Virginia’s Land Mammals: Past and Present, with Some Thoughts About Their Possible Future

John F. Pagels¹² and Nancy D. Moncrief*²

¹Department of Biology, Virginia Commonwealth University, Richmond, Virginia 23284,  
²Virginia Museum of Natural History, Martinsville, VA 24112

ABSTRACT
Mammals encountered today in Virginia’s forests and fields include native and nonnative species, feral populations, and free-ranging pets. We examine factors that have influenced Virginia’s terrestrial mammal fauna since the arrival of European colonists in the 1600s and some of the factors that are shaping the fauna today. We look in depth at changes since Handley and Patton’s (1947) first complete monograph on Virginia mammals and augment Linzey’s (1998) book, The Mammals of Virginia. We include current nomenclature, baseline information, and references to comprehensive literature. We discuss some of the current and developing anthropogenic factors that have impacted, or that likely will impact, our native land mammals as well as factors that bode well for many species, especially in areas of conservation of habitat.

BACKGROUND
Approximately 115 species of mammals live in or frequent Virginia; of these, about 28 are marine mammals (e.g., porpoises, whales, seals, and manatees) that are known from its shores, bays, and tidal rivers (Handley and Patton 1947; Linzey 1998). Including extirpated species, 77 species of native land mammals (those species that occurred here or reached here without purposeful or accidental introduction by humans) have been recorded since Europeans arrived in Virginia (Table 1). The diversity of Virginia’s land mammals reflects a complex history of evolution, adaptation, and migration that has occurred over millions of years on a varied land surface and under changing climatic conditions (Woodward and Hoffman 1991). With elevations ranging from sea level to more than 1,500 m, the east-west orientation of the long axis of the state intersects five physiographic regions (Fig. 1), which results in a wide variety of habitats. As detailed by Handley (1992), most (42 of 74 extant species) Virginia land mammals have boreal (northern) affinities and the rest have austral (southern) affinities (Table 1). As a general rule, boreal species either occur statewide or in the west. By contrast, austral species tend to occur only in the east or south if their distributions are not statewide. As a result of its latitudinal position, Virginia is near the northern edge of the distributions of about a dozen austral species and the southern edge of

* - Corresponding author -- nancy.moncrief@vmnh.virginia.gov
TABLE 1. Land mammals native to Virginia, including species present at the time of European contact and those that have naturally colonized Virginia since that time. Common or vernacular name (as suggested by Wilson and Reeder 2005) is indicated for each species, along with current classification, current distribution, distributional affinity (distrib. affinity, after Handley 1992), habitat in Virginia, and the citation for a comprehensive monograph or review of the biology of that species. Virginia’s Eastern Shore is comprised of Accomack and Northampton counties, at the southern end of the Delmarva Peninsula. For bats (Chiroptera), habitat describes roost sites, which may change seasonally. The following denote special circumstances that are detailed in text: E= extirpated; ER= extirpated (or nearly so), restoration attempted; EE = extirpated (or nearly so), range expansion from nearby states; A = augmented to increase populations and/or restore regionally.

<table>
<thead>
<tr>
<th>Scientific name</th>
<th>Common name</th>
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<th>Distrib. affinity</th>
<th>Habitat</th>
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<td>Willner et al. 1980</td>
</tr>
<tr>
<td>Synaptomys cooperi</td>
<td>southern bog lemming</td>
<td>Cricetida</td>
<td>Rodentia</td>
<td>mountains and southeast except Eastern Shore</td>
<td>boreal</td>
<td>bogs, wet meadows</td>
<td>Linzey 1983</td>
</tr>
<tr>
<td>Scientific name</td>
<td>Common name</td>
<td>Family</td>
<td>Order</td>
<td>Distribution</td>
<td>Distrib. affinity</td>
<td>Habitat</td>
<td>Citation</td>
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<tr>
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<tr>
<td>Zapus hudsonius</td>
<td>meadow jumping mouse</td>
<td>Dipodidae</td>
<td>Rodentia</td>
<td>statewide</td>
<td>boreal</td>
<td>oldfield</td>
<td>Whitaker 1972</td>
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<td>Napaeozapus insignis</td>
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<td>Dipodidae</td>
<td>Rodentia</td>
<td>mountains</td>
<td>boreal</td>
<td>forest</td>
<td>Whitaker and Wrigley 1972</td>
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<td>North American porcupine</td>
<td>Erethizontidae</td>
<td>Rodentia</td>
<td>mountains</td>
<td>boreal</td>
<td>generalist</td>
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<td>Canis latrans</td>
<td>coyote</td>
<td>Canidae</td>
<td>Carnivora</td>
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<td>boreal</td>
<td>generalist</td>
<td>Bekoff 1977</td>
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<tr>
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<td>Canidae</td>
<td>Carnivora</td>
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<td>boreal</td>
<td>not present</td>
<td>Mech 1974</td>
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<td>Vulpes vulpes</td>
<td>red fox</td>
<td>Canidae</td>
<td>Carnivora</td>
<td>statewide</td>
<td>boreal</td>
<td>oldfield, open woodlands</td>
<td>Larivière and Pasitschniak-Arts 1996</td>
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<td>gray fox</td>
<td>Canidae</td>
<td>Carnivora</td>
<td>statewide</td>
<td>austral</td>
<td>forest, brushy woodlands</td>
<td>Fritzell and Haroldson 1982</td>
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<td>Ursus americanus</td>
<td>American black bear</td>
<td>Ursidae</td>
<td>Carnivora</td>
<td>statewide except Eastern Shore</td>
<td>boreal</td>
<td>forests primarily</td>
<td>Larivière 2001</td>
</tr>
<tr>
<td>Scientific name</td>
<td>Common name</td>
<td>Family</td>
<td>Order</td>
<td>Distribution</td>
<td>Distrib. affinity</td>
<td>Habitat</td>
<td>Citation</td>
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<td>raccoon</td>
<td>Procyonidae</td>
<td>Carnivora</td>
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<td>austral</td>
<td>generalist</td>
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<td>Mustelidae</td>
<td>Carnivora</td>
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<td>boreal</td>
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<td>Powell 1981</td>
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<td>Mustela frenata</td>
<td>long-tailed weasel</td>
<td>Mustelidae</td>
<td>Carnivora</td>
<td>statewide</td>
<td>austral</td>
<td>generalist</td>
<td>Sheffield and Thomas 1997</td>
</tr>
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<td>least weasel</td>
<td>Mustelidae</td>
<td>Carnivora</td>
<td>statewide except Eastern Shore</td>
<td>boreal</td>
<td>generalist</td>
<td>Sheffield and King 1994</td>
</tr>
<tr>
<td>Neovison vison</td>
<td>American mink</td>
<td>Mustelidae</td>
<td>Carnivora</td>
<td>statewide</td>
<td>boreal</td>
<td>near water</td>
<td>Larivière 1999</td>
</tr>
<tr>
<td>Lontra canadensis A</td>
<td>North American river otter</td>
<td>Mustelidae</td>
<td>Carnivora</td>
<td>statewide</td>
<td>boreal</td>
<td>near water</td>
<td>Larivière and Walton 1998</td>
</tr>
<tr>
<td>Spilogale putorius</td>
<td>eastern spotted skunk</td>
<td>Mephitidae</td>
<td>Carnivora</td>
<td>west</td>
<td>austral</td>
<td>forest</td>
<td>Kinlaw 1995</td>
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<tr>
<td>Mephitis mephitis</td>
<td>striped skunk</td>
<td>Mephitidae</td>
<td>Carnivora</td>
<td>statewide</td>
<td>boreal</td>
<td>generalist</td>
<td>Wade-Smith and Verts 1982</td>
</tr>
<tr>
<td>Scientific name</td>
<td>Common name</td>
<td>Family</td>
<td>Order</td>
<td>Distribution</td>
<td>Distrib. affinity</td>
<td>Habitat</td>
<td>Citation</td>
</tr>
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</tr>
<tr>
<td>Lynx rufus</td>
<td>bobcat</td>
<td>Felida</td>
<td>Carnivora</td>
<td>statewide</td>
<td>boreal</td>
<td>generalist, much cover</td>
<td>Larivière and Walton 1997</td>
</tr>
<tr>
<td>Puma concolor</td>
<td>cougar</td>
<td>Felida</td>
<td>Carnivora</td>
<td>not present</td>
<td>boreal</td>
<td>not present</td>
<td>Currier 1983</td>
</tr>
<tr>
<td>Odocoileus virginianus</td>
<td>white-tailed deer</td>
<td>Cervidae</td>
<td>Artiodactyla</td>
<td>statewide</td>
<td>austral</td>
<td>generalist</td>
<td>Smith 1991</td>
</tr>
<tr>
<td>Cervus canadensis</td>
<td>wapiti</td>
<td>Cervidae</td>
<td>Artiodactyla</td>
<td>extreme southwest</td>
<td>boreal</td>
<td>clearings in high-elevation forests</td>
<td>Maehr et al. 2007</td>
</tr>
<tr>
<td>Bison bison</td>
<td>American bison</td>
<td>Bovidae</td>
<td>Artiodactyla</td>
<td>not present</td>
<td>boreal</td>
<td>not present</td>
<td>Meagher 1986</td>
</tr>
</tbody>
</table>
distribution for about as many boreal species (Hall 1981). Ranges and statuses of
several boreal species were the subject of a recent study by Campbell et al. (2010),
motivated in part by Dobson et al.’s (1997) identification of the central and southern
Appalachian mountains as a “hot spot of threatened biodiversity.” The central and
southern Appalachians have many specialized habitats, including caves, cliffs, talus,
bogs, and boreomontane forests, that support populations of 7 of the 11 extant species
listed in Virginia as threatened or endangered (Tables 1 and 2).

In this review, we summarize current information about the distribution and species
composition of Virginia’s native land mammals, with emphasis on studies that
documented changes in the land mammal fauna since Handley and Patton’s 1947
monograph. We also discuss long-term and ongoing threats to native species in the
state. In doing so, we cite key literature that directs present and future students of
Virginia mammals to pertinent resources.

HISTORICAL OVERVIEW

The history of the study of land mammals in Virginia was summarized recently by
Linzey (1998) and Rose (2013). Although many mammals, especially game species,
were documented and described by the earliest European explorers, and later by
colonists, in the late 1500s and early 1600s, Rose (2013) credits C. H. Merriam with
conducting the first systematic studies of Virginia’s mammals in the late 1800s. Both
Mammals of Virginia* as being the seminal work for chronicling the mammal fauna of
the state. Therefore, we use that book as a basis for comparison throughout this review.

Rose (2013) acknowledged contributions in recent decades by a number of
researchers that increased our understanding of mammals in particular regions of
Virginia. To Rose’s (2013) list we add W. M. Ford and J. L. Orrock, especially for their work in western Virginia, R. E. Eckerlin for work on mammals and their parasites, and J. C. Mitchell for his collaborative studies.

Handley and Patton (1947) described mammals known to occur in the state, those that were already extirpated by the early 1900s, and species from nearby states not yet recorded in Virginia. Subsequent publications of Handley (1979a, 1991) summarized information about Virginia’s threatened and endangered mammal species. In addition to detailing changes in species composition since the Pleistocene, Handley (1992) commented on destruction of habitat, climate change, and other ongoing threats to mammals. Linzey’s (1998) book, which included a comprehensive bibliography, summarized information for all mammals in Virginia.

NATIVE TAXA OVER TIME

Taxonomic changes since 1947 – In the nearly 70 years since Handley and Patton (1947), revisions in systematics and taxonomy reflect changes in our understanding of the evolutionary relationships of many mammals that inhabit Virginia (Table 3). We use the nomenclature for scientific names and vernacular, or common, names recognized by authors of taxonomic accounts in Wilson and Reeder (2005), with a few

<table>
<thead>
<tr>
<th>Scientific name</th>
<th>Common name</th>
<th>State legal status</th>
<th>Federal legal status</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Sorex palustris</em></td>
<td>American water shrew</td>
<td>endangered</td>
<td></td>
</tr>
<tr>
<td><em>Myotis grisescens</em></td>
<td>gray bat</td>
<td>endangered</td>
<td>endangered</td>
</tr>
<tr>
<td><em>Myotis lucifugus</em></td>
<td>little brown bat</td>
<td>endangered</td>
<td></td>
</tr>
<tr>
<td><em>Myotis septentrionalis</em></td>
<td>northern long-eared bat</td>
<td>threatened</td>
<td>threatened</td>
</tr>
<tr>
<td><em>Myotis sodalis</em></td>
<td>Indiana bat</td>
<td>endangered</td>
<td>endangered</td>
</tr>
<tr>
<td><em>Perimyotis subflavus</em></td>
<td>tri-colored bat</td>
<td>endangered</td>
<td></td>
</tr>
<tr>
<td><em>Corynorhinus rafinesquii</em></td>
<td>Rafinesque's eastern big-eared bat</td>
<td>endangered</td>
<td></td>
</tr>
<tr>
<td><em>Corynorhinus townsendii</em></td>
<td>Virginia big-eared bat</td>
<td>endangered</td>
<td>endangered</td>
</tr>
<tr>
<td><em>Lepus americanus</em></td>
<td>snowshoe hare</td>
<td>endangered</td>
<td></td>
</tr>
<tr>
<td><em>Glaucomys sabrinus</em></td>
<td>Carolina northern flying squirrel</td>
<td>endangered</td>
<td>endangered</td>
</tr>
<tr>
<td><em>Microtus chrotorrhinus</em></td>
<td>rock vole</td>
<td>endangered</td>
<td></td>
</tr>
</tbody>
</table>

TABLE 3. Current scientific name, scientific name (synonym) for the same taxon used by Handley and Patton (1947), if the names differ between publications, and citation(s) that documents our reason(s) for using a different name.

<table>
<thead>
<tr>
<th>Current scientific name</th>
<th>Scientific name in Handley and Patton (1947)</th>
<th>Citation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sorex hoyi</td>
<td>Microsorex hoyi</td>
<td>George 1988</td>
</tr>
<tr>
<td>Blarina brevicauda</td>
<td>Blarina telmallestes</td>
<td>George et al. 1986</td>
</tr>
<tr>
<td>Blarina carolinensis</td>
<td>Blarina brevicauda carolinensis</td>
<td>Genoways and Choate 1972; Tate et al. 1980</td>
</tr>
<tr>
<td>Myotis leibii</td>
<td>Myotis subulatus leibii</td>
<td>Glass and Baker 1968; Herd 1987</td>
</tr>
<tr>
<td>Myotis septentrionalis</td>
<td>Myotis keenii septentrionalis</td>
<td>van Zyll de Jong 1979</td>
</tr>
<tr>
<td>Perimyotis subflavus</td>
<td>Pipistrellus subflavus</td>
<td>Menu 1984; Hoofer and Van Den Bussche 2003; Hoofer et al. 2006</td>
</tr>
<tr>
<td>Sylvilagus obscurus</td>
<td>Sylvilagus transitionalis</td>
<td>Chapman et al. 1992</td>
</tr>
<tr>
<td>Ochrotomys nuttalli</td>
<td>Peromyscus nuttalli</td>
<td>Blair 1942; Carleton 1980</td>
</tr>
<tr>
<td>Myodes gapperi</td>
<td>Clethrionomys gapperi</td>
<td>Kretzoi 1964; Carleton et al. 2014</td>
</tr>
<tr>
<td>Microtus pinetorum</td>
<td>Pitymys pinetorum</td>
<td>Conroy and Cook 2000; Conroy et al. 2001</td>
</tr>
<tr>
<td>Ondatra zibethicus</td>
<td>Ondatra zibethica</td>
<td>misspelling/gender issue</td>
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<tr>
<td>Vulpes vulpes</td>
<td>Vulpes fulva</td>
<td>Lariviére and Pasitschniak-Arts 1996</td>
</tr>
<tr>
<td>Pekania pennanti</td>
<td>Martes pennanti</td>
<td>Li et al. 2014; Samuels and Cavin 2013; Koepfli et al. 2008</td>
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<tr>
<td>Mustela nivalis</td>
<td>Mustela rixosa</td>
<td>Sheffield and King 1994; Abramov and Baryshnikov 1999</td>
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<td>Neovison vison</td>
<td>Mustela vison</td>
<td>Abramov 1999; Kurose et al. 2000</td>
</tr>
<tr>
<td>Lontra canadensis</td>
<td>Lutra canadensis</td>
<td>van Zyll de Jong 1972; Bininda-Edmonds et al. 1999</td>
</tr>
<tr>
<td>Puma concolor</td>
<td>Felis concolor</td>
<td>Pocock 1917; Kratochvil 1982</td>
</tr>
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</table>
exceptions. We follow the recommendations of Hoofer and Van Den Bussche (2003) and Hoofer et al. (2006) for the tri-colored bat (Perimyotis subflavus), and those of Koepfl et al. (2008), Samuels and Cavin (2013), and Li et al. (2014) for the fisher (Pekania pennanti). For the wapiti (Cervus canadensis), we have followed the recommendations of Ludt et al. (2004), Pitra et al. (2004), and Skog et al. (2009) in recognizing it as a species that is distinct from the elk (Cervus elaphus). Handle and Patton (1947) also used the name Cervus canadensis for the wapiti, although Cervus elaphus was the name applied to this taxon by many subsequent workers (e.g., Hall 1981, Maehr et al. 2007).

Changes in the number of taxa documented since 1947 – The documentation of native taxa of land mammals in Virginia has changed since 1947 due to the collection of specimens and to changes in mammalian systematics (Table 4). One species, the Dismal Swamp short-tailed shrew (Blarina telmalestes), was judged to be conspecific with the northern short-tailed shrew (Blarina brevicauda), and we have removed it from the list. We have added the southern short-tailed shrew (Blarina carolinensis), which was formerly named Blarina brevicauda carolinensis (Tables 3 and 4), also because of systematic and taxonomic revisions.

Another taxon, the Maryland shrew (Sorex cinereus fontinalis), has been collected in Virginia (Moncrief and Dueser 1998). The systematic status of this shrew is in need of study. Based on morphology, Kirkland (1977) and others (e.g., Van Zyll de Jong 1991) assigned specimens they examined to Sorex fontinalis. On the basis of allozymic evidence, George (1988) recognized Sorex fontinalis as a distinct species. A subsequent study that examined mitochondrial DNA (mtDNA) diversification within the Sorex cinereus group (Demboski and Cook 2003) seemed to support George’s (1988) findings, and another study of relationships within the genus Sorex (Hope et al. 2012) reported high mtDNA divergence of eastern populations of Sorex cinereus that is also consistent with George’s (1988) conclusion. However, Hope et al. (2012) also reported variation at nuclear loci that places all specimens they examined from eastern localities within Sorex cinereus (sensu stricto). Neither Demboski and Cook (2003) nor Hope et al. (2012) examined specimens from Pennsylvania, Maryland, Delaware, or Virginia, where Sorex cinereus fontinalis has been documented. Additionally, as noted by Stewart et al. (1993), George’s (1988) analysis included only a few specimens (n = 7) of Sorex cinereus fontinalis and may have been subject to sampling error. In the absence of additional, convincing evidence to the contrary, we take a conservative approach and treat this taxon as a subspecies of the cinereus shrew (Sorex cinereus). Further, we suggest that additional collections and analyses of specimens of Sorex from northern Virginia may reveal the Maryland shrew to have a broader distribution than is now considered to be the case.

Another taxon that requires additional study in Virginia is the wolf (or gray wolf, Canis lupus). We note that Linzey (1998) included 2 species of wolves, Canis lupus and Canis rufus (the red wolf), in his accounts of Virginia mammals. Since the publication of Linzey’s book in 1998, numerous morphologic and genetic studies (reviewed by Chambers et al. 2012) have been conducted on Canis in North America in order to determine how many different species should be recognized in this genus and to determine the historic distributions of species of Canis on this continent. All studies of taxa in eastern North America have been hampered by a scarcity of museum
specimens, which has resulted in substantial chronological and geographic gaps in the data. None of these studies, including Nowak’s (2002) widely cited work on the historical distribution of the red wolf, examined material from Virginia. Nevertheless, Nowak (2002) and Chambers et al. (2012) included the entire state of Virginia in the historical distribution of the red wolf and considered it to have been the only species present in Virginia at the time of European contact.

Wolves were extirpated from Virginia and most of North America east of the Mississippi River by the early 1900s (Handley and Patton 1947, Linzey 1998, Nowak 2002). Linzey (1998) reported that no wolf specimens from Virginia (of either *Canis lupus* or *Canis rufus*) are known to exist in collections. Our searches of collections records and our literature review for this project revealed specimens identified as *Canis*
sp. in prehistoric deposits from Virginia (Eshelman and Grady 1986, FAUNMAP Working Group 1994). Until this material, or other evidence from Virginia, can be analyzed, we take a conservative approach and recognize a single species, *Canis lupus*, which, as defined by Wilson and Reeder (2005), includes specimens referable to *rufus*.

Species known to occur in nearby states in 1947 – Thirteen taxa have been recorded as new to Virginia since 1947 (Table 4), although many of them were known from adjacent states, and Handley and Patton (1947) speculated that seven of these species did, in fact, occur here. For example, the eastern small-footed myotis (*Myotis leibii*) and the gray myotis (*Myotis grisescens*) were known from West Virginia and Tennessee, respectively, in 1947, and Handley and Patton (1947) encouraged work to document these species in Virginia.

In several cases, the first individuals collected in Virginia were only captured by intensive survey efforts and/or by using methods that were not common in the past. Snap traps, live traps, and mist nets are often used for mammal studies. However, such trapping can be labor- and time-intensive, may not be legally permitted, or may be ineffective for detection of some species. Pitfall traps have been especially useful in studies of shrews (Handley and Kalko 1993, Padgett and Rose 1994), including the American water shrew (*Sorex palustris*; Pagels and Tate 1976, Pagels 1987). Also, largely with the use of pitfall traps, Rose (2006) found that a thought-to-be-extinct subspecies of the southern bog lemming (*Synaptomys cooperi*) was widespread in southeastern Virginia. Nest boxes attached to trees are often the most effective method for capturing arboreal squirrels (Pagels et al. 1990). Technological advances have revolutionized our ability to detect and identify species of mammals. For example, polymerase-chain-reaction analysis of DNA may only require the “capture” of hairs (Moncrief et al. 2008) or scat (Bozarth et al. 2011) to document the presence of a species. Remotely triggered digital game cameras, such as those used in the observations of the fisher and porcupine (*Erethizon dorsatum*), as discussed below, are often now used in surveys in combination with other trap types (i.e., Chupp et al. 2013). Such cameras can document species that would go undetected using traditional traps and permit broadscale survey efforts that would otherwise be cost-prohibitive (Erb et al. 2012). Similarly, increasingly sophisticated ultrasonic detectors are now used for bat surveys (Britzke et al. 2011).

Among the 13 new taxa collected since 1947 (Table 4) are the American water shrew, northern flying squirrel (*Glaucomys sabrinus*), and rock vole (*Microtus chrotorrhinus*). These species are largely confined to high elevation sites (i.e., mountain-top “islands” or nearly so) in the western part of the state (Table 1), and all are considered boreal Ice Age relicts (Handley 1992). Habitat specialization, limited geographical distributions, and apparent small population sizes of these species in Virginia reflect characteristics of threatened and endangered species (Yu and Dobson 2000).

The American water shrew lives in high-elevation moist, cool, largely undisturbed shaded habitats, which have likely prevailed throughout historic time (Pagels et al. 1991). Known from five sites in Bath and Highland counties along nearly pristine headwater streams (Pagels and Tate 1976, Pagels et al. 1998), the American water shrew is endangered in Virginia (Table 2).

The Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*), known only from Highland County, was recently delisted from federal endangered status (USFWS
VIRGINIA’S LAND MAMMALS

2008, 2013b), and it was subsequently removed from the state endangered species list (B. Gwynn, pers. comm.). We disagree with the DGIF’s actions to delist this taxon in Virginia. The Virginia northern flying squirrel occurs at only a few sites in Highland County, and its habitat (high elevation northern hardwood and northern conifer) is very rare in Virginia, as detailed below. For these reasons, we contend that this taxon is in danger of extirpation in Virginia, and therefore, warrants protection under the Virginia Endangered Species Act. A second subspecies, the Carolina northern flying squirrel (Glaucomys sabrinus coloratus) is federal and state endangered (Table 2). Populations of the northern flying squirrel in southwestern Virginia (Grayson and Smyth counties) are considered intergrades of the Virginia and Carolina forms (Fies and Pagels 1991, Sparks 2005) and are listed as federal endangered. According to Payne et al. (1989), habitat of the northern flying squirrel in the southern Appalachians is high elevation, mesic forest characterized by northern hardwood and northern conifer species [i.e., red spruce (Picea rubens) or Fraser fir (Abies fraseri)]. These forests in Virginia are now largely restricted to Whitetop and Mount Rogers in Grayson and Smyth counties, and to a few sites in Highland County (Pagels et al. 1990, Reynolds et al. 1999). Recent studies by Ford and collaborators provide habitat models and new information on the Virginia (Menzel et al. 2006, Ford et al. 2010) and Carolina northern flying squirrels (Ford et al. 2015), respectively. They found that except for increasingly higher elevations to the south (i.e., southwest Virginia and North Carolina), habitat of the northern flying squirrel in the mid- to southern Appalachians is high elevation, cool, moist forest characterized by montane conifers [such as red spruce, Fraser fir, or eastern hemlock (Tsuga canadensis)], and a northern hardwoods component [such as yellow birch (Betula alleghaniensis), sugar maple (Acer saccharum) and black cherry (Prunus serotina)]. Desirable areas for the northern flying squirrel have few, if any, hard-mast-producing trees, such as American beech (Fagus grandifolia) or oak species (Quercus spp.), which are more favorable habitat components for southern flying squirrels (Glaucomys volans).

The rock vole is known from sites in Highland and Bath counties (Pagels 1990, Orrock et al. 1999) in mixed mesophytic habitats characterized by yellow birch, with abundant large, often moss-covered rocks (Orrock and Pagels 2003). Rock voles were also captured among rocks along a roadway in Highland County where the rocks appeared to have been placed for road stabilization (W. Bulmer, R. Eckerlin, and A. Gardner, pers. comm.). That site also had abundant yellow birch. Mixed mesophytic forests (Orrock et al. 2000, McShea et al. 2003), or montane mesic forests in general (Ford et al. 2006b), are important to many small mammals, and localized areas of moss-covered rocks and associated microhabitat in these forests seem to be critical to the rock vole in Virginia. One of us (JFP) and collaborators conducted surveys for the rock vole and the American water shrew in the late 1980s and 1990s at many sites in what appeared to be prime habitat in southwestern Virginia, notably the Whitetop, Mount Rogers and Clinch Mountain areas. Despite these surveys, neither the rock vole nor American water shrew has been found there to date, indicative of their localized distribution.

The long-tailed shrew (Sorex dispar), first reported from the Mountain Lake area of Giles County (Handley 1956, Holloway 1957), was later found in several other counties in western Virginia (Pagels 1987). Often associated with talus or boulder
areas, the long-tailed shrew has a more continuous distribution than the American water shrew, northern flying squirrel, and rock vole (Table 1).

Handley and Patton (1947) stated that neither the coyote (Canis latrans) nor the red fox (Vulpes vulpes) occurred in Virginia in pre-colonial days, although Rose (1986) later reported red fox from Woodland Period archeological sites, which dated to approximately 2,000 years before European settlement. Both of these species now occur statewide (Linzey 1998). These species characteristically inhabit open woods, grasslands, and overgrown fields. However, coyotes often occupy a broader array of habitats (including inner cities; Gehrt et al. 2009) than do red foxes.

There has been debate over the source of eastern populations of both of these species. For many years, it was believed that red foxes in the eastern United States were of European origin, introduced to the American colonies for sport hunting (Churcher 1959, Linzey 1998, Kamler and Ballard 2002). Kasprowicz et al. (2016) recently presented genetic findings that European red foxes were, in fact, introduced to the mid-Atlantic region of North America. However, Kasprowicz et al. (2016) and Statham et al. (2012) also presented genetic evidence that red foxes were indigenous to the eastern United States at the time of European contact. As we noted above, red foxes were present at Woodland Period archeological sites in Virginia (Rose 1986).

Frey (2013) suggested that early naturalists in eastern North America probably believed red foxes were exotic because the colonists observed rapid range expansions and increases in abundance of this species in areas of the Southeast where, because of lack of suitable habitat, the red fox had been uncommon at the time of European settlement. Frey (2013) also provided historical information on population fluctuations of the red fox and the gray fox (Urocyon cinereoargenteus). Colonial-era clearing for agriculture and extensive deforestation increased abundance of red fox prey (e.g., rabbits and voles), whereas subsequent reforestation in some areas favored the gray fox, a woodland species, and its prey (e.g., insects, birds, and small mammals). The red fox possibly also benefitted from mesopredator release after wolves were reduced in numbers, and then extirpated in the Southeast (Frey 2013). However, the absence of wolves also likely played a role in the coyote’s eastward range expansion. Red fox populations in the eastern United States may be suppressed again, but this time by coyotes (Frey 2013; Newsome and Ripple 2015).

Handley and Patton (1947) noted that coyotes had been collected in several western counties. They went on to comment that they “hesitate to recognize [the coyote] as an authentic Virginia species because many coyote pups are brought by tourists from the west and are released or escape when they reach maturity” (Handley and Patton 1947, page 140). Linzey (1998) reported a 1965 record of the coyote from Rockingham County, a record unknown at the time of the first symposium on Virginia’s Rare and Endangered Species (Linzey 1979), when the coyote was said to be on the verge of entering Virginia (Pagels 1979). Mastro (2011) reported that prior to 1983, only eight coyotes had been recorded from Virginia. Mastro’s (2011) review of literature on coyotes includes a time-line of range expansion into the mid-Atlantic states, observations on life history and ecology, and information about hybridization with other canids. Bozarth et al. (2011) provided mtDNA evidence that coyotes expanded their range into Virginia from northern and southern fronts, and they and Mastro (2011) observed that the mid-Atlantic states are the terminus of coyote range expansion in the continental US. Translocation by humans cannot be ruled out for spotty coyote
introductions (Hill et al. 1987, Linzey 1998); however, like others, we suggest habitat alteration and the extirpation of wolves were dominant factors in the colonization of Virginia by coyotes. We consider the coyote to be part of Virginia’s native fauna and its presence in the state to be the result of natural range expansion. The coyote is an opportunistic feeder and known to predate white-tailed deer (Odocoileus virginianus). Montague (2014) found deer to be the most frequent food item of coyotes during all months of the year in western Virginia. Perhaps the abundance of white-tailed deer since the 1970s has played a complementary role in the rapid range expansion of the coyote in the state, including (as in other regions, see Gehrt et al. 2009), suburban and urban areas.

Range expansions of species not included in Handley and Patton (1947) – Six taxa not mentioned by Handley and Patton (1947) have naturally expanded their ranges into Virginia since 1947 (Table 4). Bats added to the list include the Brazilian free-tailed bat (Tadarida brasiliensis), which may be a very recent arrival. It was first reported by Cranford and Fortune in 1994 based on two specimens captured in Giles County, far north of its published geographic limits in North Carolina at the time, where it was considered a recent arrival (Wilkins 1989). Reynolds and Fernald (2015) reported on a specimen from southeastern Virginia in the 1990s and a pup collected in Charlottesville in 2014. More recently, R. Reynolds (pers. comm.) learned of an additional record from southeast Virginia and another from the Richmond area. This species has a surprisingly broad distribution in the state, given its recent range expansion.

Two species of bats are known from single records in the southeast: the Seminole bat (Lasiurus seminolus) from the Great Dismal Swamp (Padgett 1987) and the northern yellow bat (Lasiurus intermedius) from what is now the City of Norfolk (Rageot 1955). The southeastern myotis (Myotis austroriparius) was first recorded in the Great Dismal Swamp in 1998 (Hobson 1998), but it is now known to also occur at inland sites in the upper Coastal Plain (Reynolds and Fernald 2015). Virginia is at the northern edge of the range of each of these species. Another bat, Townsend’s big-eared bat (Corynorhinus townsendii), occurs only in westernmost, mountainous portions of the state (Table 1). The subspecies of Townsend’s big-eared bat that occurs here, Corynorhinus townsendii virginianus, is on the state and federal endangered lists (Table 2).

A subspecies of the North American deermouse (Peromyscus maniculatus), the prairie deermouse (Peromyscus maniculatus bairdii), was first collected in northern Virginia in 1960 (Table 4; Peacock and Peacock 1962). Another subspecies (Peromyscus maniculatus nubiterrae), which was included in Handley and Patton (1947), is a long-tailed mouse that is abundant in mountainous areas of Virginia at relatively high elevations and typically occupies mesic forests (McShea et al. 2003). In contrast, the prairie deermouse is a short-tailed mouse that is abundant in the Midwestern US. It is found in early successional and agricultural habitats and has been recorded in the Shenandoah Valley as far south as Harrisonburg (Hensley 1976). Francl and Meikle (2009) included the North American deermouse and white-footed mouse (Peromyscus leucopus) among other species captured with the hispid cotton rat (Sigmodon hispidus) at an early successional, relatively low-elevation site, 510 m, in Montgomery County in southwestern Virginia. Specimens were assigned to species based on tail length; the long-tailed specimens were identified as deermice and those...
with shorter tails as white-footed mice (K. Powers, pers. comm.). They did not assign the deermice to subspecies. The forest subspecies of deer mouse (Peromyscus maniculatus nubiterrae), is usually found above 800 m (Handley and Patton 1947). Except for a Rockbridge County record (Pitts and Kirkland 1987), we know of no other efforts to document the presence of the prairie deer mouse in Virginia. However, we suspect Peromyscus maniculatus bairdii has a broader and more southerly distribution in the Shenandoah Valley than is indicated by published records.

Augmentation, regional translocations, undetected occurrence, and natural range expansions within Virginia since 1947 – Handley and Patton (1947) indicated that several species were absent from one or more regions of Virginia. In some cases, the Virginia Department of Game and Inland Fisheries (VDGIF) translocated animals from other regions of Virginia and from other parts of North America, in an attempt to restore populations of those species. In other cases, we believe natural range expansion has occurred, and we provide details and explanations for these expansions. The white-tailed deer was restricted to far southeastern Virginia and a few counties in the mountains by the early 1900s (Handley and Patton 1947). Between 1930 and 1950, more than 2000 animals from Florida, Michigan, North Carolina, Pennsylvania, and Wisconsin were released in Virginia (Linzey 1998). The augmentation efforts were successful. By the 1990s their numbers had rebounded to the point that the VDGIF sold some “limitless” tags to reduce populations and curtail damage to crops and ornamental plantings (Thompson and Franch-Powers 2013).

In 1947, Handley and Patton reported that the northern river otter (Lontra canadensis) was rare in the mountains. In the late 1980s, to supplement natural re-expansion of its range, VDGIF translocated animals from the Coastal Plain of Virginia and from Louisiana to areas west of the Blue Ridge (Handley 1991), and the northern river otter again occurs statewide (Linzey 1998).

Handley and Patton (1947) indicated that the eastern fox squirrel (Sciurus niger) was rare and localized in most regions of the state in 1947. More recently, Fies (1993) provided evidence that populations of eastern fox squirrels west of the Blue Ridge may be naturally expanding eastward. Although this species occurs in the Coastal Plain, its distribution is highly fragmented and population densities are low (Linzey 1998). In an effort to restore this species to Virginia’s Eastern Shore (where it was listed as federal endangered until December 2015, USFWS 2015a), the US Fish and Wildlife Service translocated animals from Maryland to Accomack County between 1968 and 1971, and then from Accomack to Northampton County in 1982 and 1983 (Handley 1991).

Handley and Patton (1947) reported very restricted distributions for several taxa that are now known to be more widespread. Their records indicated that a subspecies of the southeastern shrew (Sorex longirostris), the Dismal Swamp southeastern shrew (Sorex longirostris fisheri), was restricted to the historic Dismal Swamp of extreme southeastern Virginia and extreme northeastern North Carolina. This taxon subsequently was found to occur throughout the Coastal Plain of North Carolina and well west of the Dismal Swamp in Virginia (Webster et al. 2009). Handley and Patton (1947) also reported the star-nosed mole (Condylura cristata) was unknown from most of the Piedmont and that the hoary bat (Lasiurus cinereus) had only been recorded at three localities. These three species now have statewide distributions (Linzey 1998), and it is likely they occurred statewide in 1947, but had gone undetected. Handley and Patton (1947) also reported that the American pygmy shrew (Sorex hoyi) was rare and
known from only two localities. Because of extensive studies using pitfall traps (Pagels 1987), this species is now known to occur statewide (Linzey 1998), and it is sometimes locally abundant (Bellows et al. 2001).

The hispid cotton rat, a species that inhabits oldfields, was first collected in southern Virginia in 1941 (Patton 1941), then in Chesterfield County (Pagels and Adleman 1971), and later at many sites in southcentral Virginia (Pagels 1979). It has been reported from many locations across the southern half of the state: the Great Dismal Swamp (Rose 1999), Buckingham County (Pagels et al. 1992), a Blue Ridge site in Nelson County (Francl and Meikle 2009), sites in Botetourt and Montgomery counties (Francl and Meikle 2009), and Lee County in southwestern Virginia (Pagels 1979). It is likely that more northerly expansion will ensue in the Great Appalachian Valley (which includes the Shenandoah Valley) and in portions of the Piedmont and Coastal Plain.

The least weasel (Mustela nivalis) was only known from Montgomery and Rockingham counties in 1947, but Handley and Patton (1947) suggested that it probably occurred in all montane counties. More recently, the species was recorded from scattered mountain localities and two sites in the upper Piedmont (Handley 1991), and it was subsequently captured in the Coastal Plain (Bellows et al. 1999). Sheffield and King (1994) noted reports of many range extensions by the least weasel. Unlike several of the aforementioned species that have demonstrated range expansions, the least weasel is not a habitat specialist, but it is a predator specialist of small mammals, especially voles and other mice (Sheffield and King 1994).

The bobcat (Lynx rufus) was absent from the lower Piedmont and Coastal Plain, except it occurred in the Dismal Swamp and was “common in the mountains” (Handley and Patton 1947). Similarly, at the time of Handley and Patton’s (1947) publication, the distribution of the black bear (Ursus americanus) was restricted to montane counties and the Dismal Swamp. Although still most abundant in those areas, both species now have statewide distributions (Linzey 1998); these reestablishments are likely the result of management and enforcement of game regulations by VDGIF.

Extirpations without reintroductions – At least three species of native land mammals present in Virginia at the time of the establishment of Jamestown were extirpated between 1607 and 1947 (Table 1) and remain absent today: wolf, cougar (also known as puma or mountain lion, Puma concolor) and American bison (Bison bison). Wolves and the cougar were eliminated from most of eastern North America by the early 1900s because of their reputation as predators of livestock. Handley and Patton (1947) stated that the last wolf was killed in the winter of 1909-1910 in Tazewell County, and the last known cougar was killed in Washington County in 1882. Linzey (1998) summarized what he considered to be reliable reports of cougars in Virginia between 1979 and 1998, but none of these were accompanied by verified physical evidence (specimens, hair, scat, or photographs). Our searches of museum databases (see Acknowledgments) returned one record of a Puma concolor specimen at the US National Museum (USNM, catalog number 270142) collected in 1940 at an archeological deposit (Keyser Farm site) in Page County, and another specimen at the Museum of Comparative Zoology (catalog number BOM-7120) of unknown date from Lee County. The US Fish and Wildlife Service (McCollough 2011) recently reviewed evidence of cougars in the eastern United States and recommended delisting the eastern
cougar (*Puma concolor couguar*) because it is extinct. Most biologists consider the cougar to be extirpated in Virginia (Kocka and McShea 2011).

Handley and Patton (1947) reported that American bison were common in the early 1600s. William Byrd II in his 1728 survey of the “dividing line” between Virginia and North Carolina reported that a member of his party shot a two-year-old male American bison on 11 November (Rose 2013). Byrd wrote an extensive description of the massive shoulders of the animal, as well its legs, horns, hair, and herding behavior (Rose 2013). American bison were also reported in other early historical accounts of Virginia (Rose 1986). Skeletal remains of the American bison have been reported from archaeological deposits from one site in extreme southwestern Pennsylvania (Gilmore 1946). However, none have ever been reported from Virginia (E. Moore, pers. comm.). Although herds of the American bison were certainly present east of the Mississippi by the 18th Century, the lack of archaeological evidence in Virginia suggests they occurred in this region irregularly (if at all) prior to European colonization (E. Moore, pers. comm.). Handley and Patton (1947) cite Coues (1871) in reporting that the last remaining American bison in this region was killed in western Virginia (possibly what is now eastern West Virginia or eastern Kentucky) in the late 1790s.

Reintroductions and range expansions following extirpations and near extirpations – Several native species were extirpated, or nearly so, following arrival of Europeans; efforts have been made to restore most of these species to their former ranges through translocation of individuals (Table 1). Handley and Patton (1947) indicated that the snowshoe hare (*Lepus americanus*) probably occurred at high elevations throughout the mountains of Virginia, but by 1947 it was restricted to Highland County. Between 1961 and 1978, hundreds of animals from New Brunswick, Canada were released at several sites in Virginia; however, these attempts to establish populations of snowshoe hares failed (Fies 1991). In 1989, 26 animals captured in West Virginia were released in Highland County (Fies 1992), but by 1991 hares were absent in some previously occupied areas (Fies 1991). Fies (1991) noted that lack of understory threatened the remaining populations of snowshoe hares in Virginia, and Handley (1991) predicted that snowshoe hares could not survive in Virginia without appropriate habitat management. Our searches of museum databases (see Acknowledgments) returned electronic records of three specimens (skulls only) of *Lepus americanus* (USNM catalog numbers 448849-448851) collected in 1986 from Highland County. Also, a road-killed specimen (VMNH 134967, formerly VCU 4968) was collected in 1986 in extreme eastern Pocahontas County, West Virginia, near the Virginia border. The portion of the George Washington-Jefferson National Forest in northwestern Highland County where the hare was last seen is managed as the US Forest Service’s Laurel Fork Special Management Area. This designation generally prohibits habitat alteration that otherwise could benefit the snowshoe hare. Although extant populations are present nearby in West Virginia within a few km of the state line, the conservation status of the snowshoe hare in Virginia is questionable, and this species may be extirpated.

The American beaver (*Castor canadensis*) is among the species that were extirpated and later successfully reintroduced (Table 1). Handley and Patton (1947) reported that American beavers were absent from Virginia by 1910, due to overtrapping. Linzey (1998) provides details of the restocking program implemented by VDGIF in the 1930s.
and 1940s. The American beaver is now considered to be a pest or nuisance species in some locations in the state (Linzey 1998).

The presence (or not) of the North American porcupine in Virginia at the time of European contact and recent evidence that it now occurs here present an enigma. Handley and Patton (1947) considered the porcupine to be “vanished” (extirpated) from Virginia’s fauna, based on an anecdotal account from the 1730s. In the late 1800s, credible reports of live porcupines in West Virginia and Maryland were published in the Proceedings of the National Museum of Natural History; Goode (1878) described a live specimen from West Virginia, and Lugger (1881) provided details of specimens, including a live and a recently killed animal, from three localities in Maryland. Harman and Thoerig (1968) and Feldhamer et al. (1981) reported on porcupines killed by hunters in western Maryland, and Paradiso (1969) stated that the porcupine had been extirpated from Maryland, even though he mentioned “records and reports of the porcupine in the western part of Maryland right up to the present time.” More recently, Linzey (1998) cited literature of occasional reports of animals in western Maryland, West Virginia, and Virginia through the late 1980s.

Our searches of museum databases returned one record (USNM catalog number 570136) of a porcupine found by D.E. Carr in 2006; it was dead on a road on North Mountain in Frederick County. M. Fies also reported (pers. comm.) a roadkill porcupine in 2010 near Swoope in Augusta County and two animals that were killed between September 2010 and July 2011 near I-81 in Frederick County. Joseph and Janet Trout used game cameras on Stone Mountain (in western Frederick County) to obtain numerous photographs of porcupines during 2008-2011. Among the photographs (which were examined by M. Fies, J. Pagels, and S. Roble, in litt.) were adults with young that apparently represent the first breeding records of the porcupine for Virginia. M. Fies (pers. comm.) also reported photos of porcupines from game cameras in western Shenandoah County (adjacent to Frederick County) in 2010 and 2013. More recently, a porcupine that had been hit by an automobile in western Frederick County in September 2014 was rehabilitated and released (Fies, pers comm.). Almost all recent evidence of the porcupine in the state was from areas near the border with West Virginia and Maryland. This is consistent with a statement in October 2015 by B. Sargent (pers. comm.) that the porcupine is “becoming more commonly reported in northeastern West Virginia.” While we concede that it is possible that some animals have been accidentally transported to Virginia and nearby states on logging trucks heading south through Pennsylvania (Handley 1991), we concur with M. Fies (pers. comm.) that most of the porcupines recently observed in Virginia likely are the result of dispersal from expanding populations in West Virginia and Maryland. Regardless of origin and political boundaries, there is a breeding population of porcupines in western Maryland, northeastern West Virginia, and portions of northwest Virginia; the porcupine is once again part of our mammal fauna.

The fisher probably was present in western Virginia before being extirpated in the late 1800s (Handley and Patton 1947), although no specimen from Virginia was reported in a museum collection until very recently (Moncrief and Fies 2015). In 1969, the West Virginia Division of Natural Resources released 23 animals from New Hampshire at two sites in eastern West Virginia; at the time, no fisher population was known within 460 km of West Virginia (Pack and Cromer 1981). Periodic observations of fishers in Virginia, which Handley (1979a, 1991) considered to be reliable, were
reported between 1969 and 1990, including one by JFP in 1989. However, none of these reports were accompanied by verified physical evidence of fishers (specimens, hair, scat, or photographs). In 2008, personnel from VDGIF examined and photographed two taxidermy mounts of fishers that were killed by hunters in Frederick Co., Virginia during 2006 and 2007 (Moncrief and Fies 2015). Trail cameras provided photographic evidence that documented fishers in five western counties between 2009 and 2015 (Moncrief and Fies 2015). In addition, four animals were collected in two of those counties between 2011 and 2015, and these specimens were deposited in the Mammal Collection of the Virginia Museum of Natural History (Moncrief and Fies 2015). According to Moncrief and Fies (2015), fishers that are now present in Virginia almost certainly dispersed from expanding populations in eastern West Virginia and western Maryland. Based on fisher sightings nearly 25 years ago, as well as the more recent specimens and photographic evidence, it is likely there will be documentation of reproduction in Virginia fishers in the near future.

The wapiti was hunted to extinction in Virginia by 1855 (Handley and Patton 1947). In 1917, animals from Yellowstone National Park were released into several western counties, and the population was estimated at about 300 individuals by 1922 (Handley 1979a). However, after a nematode parasite \[Pneumostrongylus \text{ (syn. Parelaphostrongylus) tenuis}\] lethal to the wapiti was introduced by translocated white-tailed deer, the wapiti again disappeared (Handley 1979a). Another attempt to restore the wapiti in Virginia has been made within the past decade. A total of 71 animals from Kentucky was released from 2012 to 2014 in Buchanan County (part of the three-county restoration area that also includes Dickenson and Wise counties). Each year, the animals (16 in 2012, 10 in 2013, and 45 in 2014) were held for quarantine and disease testing before they were released. Including individuals that have entered Virginia from Kentucky on their own, the estimated population size was 150 to 200 animals following the 2016 calving season (D. Kalb, pers. comm.).

ONGOING AND NEW LONG-TERM THREATS TO VIRGINIA’S NATIVE LAND MAMMALS

Clearing for agriculture and other purposes, roadways, invasive plants, nonnative mammals, disease, climate change, and wind turbines are among the threats to native land mammals in Virginia. Before humans arrived, natural forces such as floods, wind, ice storms, and landscape-level wildfires (c.f. Francl and Small 2013), initiated or retarded succession. Both Native Americans and Europeans often used burning and clear cutting to prepare the land for crops and to manage habitat for early successional wildlife. Changes in land-use patterns since the arrival of Europeans have undoubtedly affected the distributions and abundances of our mammals, and some of these changes threaten continued existence of some species. Forests have been alternately cleared for agriculture and replanted. Networks of roadways have been established to move goods and people. Some introduced plants and animals have become invasive, compete with native organisms, or spread diseases to other mammals, including humans. Reliance on fossil fuels and the resultant climate change are altering distributions of species. These and other factors will continue to impact Virginia’s land mammals. In the following sections, we provide details of the current status of these threats and efforts to mitigate them.
Virginia's landscape today – In western Virginia, as a result of reforestation after extensive early timbering and the abandonment of small farms, plus many years of control of natural fires, there is less early successional habitat than in the past. Forest abundance may be returning to pre-Colonial times, although tree species composition has been altered (e.g., American chestnut, Castanea dentata, is almost absent, Stephenson et al. 1992). Old-growth forests and forest types critical to uncommon plants and animals must be preserved, and connectivity must be encouraged in our mountainous areas. However, well-planned wildlife “openings,” regardless of how they are produced, and continued USFS burning at previous fire intervals will benefit forest species and nongame and game species of mammals and birds.

In eastern Virginia, land use changes, increased urbanization, and changes in agricultural practices have decreased abundance of early successional habitats that benefit many species of wildlife. In most agricultural areas, early successional habitat is nearly non-existent because fields are cultivated, mowed or bush-hogged to the forest edge, the fields and pastures are of great acreage, and the fence rows, which provided cover and food in the past, are now nearly non-existent. Fies et al. (1992) described effects of changing land-use patterns on habitat for northern bobwhite (Colinus virginianus), including the impact of “clean farming” methods. The same effects and impacts apply to numerous old field and generalist mammals.

Nearly all human activities lead to fragmentation of habitat far beyond the levels caused by natural factors such as fires and floods. Studies in landscape ecology have demonstrated that habitat fragmentation and the resultant size, shape, and isolation of patches and the inter-patch matrices have far-reaching effects on populations of organisms (Watling et al. 2011). Regardless of scale, habitat fragmentation will have lasting impacts on earth’s ecosystems (Haddad et. al 2015). Whether viewed positively or negatively, managed forests, agroforestry, deforestation, reforestation, agricultural development, urbanization, suburbanization and exurbanization (low density rural development) all impact many of the state’s 10.2 million ha. In 1630, about 9.9 million ha was forested. About 800,000 ha of reforestation followed extensive timbering in the early 1900s, so that a total of about 6.4 million ha, including plantation forests or otherwise highly managed sites, are forested today (VDOF 2015a,b). More than 3.3 million ha, or about 33% of Virginia’s area, is agricultural land (VDACS 2015). In a nutshell, Virginia’s landscape has become increasingly fragmented in modern times.

Roadways – Roadways are a major part of our environment and can affect both the biotic and the abiotic components of landscapes by changing the dynamics of populations of plants and animals, introducing exotic elements, and changing levels of available resources, such as water, light and nutrients (Coffin 2007). Virginia maintains more than 14,000 km of interstate and primary roads and 77,000 km of secondary roads (VDOT 2015). Among the most obvious, negative impacts are dead animals on or along roadways. Romin and Bissonette (1996) estimated the number of deer (all species) killed on US roadways to be at least 500,000 in 1991. In the mid-1980s, Pagels and French (1987) estimated that about 24 small mammals, primarily shrews, were entrapped in discarded bottles per km of Virginia’s secondary roads. Forman (2000), who earlier coined the phrase “road ecology” (Forman and Alexander 1998), estimated one-fifth of the land area in the United States is affected by the cumulative effects of public road systems. Beckmann et al. (2010) encouraged road engineers and planners to consider impacts on animal movement in their design of new roadways. Methods are
available for reducing wildlife mortality on roads. One solution includes fencing that
directs wildlife to existing culverts or specially constructed underpasses. Sparks and
Gates (2012) found that at least 57 wildlife species used culverts in western Maryland.
In a novel approach, Kelly et al. (2013) installed gliding posts (modified wooden utility
poles) that allowed successful gliding by the northern flying squirrel across a scenic
byway in the mountains of North Carolina. In brief, many management tools are
available to reduce the carnage of wildlife on our highways.

Invasive plants – Habitats in Virginia and elsewhere are becoming increasingly
altered by invasive plants, which disrupt ecosystem processes and alter plant
community composition and structure (Vilà et al. 2011). Some plants (e.g., *Elaeagnus
umbellata*, autumn olive) were introduced in an attempt to benefit wildlife, yet they are
now known for their negative impact on native habitats. Japanese stilt grass
(*Microstegium vimineum*) is spreading rapidly in much of Virginia, including sites in
the Coastal Plain, Piedmont, Blue Ridge, and Ridge and Valley provinces (JFP, pers.
obs.). This invasive species can dominate ground-level habitats and shade out important
native plants, and its high allelopathic potential (Pisula and Meiners 2010) is perhaps
the reason for the large monocultures seen in many areas. A non-native form of
common reed (*Phragmites australis*), which forms 2-m tall thickets where few native
biota can coexist, dominates edges of salt and freshwater marshes and other damp
places in the Coastal Plain and undoubtedly impacts many organisms, including
mammals. Further, cold season fescue grasses (*Festuca arundinacea* varieties), of
European origin, are often planted along roadsides, stream embankments, pastures, and
cultural areas (including battlefield parks). The thick, matted growth form of fescue
grain nearly prevents the germination of warm-season grasses and forbs, and severely
limits movement of ground-nesting and ground-feeding wildlife (IDFW 2006).
Allelopathic compounds produced by fescue grass also inhibit germination and
establishment of native herbaceous species, and fescue grass often has a high
occurrence of an endophytic fungus (*Acermonium coenophialum*) that produces
alkaloids toxic to many organisms, including certain insects, wildlife, and many
domestic animals (Conover 1998, IDFW 2006). These are but a few examples of the
invasive plants and the damage caused by them in Virginia (VDCR 2015a). Some of
the fescue fields are being reconverted to animal- and plant- friendly warm-season
grasses and herbs. In general, some of the best efforts for countering loss of old-field
habitats are found in groups working for recovery of game species (e.g., northern
bobwhite quail), which benefits numerous other bird species and mammals, including
the eastern cottontail (*Sylvilagus floridanus*).

Wildlife diseases and parasites – In recent decades, several diseases that affect free-
living wildlife have been labeled emerging infectious diseases (EIDs), which can be
placed into three broad categories: 1) diseases that “spill-over” to domestic animals and
wildlife living nearby; 2) diseases resulting from human translocation of hosts and/or
parasites; and 3) diseases with no obvious direct involvement of domestic animals or
humans (Daszak et al. 2000). Emerging infectious diseases are frequently associated
with changes in the ecology of the host, the pathogen, or both. These ecological
changes are, in turn, often caused by anthropogenic habitat modification (e.g.,
deforestation, habitat fragmentation, agricultural development; Colwell et al. 2011,
Gottdenker et al. 2014).
Wildlife diseases sometimes threaten the health of humans or domestic animals (Sleeman 2006, Joseph et al. 2013). Sleeman (2006) provided a comprehensive review of potential risks and instructions to prevent or reduce exposure to several notable wildlife diseases, including hantavirus pulmonary syndrome, tularemia, and tick-borne diseases such as Lyme disease and Rocky Mountain spotted fever.

Rabies, which can infect any mammal and is nearly always fatal, provides an example of a disease that was rapidly, and unintentionally, spread to Virginia by translocation (Smith et al. 1984). In the late 1970s, an outbreak of raccoon rabies occurred on the border of Virginia and West Virginia. It was later attributed to the interstate translocation of infected raccoons (*Procyon lotor*) that were captured in the southeastern United States and relocated to the mid-Atlantic region as part of an effort by hunting clubs to restock dwindling raccoon populations in this region (Guerra et al. 2003).

Another disease associated with raccoons is caused by the ascarid roundworm parasite *Baylisascaris procyonis*. This parasite has been documented in Virginia (Davidson 2006), and it has been described as an emerging zoonosis (Sorvillo et al. 2002) because of the increasing abundance and proximity of raccoons, its primary host, to humans. The ingestion of *Baylisascaris procyonis* eggs from soil or materials contaminated by raccoon feces, although very rare, may be fatal in humans. The parasite is also known to impact many wild mammals and some birds (Sorvillo et al. 2002), and it has been implicated in the extirpation of the Allegheny woodrat (*Neotoma magister*) in New York and New Jersey (LoGiudice 2003, Page 2013). In a study of Allegheny woodrats in the mid-Atlantic Highlands of Maryland, Virginia, and West Virginia, Ford et al. (2006a) indicated that, although the status of *Baylisascaris procyonis* throughout this region is uncertain, the parasite has been documented from raccoon feces in northern West Virginia and much of Maryland. These authors (Ford et al. 2006a) also cautioned that raccoons have been observed in rock outcrops with Allegheny woodrats in this region, so that a potential transfer mechanism is in place if *Baylisascaris procyonis* becomes a common enzootic in the mid-Atlantic Highlands, as may already be occurring north of the Potomac River.

Another parasite, *Toxoplasma gondii*, is a protozoan that can infect all birds and mammals. It relies on felids to complete its life cycle, and it is an emerging threat from free-roaming domestic cats (*Felis catus*). A recent study (Bullash et al. 2015) concluded that feral cats are likely the primary cause of white-tailed deer infections of *Toxoplasma gondii* in northeastern Ohio. Feces of a single cat can deposit hundreds of millions of oocysts that may remain infectious for up to 18 months (Tenter et al. 2000). The implication for humans for the disease, which has been linked to schizophrenia, miscarriages, blindness, memory loss, and death (Torrey and Yolken 2013, Gajewski et al. 2014), is that humans can acquire toxoplasmosis from cysts in venison of undercooked white-tailed deer, a situation that may be exacerbated by the close association of humans, cats and deer in urban and suburban areas.

Although many studies of diseases in wildlife are motivated by concerns related to the health of humans and livestock, a number of diseases mainly or only affect wild mammals. Hemorrhagic disease, which is the most important infectious disease of white-tailed deer in the southeastern United States and in Virginia (VDGIF 2015c), seems to be in this category. Chronic wasting disease (CWD) is another disease that seems to naturally occur only in wild mammals, including white-tailed deer and wapiti.
In this case, the disease agent appears to be abnormally shaped proteins called prions that affect the central nervous system and lymphatic tissues (Davidson 2006). The first Virginia case of CWD was confirmed in Frederick County in 2009 (VDGIF 2015a).

In some instances, EIDs may lead to extirpation and/or extinction (Daszak et al. 2000, Joseph et al. 2013). For example, white-nose syndrome, which is caused by the fungal pathogen *Pseudogymnoascus destructans*, has been documented in numerous cave-dwelling bats, including species that occur in Virginia (Zukal et al. 2014, Powers et al. 2015). This pathogen is responsible for killing millions of bats in North America; it may alter the structure of bat communities and change ecosystem function (Jachowski et al. 2014), and it may extirpate one or more species of bats (listed in Table 2) that inhabit Virginia (Thogmartin et al., 2013). Additional parasites and diseases that cause mortality in native land mammals of Virginia are described in Davidson (2006).

*Introduced and feral mammals* — Ten species of mammals have been introduced intentionally or accidentally since the arrival of Europeans in Virginia, and many of these negatively impact our native environment. The house mouse (*Mus musculus*), the brown rat (*Rattus norvegicus*), and the roof rat (*Rattus rattus*) accompanied Europeans and remain commensals of humans (Table 5). Efforts to control these rodents and their damage to stored grains and foods result in great economic costs. However, their impact on native mammals, though largely unmeasured, probably is slight. More recent, and intentional, introductions were those of the sika (*Cervus nippon*) to Assateague Island (Accomack County) and the black-tailed jackrabbit (*Lepus californicus*) to Cobb Island (Northampton County). Introduced for hunting around 1960 (Linzey 1998), both species survive on their respective islands. The coypu (or nutria, *Myocastor coypus*) is a semiaquatic rodent native to South America. It was held in captivity for its fur in the 1930s, but animals escaped or were released when the fur market collapsed, and populations have become established on the Coastal Plain (Klopfer and St. Germain 2012). The coypu consumes large amounts of aquatic vegetation, can damage earthen dams, and likely competes with, and displaces, the (native) muskrat (*Ondatra zibethicus*, USFWS 2013a). Klopfer and St. Germain (2012) provide details about the distribution of the coypu in Virginia and adjacent states, and recent collaborative efforts to eradicate this invasive species.

Free-ranging and feral domestic mammals in Virginia (Table 5) include the horse (*Equus caballus*), the wild boar (pig or hog, *Sus scrofa*), the domestic cat, and the domestic dog (*Canis lupus familiaris*). Feral horses are restricted to Assateague Island ( Accomack County) and Mount Rogers (Grayson and Smyth counties). The herd of horses on Assateague Island (the “Chincoteague ponies”) is maintained at 150 head, and it is managed by local and federal guidelines. A goal of the 2013 Interim Chincoteague Pony Management Plan is to ensure the horses remain healthy and do not detract from the island’s diverse natural resources (USFWS 2013c). Similarly, there are about 120 horses on the grassy balds near Mount Rogers (two herds on the Mount Rogers National Recreational Area with about 90 animals and one herd on Grayson Highlands State Park of about 30 animals) that are maintained by the Wilbur Ridge Pony Association (H. Thompson, pers. comm.). Such grassy, high elevation balds as those at Mount Rogers are being lost to encroachment by weedy vegetation and surrounding forests in the US and elsewhere. Weigl and Knowles (2014) hypothesized these areas owe their origin and persistence to past climatic extremes and activities of
TABLE 5. Land mammals introduced to Virginia, either accidentally or intentionally. Common or vernacular name (as suggested by Wilson and Reeder 2005) is indicated for each taxon, along with current classification and the citation for a comprehensive monograph or review of the biology of that taxon. Asterisks denote taxa with feral and/or free-ranging individuals.

<table>
<thead>
<tr>
<th>Scientific name</th>
<th>Common name</th>
<th>Family</th>
<th>Order</th>
<th>Citation</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Lepus californicus</em></td>
<td>black-tailed jackrabbit</td>
<td>Leporidae</td>
<td>Lagomorpha</td>
<td>Best 1996</td>
</tr>
<tr>
<td><em>Mus musculus</em></td>
<td>house mouse</td>
<td>Muridae</td>
<td>Rodentia</td>
<td>Laerm and Webster 2007a</td>
</tr>
<tr>
<td><em>Rattus norvegicus</em></td>
<td>brown rat</td>
<td>Muridae</td>
<td>Rodentia</td>
<td>Laerm and Webster 2007b</td>
</tr>
<tr>
<td><em>Rattus rattus</em></td>
<td>roof rat</td>
<td>Muridae</td>
<td>Rodentia</td>
<td>Laerm and Webster 2007c</td>
</tr>
<tr>
<td><em>Myocastor coypus</em></td>
<td>coypu</td>
<td>Myocastoridae</td>
<td>Rodentia</td>
<td>Woods et al. 1992</td>
</tr>
<tr>
<td><em>Canis lupus familiaris</em></td>
<td>domestic dog</td>
<td>Canidae</td>
<td>Carnivora</td>
<td>Serpell 1995</td>
</tr>
<tr>
<td><em>Felis catus</em></td>
<td>domestic cat</td>
<td>Felidae</td>
<td>Carnivora</td>
<td>Turner and Bateson 2013</td>
</tr>
<tr>
<td><em>Equus caballus</em></td>
<td>horse</td>
<td>Equidae</td>
<td>Perissodactyla</td>
<td>Mills and McDonnell 2005</td>
</tr>
<tr>
<td><em>Sus scrofa</em></td>
<td>wild boar</td>
<td>Suidae</td>
<td>Artiodactyla</td>
<td>Chapman and Trani 2007</td>
</tr>
<tr>
<td><em>Cervus nippon</em></td>
<td>sika</td>
<td>Cervidae</td>
<td>Artiodactyla</td>
<td>Feldhamer 1980</td>
</tr>
</tbody>
</table>
large mammalian herbivores, many of which are now extinct or extirpated. The horses largely fulfill that maintenance role today.

Feral wild boars consume wildlife and plants, destroy food caches of small mammals, compete with native wildlife for hard mast, and often severely damage plant communities and habitats (Campbell and Long 2009). Although populations of feral wild boars are localized in Virginia, they seem to be increasing and are being monitored by the VDGIF (2015b).

The literature is voluminous on the negative impact of domestic cats on native wildlife. Loss et al. (2013) estimated that free-ranging pets and feral cats kill 1.4-3.7 billion birds and 6.9 to 20.7 billion mammals annually in the US. Loss et al. (2013) also found that the majority of mortality is caused by truly feral cats and un-owned, stray cats (i.e., those without habitation but perhaps being fed). However, even house pets that spend only part of the day or night outside kill large numbers of small, native animals. A study that used “kittycams” to monitor hunting by such house pets in a suburban area of the southeastern USA found that almost half of them hunted wildlife, with an average of 2.4 kills per week (Loyd et al. 2013). These authors also showed that domestic cats brought home fewer than one in four kills, a finding that greatly increases earlier mortality estimates (e.g., Mitchell and Beck 1992). Loss et al. (2013) suggested that free-ranging pets and feral cats likely are the greatest source of anthropogenic mortality for US birds and mammals. Further, abundance of native predators typically reflects prey numbers and habitat quality of prey, and crashes of prey populations are followed by crashes of predator populations. In contrast, predation by free-ranging pet or feral cats (including those in trap, neuter, release programs) occurs regardless of prey numbers. Even those cats fed by humans continue to hunt, to the detriment of native wildlife (see Hawkins et al. 2004, among others).

The domestic dog has a long history in North America, perhaps as long as that of Native Americans. Companion, hunter, protector, herder, guide, and law enforcement describe some of the roles of modern dogs. Dogs also can adversely affect wildlife, but differ from cats in a number of ways, including mechanisms of disturbance, numbers of prey individuals consumed, and prey size. Free-ranging dogs, even when accompanied by their owners, often disturb and harass wildlife species (see Hughes and Macdonald 2013). Leashed dogs jumping after squirrels or depositing scent (that of a predator) while on a casual walk provide familiar examples of such harassment, potential or real.

Climate change – In the past 50 years, human-induced modification of climate has caused temperatures to rise, precipitation regimes to change, and icecaps to melt (Duffy and Tebaldi 2012, Abatzoglou and Barbero 2014, McCain and King 2014). Handley (1992) noted that regional disasters such as the gypsy moth (Lymantria dispar), acid rain, and the chestnut blight fungus (Cryphonectria parasitica) can have long-lasting or permanent impacts on the environment, but that all of these pale in comparison to the destructive potential of climate change. Handley (1992) and many others (e.g., Lawler et al. 2009) predicted a shift in the distributional ranges of some flora and a concomitant shift in the range of some mammals in response to climate change. Such shifts will change the composition, but not necessarily change the species richness, of mammal communities in Virginia (Handley 1992).

Recent models (McCain and King 2014) have identified factors (body size and activity time) that may mediate response of individual mammal species to climate
change. We suggest that in the short-term, several species isolated in high elevation habitats in Virginia (e.g., American water shrew, northern flying squirrel, and rock vole) face the greatest threat of local extirpation due to climate change. Despite certain, often political, arguments that climate change is part of a natural cycle, we note extinction is also natural, but that both extinction and climate change are exacerbated by human activities. There is no evidence that Virginia is being spared the effects of climate change. In fact, the state has recently taken an active role to address climate change by developing a strategy to safeguard species of greatest concern (VDGIF et al. 2009). In addition, Kane et al. (2013) recently conducted a suite of climate modeling and species vulnerability assessments. Although their models did not explicitly include any mammals, we deem the animals used in that study to be appropriate surrogates for Virginia’s mammals.

Wind energy and wind turbines — Large numbers of bats and other wildlife are killed by wind turbines each year (Kunz et al. 2007, Arnett et al. 2008). For years, arguments in support of wind energy development noted that wind is free, that fossil fuel costs are high, oil production is subject to political disruption in other countries, and the US is exhausting its coal deposits. More often now we hear from promoters of wind energy that wind is (still) free and that turbines produce zero greenhouse gas emissions and hence do not promote climate change. These arguments of the American Wind Energy Association and the American Wind Wildlife Institute can be compelling. However, wind turbines are substantial potential threats to Virginia bats, especially the hoary bat, the eastern red bat (Lasiurus borealis), and the silver-haired bat (Lasionycteris noctivagans; R. Reynolds, pers. comm.).

WILDLIFE MANAGEMENT AND HABITAT PROTECTION
Thompson and Francl-Powers (2013) recently summarized the history of wildlife management in Virginia. Between 1607 and the early 1900s, many species of mammals were hunted or trapped for sustenance, for sport, or for their pelts and other body parts. By 1916, the VDGIF was established to conserve, protect, and manage wildlife and non-marine fishes of the state. This mission continues today, and this state agency is charged with managing all land mammals, whether game or non-game species.

Over time, the mandate of the VDGIF has expanded to include management and conservation of land and habitat as well as the wildlife species themselves (Thompson and Francl-Powers 2013). In 2015, VDGIF maintained 41 management areas totaling more than 82,000 ha (VDGIF 2015d). Two other state agencies, Virginia Department of Conservation and Recreation (VDCR) and Virginia Department of Forestry (VDOF), also conserve natural resources and manage land for wildlife. In 2015, VDOF managed 22 state forests that total more than 27,000 ha (VDOF 2015c), and VDCR maintained more than 48,000 ha, including 36 state parks and 62 natural areas and preserves (VDCR 2015b).

In 2015, federal lands under management for wildlife and habitat conservation in Virginia included the George Washington and Jefferson National forests, which comprised more than 647,000 ha in Virginia (USDA 2015), 14 USFWS National Wildlife Refuges, which protected more than 52,000 ha of habitat (USFWS 2015b), and 21 national parks and other sites totaling more than 80,000 ha that are administered by the National Park Service (NPS 2015). In addition, the federal Department of Defense (DOD) properties in Virginia comprised 104,814 ha (Gorte et al. 2012), and
most undeveloped area on DOD sites is managed as habitat for local wildlife. In 2015, the Virginia Outdoor Foundation (VOF) administered conservation easements on more than 300,000 ha of private land, including some of the highest-quality forests, cleanest waterways, and richest wildlife habitat in the state (VOF 2015). In sum, about 16.7 percent (about 1.7 million ha) of the estimated total land area of Virginia is protected in 2015 (VDCR 2015c).

SUMMARY

Although species richness, abundance and distribution of Virginia’s land mammals reflect natural processes, the consequences of long-term human activities are also evident. As we described above, the recent range expansion of the hispid cotton rat provides an example of how humans have influenced the roles of habitat availability and habitat contiguity, in part through climate change. Further, with continued warming, we predict subsequent expansion of the ranges of additional species and contraction of the ranges of others. This will change species composition, but not necessarily species richness, as certain boreal species are lost from Virginia’s fauna and replaced by austral species.

We suggest early successional habitats are more abundant now in much of the Piedmont and Coastal Plain than at the time of European settlement. In those same regions, future land use patterns may cause those early successional associations to persist, except in areas where cover is removed (e.g., modern clearing of vacant land and “clean farming”). In western Virginia, especially on large expanses of public lands, reforestation has reduced the amount of early successional habitat, and creation of additional openings would benefit certain wildlife.

Invasive plants will increasingly alter our native communities, degrading and eliminating habitats suitable for native mammals and other organisms. Feral and free-ranging cats and dogs will continue to harass and kill native wildlife. Lessening the impact of these non-native predators will require measures that evoke emotional reactions and cause contentious situations; it is unlikely this problem will be solved anytime in the near future. The public must be educated regarding the potential negative consequences (e.g., habitat destruction, competition with native species, new diseases) of introductions of exotic species, translocated game species, and the free rein given to domestic species.

The quest for alternative, renewable energy sources is urgent and includes capturing solar and wind energy. We caution that wind energy is not a panacea to the ills of fossil fuels. Animals may be killed by turbines, and habitat destruction on ridgetops, somewhat akin to surface mining, must be considered in the siting of wind facilities. We urge decision makers to seek information from qualified biologists and from refereed journals and to otherwise be aware of conflicts of interests when considering sources of information regarding the effects of wind turbines on wildlife.

Demands placed on our environment by an ever-increasing human population and the ongoing perturbations of natural systems portend that protection, management, and conservation of our natural resources will continue to be major challenges. Most of the lands under management for wildlife and habitat conservation in Virginia, especially east of the mountains, are not contiguous. Moreover, much of the habitat in the matrices surrounding managed areas is unsuitable for many species. Challenges will be greatest for maintenance of viable populations of species considered to be habitat
specialists, whether in mesic forests, overgrown fields, swamps, marshes, or clear, 1st-
2nd order headwater streams. Despite these and other ongoing challenges, many of
Virginia’s land mammals have demonstrated resilience in their ability to persist during
the more than 400 years since European contact. With the combined efforts of state and
federal agencies and non-governmental organizations, most species should continue to
be a part of our natural heritage well into the future.

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quickly provided helpful information related to their areas of expertise. J. Davenport
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obtain details for museum records, we sent information requests to Academy of Natural
Sciences of Philadelphia on 11 August 2014 and Carnegie Museum of Natural History
on 27 August 2014. We also searched the following institutions through the VertNet
portal on 16 August 2014 and 9 January 2015: American Museum of Natural History,
California Academy of Sciences, Centennial Museum, Charles R. Conner Museum,
Cheadle Center for Biodiversity and Ecological Restoration, Cincinnati Museum
Center, Cornell University Museum of Vertebrates, Delaware Museum of Natural
History, Denver Museum of Nature & Science, Field Museum of Natural History,
Florida Museum of Natural History, Georgia Southern University, Humboldt State
University Wildlife Department, James R. Slater Museum of Natural History, John
Wesley Powell-Dale Birkenholz Natural History Collections, University of Kansas
Biodiversity Institute, Louisiana State University Museum of Natural Science,
Michigan State University Museum, Milwaukee Public Museum, Moore Laboratory
of Zoology, Museum of Comparative Zoology Harvard University, Museum of
Southwestern Biology, Museum of Texas Tech University, Museum of Vertebrate
Zoology University of California at Berkeley, United States National Museum of
Natural History Smithsonian Institution, Natural History Museum of Los Angeles
County, New Mexico Museum of Natural History and Science, New York State
Museum, North Carolina Museum of Natural Sciences, Ohio State University, Oregon
State University, Perot Museum of Nature and Science, Royal Ontario Museum, Sam
Noble Oklahoma Museum of Natural History, San Diego Natural History Museum,
Santa Barbara Museum of Natural History, Schmidt Museum of Natural History
Emporia State University, Tall Timbers Research Station and Land Conservancy,
Texas A&M University Biodiversity Research and Teaching Collections, The
University of Texas at Austin Natural History Collections, Tulane University,
University of Alabama Biodiversity and Systematics, University of Alaska Museum,
University of Arkansas Collections Facility, University of British Columbia Beatty
Biodiversity Museum, University of Colorado Museum of Natural History, University
of Michigan Museum of Zoology, University of Nevada at Reno, University of
Washington Burke Museum, University of Wyoming Museum of Vertebrates, Western
Foundation of Vertebrate Zoology, Western New Mexico University.
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