave of ecological adjustments through our eastern forests. In fact, it has been speculated that this event set the stage for the decline of *N. magister*. Certainly, small mammals such as the Allegheny woodrat are important contributors to the prey base for larger mammals and raptors. But perhaps, the only thing we can say with certainty is that the loss of any species leaves us poorer, whether it is the loss of the passenger pigeon that once darkened our skies or of the most secretive species that share our earth. The biologists who contributed to this volume have not only spent significant amounts of time conducting research on Allegheny woodrats, but also have contributed untold volunteer hours to help in ensuring their survival. Writing in *A Sand County Almanac*, a work that has inspired several generations of conservationists, Aldo Leopold asserted that "There are some who can live without wild things and some who cannot." This book is clearly the product of those who cannot.

Indiana, PA Alicia V. Linzey

Preface

In the early 1980s, the Pennsylvania Biological Survey—a research advisory body to the Pennsylvania Game Commission—recommended two priorities regarding the Allegheny woodrat (*Neotoma magister*): (1) surveys to determine the present distribution of the species; and (2) investigations to understand its ecological requirements. These recommendations reflected the magnitude of the task facing biologists in Pennsylvania and many other states at that time. The task was to document the extent and progress of the decline for a species about which little was known. Implied in the recommendations also was the need to understand the reasons for the decline of the Allegheny woodrat.

For nearly two decades, biologists employed by state agencies devoted many hours to documenting the extent of the Allegheny woodrat's distribution and monitoring the status of existing populations. These were pioneering studies, in that the status of nongame species was a relatively new focus for these agencies. While biologists from academic settings assisted with the monitoring process, most of their efforts were focused on understanding the systematics, ecology, and natural history of woodrats—the business of classical mammalogy. Although a great deal of potentially valuable information was gained from the efforts of both groups, much of it remained unpublished or available only through reports to state agencies. In some cases, this was due to time constraints faced by biologists within those agencies. In other cases, the lack of published information on *N. magister* reflected the difficulties in collecting statistically rigorous data in small populations that are subject to fluctuations in time and space. In fact, the first publications reporting empirical research on woodrats did not appear until very recently as researchers in West Virginia, where populations are relatively stable, began to take interest in this species.

In September 2005, a workshop on the Allegheny woodrat—organized by Jerry Hassinger—was held at Dickinson College to facilitate communication among researchers and field personnel about the status of our knowledge of this species. Such conferences are useful, but one of us (JP) came away with a conviction that there was a large, diffuse body of information that begged to be summarized in book form. From this idea developed our partnership to coedit the project. As mammalogists who have devoted a great deal of time and energy to the study of the Allegheny woodrat, initially our primary purpose was to synthesize current knowledge of the

species. Thus, this book answers questions such as: What is the current distribution and status of *N. magister*? What factors have contributed to its decline? What do we know about its ecology and genetics? What is the future of conservation and management for this species?

In this book, we use the term *decline* to refer to a long-term trend of decreasing abundance and distribution of a species within all or part of its historical range. As we considered the implications of this definition, we realized that this term likely applies to many species in North America and elsewhere. Thus, much of what we have learned from the study of the relatively obscure Allegheny woodrat has the potential to make a valuable contribution to the field of conservation biology. Consequently, the second purpose of this book is to highlight general principles that may be applied to the study of other declining species. In fact, we were encouraged by a reviewer of the original book prospectus to include a chapter on the status of other species of *Neotoma* based on the knowledge that several species or subspecies within this genus have experienced decline.

Most of the contributors to this book represent researchers currently involved in the study of the Allegheny woodrat. In some cases, authors who have previously published on a topic have integrated their own work with other published and unpublished data to provide a synthesis of our current knowledge on that topic. Other chapters represent the synthesis of data on a topic that has not previously appeared in the published literature. In fact, a particular goal was to use this book as an opportunity to present previously unpublished data that contribute to the synthesis of our current knowledge on the topic. All chapters were peer reviewed and underwent significant revision following the review and editorial processes. Our goal has been to bring together what has been a disparate, diffuse patchwork of information into a coherent, integrated picture. Our hope is to provide both good models and some caveats from hard lessons learned for those approaching these same questions for other species in decline.

We are grateful to Janet Slobodien and Ann Avouris at Springer for their support of this project and their assistance in the publication process. Several external reviewers of the prospectus for this book provided helpful suggestions. George Feldhamer, Mark Ford, Alicia Linzey, Kathleen LoGiudice, Carolyn Mahan, Joe Merritt, Gene Rhodes, Tim Smyser, and Petra Wood provided helpful comments on one or more chapters in the book. Most of all, we appreciate the spirit of the authors in their shared concern for the future of this unique animal.

Mckeesport, PA, USA — John D. Peles
Carlisle, PA, USA — Janet Wright

Contents

Contributors

Calvin M. Butchkoski
Pennyslvania Game Commission, Harrisburg, PA 17110

Nikole L. Castleberry
Georgia Department of Natural Resources, Nongame Conservation Section, Social Circle, GA 30025

Steven B. Castleberry
Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA 30602

Duane R. Diefenbach
U.S. Geological Survey, Pennsylvania Cooperative Fish and Wildlife Research Unit, Pennsylvania State University, University Park, PA 16802

George A. Feldhamer
Department of Zoology, Southern Illinois University, Carbondale, IL 62901

Daniel J. Feller
DNR-WHS Natural Heritage Program, Appalachian Laboratory, University of Maryland, 301 Braddock Road, Frostburg, MD 21532

Jerry D. Hassinger
Pennsylvania Biological Survey, 105 Adams Lane, Millersburg, PA 17061

Scott A. Johnson
Indiana Department of Natural Resources, 553 East Miller Drive, Bloomington, IN 47401

Alicia V. Linzey
Department of Biology, Indiana University of Pennsylvania, Indiana, PA 15705

Kathleen LoGiudice
Department of Biological Sciences, Union College, Schenectady, NY 12308

Michael T. Mengak
Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA 30602

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

Aaron K. Poole
Department of Zoology, Southern Illinois University, Carbondale, IL 62901

Olin E. Rhodes, Jr.
Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN 47906

Thomas L. Serfass
Department of Biology, Frostburg State University, Frostburg, MD 21532

Timothy J. Smyser
Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN 47906

Petra Bohall Wood
U.S. Geological Survey, West Virginia Cooperative Fish and Wildlife Research Unit, Division of Forestry and Natural Resources, West Virginia University, P.O. Box 6125, Morgantown, WV 26506

Janet Wright
Department of Biology, Dickinson College, Carlisle, PA 17013

Section I
History and Current Status

The decline of few species has been as mysterious as that of the Allegheny woodrat (*Neotoma magister*). The chapters in this section show why understanding the disappearance of this species has been such a knotty problem. Reference to a species as "declining" implies documentation of a decrease in abundance and distribution within at least some part of the species' range. In the case of the Allegheny woodrat, this seemingly simple task was confounded by its uncertain taxonomic status. In Chapter 1, Janet Wright reviews the complicated taxonomic history of *N. magister* and discusses how this and other factors contributed to the delay in recognizing the decline of this species. She then provides a review of the current distribution of this species and its conservation status as designated in the states of its range.

Once the decline of a species is recognized, the next step is to understand the underlying causes. For many years, biologists used a single-factor approach to explain the decline of the Allegheny woodrat. Kathleen LoGiudice (Chapter 2) provides a review of the main hypotheses to explain the decline, and reviews the shortcomings of each of these single-factor hypotheses. She presents a convincing case for considering interactions among multiple factors within a historical framework to explain the woodrat's decline. A careful examination of our attempts to understand the reasons for the disappearance of the Allegheny woodrat should provide a lesson to conservation biologists that context, including taxonomy and history, must be a part of the analysis of any species in decline.

John D. Peles
Janet Wright

Chapter 1
History and Current Status of the Allegheny Woodrat

Janet Wright

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

J. Wright
Department of Biology, Dickinson College, Carlisle, PA 17013

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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 Witmer 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 "austroriparian 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

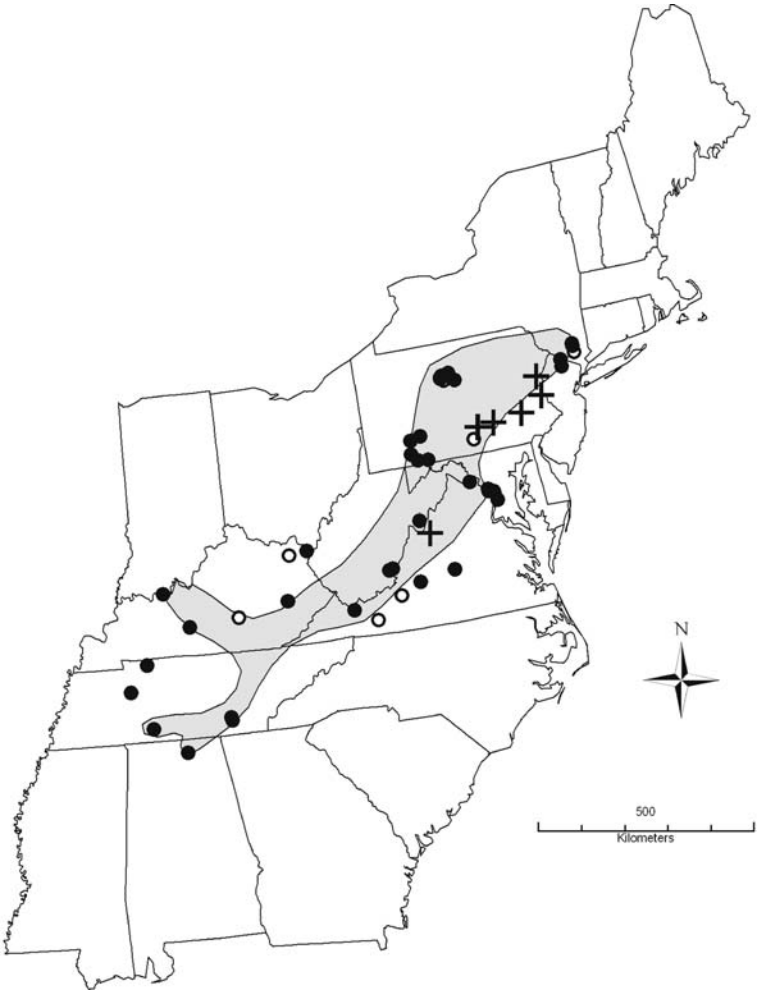

Fig. 1.1 Early collecting localities for museum specimens of *Neotoma magister*, with range of the species (shaded) as depicted by Goldman (1910). Open circles represent specimens collected by the time of Merriam's (1894) taxonomic revision. Closed circles represent additional specimens collected by the time of Goldman's (1910) revision. Crosses represent fossil specimens collected before 1910

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 reexamined 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-1900 s: 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

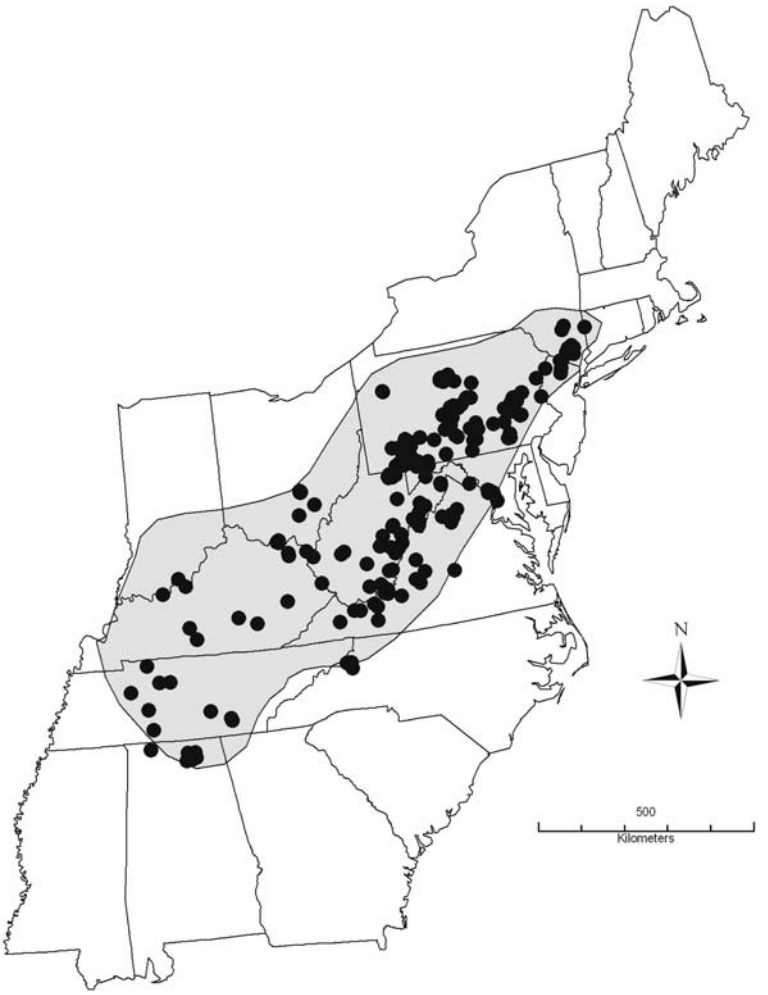

Fig. 1.2 Collecting localities for museum specimens of *Neotoma magister* by the time of Schwartz and Odum's (1957) revision (*closed symbols*), and complete range (*shaded*) as depicted in Hall (1981)

were collected in intermediate localities. By the mid-1950 s, 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 1960 s–1980 s, 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 1990 s 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