

Biology and Management of White-tailed Deer



Edited by David G. Hewitt

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Preface

The white-tailed deer is an American original, having evolved in North America. The white-tailed deer is a survivor. During its existence in the Americas, innumerable other species have come, through migration and speciation, and gone, through extinction. The whitetail is a survivor because it is highly adaptable. Whitetails are found from the boreal forests of central Canada to the equatorial savannahs and forests of Peru, from the Rocky Mountains and Andes to the llanos of Venezuela and swamps of the United States Gulf Coast. The species' adaptability over this broad range is shown not only in the habitats it uses, but in the diets it selects, a twofold difference in body size, variable pelage, and reproduction that varies from highly seasonal to year-round.

Interactions between humans and white-tailed deer began as soon as people migrated to the Americas. Hunting and eating deer were surely important to early humans. Deer also became prominent in the art and religion of the first Americans, and once agriculture arose, the concept of deer causing damage also developed.

Across the species' vast range and during the past 200 years, management of white-tailed deer has encompassed all aspects of wildlife biology. In some places at times, white-tailed deer have become endangered and even extirpated. In other places at times, white-tailed deer have been managed sustainably for decades. And in still other places at times, especially during the past 25 years, white-tailed deer have become too numerous relative to society's desires and even have negatively impacted diverse and naturally functioning ecosystems. In line with other wildlife conservation issues of the day, biologists are beginning to consider the effects of changing climate on deer distribution, particularly in the southwestern United States and along northern edges of the species' range.

To complicate this already complex management milieu, white-tailed deer have both positive and negative values to society and have constituencies promoting these diverse values. Many people have positive feelings toward deer because whitetails are large, graceful, and beautiful animals. Other people value deer as a challenging species to hunt. Some constituencies advocate much smaller deer populations because of damage to vehicles, landscaping, crops, forest products, and ecosystems. Balancing these competing desires of society is the challenge of wildlife biologists and agency administrators.

This book seeks to compile current understanding of white-tailed deer biology and management. This goal was last attempted over 25 years ago by Halls (1984). During the past quarter century, deer populations have flourished, particularly in urban areas. Hunting, the traditional tool used to manage deer population size, is difficult to apply in some instances and is becoming less effective in others. Thus, managing conflicts between people and whitetails is increasingly difficult and complex. Another prominent change in deer management concerns the time and resources landowners and hunters invest in deer management. A growing realization that a quality hunting experience is based on a quality deer herd has changed deer management paradigms from buck-only harvest and high deer densities toward more natural age structures and balancing deer density with the habitat. The intensity of deer management has reached its zenith in the captive deer facilities that occur where allowed by state law.

The prominence of and interest in white-tailed deer has spurred a great deal of research on the species' ecology and management. An exceedingly conservative estimate of research involving white-tailed deer can be obtained by a literature search of JSTOR, which, in June 2010, found 631 papers published before 1985 and 834 papers published since January 1, 1985 that contained the words "white-tailed deer" in the title or abstract. Summarizing this body of research and the vast amount of gray literature on white-tailed deer for this book was accomplished by 35 authors from throughout the white-tail's range, including personnel from state and federal agencies, nongovernmental organizations, private consulting companies, and universities. These experts found time in their busy schedules to review the literature for their respective chapters, decide which issues were essential to cover and which would need to be

omitted because of space limitations, and rendered the stacks of research papers and knowledge into the chapters of this book. These chapters can serve as the gateway for white-tailed deer enthusiasts to a greater understanding of this fascinating species.

Also to enhance reader understanding, this book includes a companion CD-ROM disc containing full-color versions of all figures from the book.

As editor of this volume, I would like to thank Fred Bryant, Director of the Caesar Kleberg Wildlife Research Institute (CKWRI), for encouraging such a project and providing the freedom and resources to complete it. I appreciate the support and confidence of Stuart Stedman, a generous benefactor of the Deer Research Program at the CKWRI and the professors' professor when it comes to insight in producing giant white-tailed deer in southern Texas. The invigorating work environment and interactions provided by my colleagues and graduate students at Texas A&M University–Kingsville have been invaluable. I am thankful to Judy Hartke who graciously provided beautiful and original artwork for the book's cover and section breaks. John Sulzycki and Jill Jurgensen with CRC Press, Taylor & Francis Group, were a pleasure to work with; I appreciate greatly their support and productive input as this project developed. My grandfather, W. L. Robinette, through his pioneering research on mule deer and his spending time outdoors with his grandchildren, showed me that it is possible to make a living while pursuing your passion. And finally, my parents, Glenn and Lee Hewitt, my wife Liisa, and my kids Nicole and Matt deserve all the accolades I can bestow for their support in this project and throughout my career.

David G. Hewitt

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Editor

David Glenn Hewitt is the Stuart Stedman Chair for White-tailed Deer Research at the Caesar Kleberg Wildlife Research Institute at Texas A&M University–Kingsville. He graduated with highest distinction and honors from Colorado State University in 1987 with a bachelor of science degree in wildlife biology. He earned a master's degree in wildlife biology from Washington State University and then worked for a year as a research associate at the Texas Agriculture Experiment Station in Uvalde, Texas. In 1994, David completed a PhD in wildlife biology at Virginia Tech. David taught wildlife courses at Humboldt State University during the 1994–1995 academic year and then spent a year as a postdoctoral scientist at the Jack Berryman Institute at Utah State University. In 1996, he was hired as an assistant professor at Texas A&M University–Kingsville. His primary research interests are in wildlife nutrition and white-tailed deer ecology and management. He has authored or coauthored more than 60 peer-reviewed scientific publications and three book chapters and has co-edited the book *Wildlife Science: Linking Ecological Theory and Management Applications*.

David served as associate editor of the *Journal of Wildlife Management* during 1997–1998 and *Rangeland Ecology and Management* during 2004–2006. He was recognized as the Outstanding Young Alumnus from the College of Natural Resources at Virginia Polytechnic Institute and State University in 1999 and received the Javelina Alumni Award for Research Excellence in 2004, the Presidential Award for Excellence in Research and Scholarship from the College of Agriculture and Human Sciences, Texas A&M University–Kingsville in 2004, and the Educator of the Year Award from the Texas Chapter of The Wildlife Society in 2010.

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Part I

The Past



1

Taxonomy, Evolutionary History, and Distribution

James R. Heffelfinger

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Taxonomy

Taxonomy is the process of naming, describing, and organizing plants and animals into categories based on similarities and differences. These categories indicate evolutionary relationships because similar animals generally have common ancestors. This structured system of classification was originally based on morphology, but as molecular analyses became refined, genetic data became very useful in elucidating relationships that remained unresolved. Both morphological and genetic evaluations have shortcomings, and so it is important to use all available information when inferring taxonomic relationships.

In 1758, Swedish physician and botanist Carl von Linnaeus finalized a system for naming plants and animals in a classification scheme he called *Systema Naturae* (Linnaeus, 1758). Linnaeus' naming convention consisted of a hierarchy of seven classifications that grow progressively more specific (Table 1.1). This system is still called *binominal nomenclature* because it uses two names for each species; the first name is the *genus* and the second is the *species*.

TABLE 1.1

Classification of White-tailed Deer within Linnaeus' *Systema Naturae* (Linnaeus, 1758)

Kingdom	Animalia (Animal Kingdom)
Phylum	Chordata (animals with a backbone)
Class	Mammalia (mammals)
Order	Artiodactyla (even-toed hoofed mammals)
Family	Cervidae (the deer family)
Genus	<i>Odocoileus</i> (medium-sized North American deer)
Species	<i>virginianus</i> (white-tailed deer)

With this naming system each plant and animal in the world has a unique scientific name (*Genus species*) used by scientists in all countries regardless of their primary language. Scientific names are sometimes in Greek, but usually Latin. Because Latin is a “dead” language and not subject to continual change, it is the international language of science. The *subspecies* category was not part of the original classification system, but was added later in an attempt to describe variations (sometimes called *races* or *ecotypes*) within the same species. The subspecies name is added to the end of the two-word scientific name (*Genus species subspecies*). In the field of taxonomy, there are some biologists who are considered “lumpers” and others who are “splitters.” Lumpers prefer to focus on the similarities among animals and group several similar forms into one category. Splitters, on the other hand, prefer to separate even slightly different forms into different taxonomic categories.

Taxonomy was a full-time job for many early naturalists. Historically, especially in the eighteenth and nineteenth centuries, taxonomic splitting was very common. There were very few specimens available and the exploration of new lands resulted in new specimens that seemingly had unique characteristics. Many new categories were established based on only a few specimens. In some cases, a small and barely discernible difference resulted in the naming of a new species. Merriam (1918) examined grizzly bear skulls and declared that there were 86 species of grizzlies in North America, with 27 species in Alaska alone.

Many of these early “species” were later reduced to subspecies status or dissolved completely resulting in a series of synonyms for many subspecies. These early efforts at categorizing animals introduced much confusion and bad science into the taxonomic realm when further analysis of many more samples showed characters not to be diagnostic of anything meaningful. Unfortunately, one only needs a single specimen and a short mention in print to establish a scientific name, leaving the scientific community the burden of conducting a comprehensive morphologic, genetic, and ecological study throughout the animal’s entire range to properly evaluate its validity.

Deer and Other Ungulates

Deers are members of the Class Mammalia; which contains all warm-blooded animals that produce milk for their young, usually have fur, and possess seven neck vertebrae. Within the Class Mammalia are 26 Orders; two of these are groups of animals that walk on thick, modified toenails called hooves (Wilson and Reeder, 2005). These animals are called ungulates from the Latin word *unguis* meaning “claw” or “toenail” (Gotch, 1995).

Ungulates with an odd number of toes (one or three) on each hoof belong to the Order Perissodactyla (horses, rhinos, tapirs), while the Order Artiodactyla (“artios”= even, “daktulos”= toes) contains all even-toed ungulates like cattle, deer, goats, antelope, and pigs. Within Artiodactyls, there are many different taxonomic families that have been traditionally recognized, but only four occur naturally in North America: Bovidae (sheep, cattle, goats, bison), Antilocapridae (pronghorn antelope), Tayassuidae (collared peccary), and Cervidae (deer, elk, moose) (Nowak, 1999).

The most remarkable taxonomic discovery in recent years is the well-supported placement of whales and dolphins (Cetacea) deep within the Order Artiodactyla. Genetic and fossil evidence (astragalus

bones) confirms that Cetacea evolved from an artiodactyl ancestor, similar to hippopotamus (Geisler et al., 2007). Some are now calling the order “Cetartiodactyla.”

White-tailed Deer and Other Cervids

The deer family (Cervidae) is comprised of all animals that shed antlers annually, including moose, elk/red deer, caribou/reindeer, white-tailed and mule deer, as well as several Asian, European, and South American species. Only males have antlers, except for caribou/reindeer in which females bear a smaller version of the males'. Cervids, as members of the family are called, walk on the hooves (toenails) of the third and fourth toes, but no longer have the first digit (thumb or big toe). The second and fifth toes have been reduced and assume a nonfunctioning role in what are called dew claws. True cervids have a four-chambered stomach like other ruminants, but lack a gall bladder.

Worldwide, there are 18 genera in the deer family (Groves, 2007) containing about 51 species (Wilson and Reeder, 2005). There is still some question about the distinctness of some of these species and some disagreement about what constitutes species versus subspecies differences. Taxonomic revision is a continual process as additional morphometric and especially genetic information become available. Regardless of the number of species, there is little doubt about the worldwide success of the deer family, which is native to all continents except for Australia and Antarctica. The family ranges from the 4-kg pudu of South America to the 725-kg Alaskan moose and occupies habitats from arctic tundra to tropical forest.

Chinese water deer are included in Cervidae even though this species lacks antlers. Rather than antlers, male Chinese water deer have the large protruding upper canines reminiscent of several extinct cervids. This species has been used as an example of a cervid that retained its primitive form, but there are indications that it may have had antlers in the past and reverted to an antlerless and tusked condition secondarily (Groves, 2007).

Two deer-like ruminants have been associated with the deer family at times, but are not true cervids. The first are the diminutive (2.3 kg) mouse deer and chevrotains. The chevrotain is a small antlerless animal that lives in the tropical forests of Africa and Southeast Asia. These solitary animals have upper canines, no antlers, and represent a very primitive form of ruminant. The musk deer is a 7–15-kg animal resembling the Chinese water deer with enlarged saber-like canines. This too was originally considered a cervid, but some morphologic differences, such as the presence of a gall bladder and abdominal musk gland, have always been enigmatic. Increasingly sophisticated genetic work has recently shown it to be more closely related to the cattle family, Bovidae (Groves, 2007). Separate taxonomic families are now used for both the chevrotain (Tragulidae) and musk deer (Moschidae).

The genus *Odocoileus* includes two species of medium-sized deer whose distribution is centered on North America: the mule deer and the white-tailed deer. This genus name was given by Constantine Rafinesque based on a few teeth given to him by a colleague who had broken them out of a jaw protruding from the wall of a limestone cave in Pennsylvania. Rafinesque returned to the cave in hopes of finding more material to examine, but found none. Although he described the teeth in detail, he was unsuccessful in matching them to any living animal. Despite naming not only the genus *Odocoileus*, but also giving mule deer their scientific name, it is apparent that Rafinesque had not yet seen deer teeth for comparison. He named his mysterious cave teeth with the genus “*Odocoileus*,” meaning “teeth well hollowed” because of the crescent-shaped infundibula in the chewing surface of the teeth (Rafinesque, 1832). Later taxonomists realized these teeth were from white-tailed deer and designated this publication as the first to assign a valid genus to these North American deer.

The name *Odocoileus* was used widely without question, until Hershkovitz (1948) pointed out that it was wrong. The genus name *Dama* was used for white-tailed deer by Zimmerman (1780), 52 years before Rafinesque pondered the origin of his cave teeth. Under taxonomic rules this makes *Dama* the correct genus name for white-tailed and mule deer in North America. Shortly thereafter, some sources began to use “*Dama virginianus*” for white-tailed deer (Hall and Kelson, 1959). This caused considerable confusion in the taxonomic community since *Dama* was already being used for European fallow deer (*Dama dama*). These New World and Old World deer are not closely related, which necessitated finding a new genus name for fallow deer. The cascading confusion of changing at least two well-established genera was deemed unacceptable and so the International Commission on Zoological Nomenclature used its

plenary powers to issue Opinion 581. This decision acknowledged that although *Dama* is technically correct, *Odocoileus* would be recognized as the official genus name for white-tailed and mule deer (International Code of Zoological Nomenclature, 1960).

White-tailed deer were first described in notes made by Thomas Hariot, who was part of Sir Walter Raleigh's attempt to establish a settlement on the North Carolina coast in 1584 (referred to generally as "Virginia" at the time). At the age of 25, Hariot produced the first detailed account of the New World published in English. His *A Briefe and True Report of the New Found Land of Virginia* included a notation that deer were common and that the native inhabitants traded thousands of deer hides annually for firearms (Hariot, 1588). He also offered that deer were of "ordinary" size near the sea coast and larger inland where the habitat was better. Having only red deer and roe deer as reference, Hariot (1588) described this new deer species by writing that "... they differ from ours onely in this, their tails are longer and the fnags [snags] of their hornes looke backward." The species name *virginianus* reflects the location where it was first described by Hariot (1588) and the species is still commonly referred to as "Virginia Deer." Ironically, Thomas Hariot was describing deer in what is now North Carolina.

Evolutionary History

The earliest hoofed animals with an even number of toes (Artiodactyls) appeared during the early Eocene Epoch, 56–34 million years ago. Rabbit-sized ungulate ancestors, such as *Diacodexis* and other similar forms, were distributed throughout North America and Eurasia (Theodor et al., 2007). *Diacodexis* possessed a unique ankle bone, called the astragalus, which acts as a double pulley providing great flexibility in the hind foot. This bone marks this animal unmistakably as the first known artiodactyl; all even-toed ungulates have this bone. Like the artiodactylids that followed, these animals possessed long limbs for running. Although they walked on all four (rear) or five (front) hoofed toes, they supported most of their weight on the two central toes on each foot. Thus, even at this early stage, one can see the development toward the two-toed ungulates of today and their unused lateral dew claws.

Primitive artiodactyls diversified and increased in abundance throughout the Eocene as the climate became dryer and possibly cooler, allowing ruminants to flourish (Metais and Vislobokova, 2007). By the close of the Eocene there were several groups of primitive ruminants that were precursors to the cattle, pronghorn, camel, and deer families. A small ruminant like the *Archaeomeryx* in Asia gave rise to a subsequent diversification and radiation into forms exemplified by *Eumeryx* in Eurasia. *Eumeryx* already possessed many characteristics seen in today's deer and bovids, such as no upper incisors, incisor-like lower canines, low-crowned molars, and much reduced first lower premolars (Figure 1.1) (Stirton, 1944).

Evolutionary development of these ruminants continued through the Oligocene Epoch (34–24 million years ago) with the appearance of increasingly complex forms such as the Moschidae family.



FIGURE 1.1 The Eurasian *Eumeryx* represents the transition between very primitive artiodactyls and the more graceful forms that eventually evolved into deer. (Illustration by R. Babb from Heffelfinger, J. R. 2006. *Deer of Southwest*. College Station: Texas A&M University Press.)

Moschids, like the North American *Blastomeryx* and the Eurasian *Dremotherium*, are primitive deer-like mammals with no antlers, but exaggerated tusk-like canines (Prothero, 2007). A Eurasian form of these sabre-toothed deer, such as *Dremotherium*, is the most probable ancestor to all cervids. Moschids disappeared by the end of the Miocene, with the exception of one genus, the present-day musk deer. Musk deer of eastern Asia are not actually cervids, but represent direct descendants of these primitive Moschid forms. Canine tusks are not normally associated with Cervidae today, but the Chinese water deer provides an example of a true deer that lacks antlers and possesses large canines remarkably similar to fossil deer.

Antlered Deer Appear

Despite the abundance and diversity of ruminants in North America, none of these forms gave rise to North American deer. Eurasian deer-like animals such as the tusked and antlerless *Dremotherium* are recognized as the types of primitive ruminants that eventually gave rise to all cervids. Later Miocene forms in the Family Lagomerycidae offer important clues, and a probable “missing link,” to the early development of deer (Gentry, 1994). Many of the Lagomerycids, such as *Procervulus*, not only possessed large canine tusks, but also forked or palmated antlers that were shed, but probably not every year (Figure 1.2). Thus, with the occasional casting of antlers, *Procervulus* and related forms were positioned precisely at the genesis of the deer family.

The earliest true deer (Cervidae) appeared in Eurasia in the middle of the Miocene (Scott and Janis, 1987). One of these ancestral deer had small antlers that normally formed a single fork (Figure 1.3) (*Dicrocerus*). Another Miocene deer, *Stephanocemas*, had tusk-like canines and antlers that formed a bowl-shaped palm (Figure 1.3) (Gentry, 1994). The antlers of these early deer were shed annually from long antler bases much like the present-day muntjac of Asia (Figure 1.4).



FIGURE 1.2 The increasingly deer-like forms such as *Dremotherium* (left) and *Procervulus* (right) appear in the Eurasian fossil record during the Miocene. *Dremotherium* had no antlers, but the males had large saber-like canines. The horns/antlers of *Procervulus* may have been shed at irregular intervals. (Illustration by R. Babb from Heffelfinger, J. R. 2006. *Deer of Southwest*. College Station: Texas A&M University Press.)



FIGURE 1.3 *Stephanocemas* (left) and *Dicrocerus* (right) are the first animals to shed their antlers on a regular and recurrent basis. All of today's true (antlered) deer arose from early deer such as these. (Illustration by R. Babb from Heffelfinger, J. R. 2006. *Deer of Southwest*. College Station: Texas A&M University Press.)



FIGURE 1.4 The musk deer (left), muntjac (center), and roe deer (right) provide an illustrative example of the evolutionary progression from oral to cranial weaponry in Cervidae. (Photo by P. Myers. With permission.)

With the evolutionary development of increasingly elaborate antlers, the occurrence of tusk-like canines was much reduced in the deer family (Figure 1.4) (Eisenberg, 1987). The antlerless Chinese water deer have prominent canines, while other antlered deer have lost their canines entirely or they are very much reduced (as in elk). The muntjac and tufted deer of Asia occupy an intermediate position with small antlers and small canines. It has been hypothesized that the reduction of large canines occurred because the development of elaborate antlers supplanted the need for these teeth as weapons or sexual display organs. An alternate theory surmises that the reduction of these enormous canines was caused simply by a change to a browse-dominated diet and the need to grind food with side-to-side jaw movements.

The First North American Deer

There is no record of true (antlered) deer in North America until the close of the Miocene (Webb, 2000), when an ancestral stock immigrated from Eurasia by way of the Bering Land Bridge seven to five million years ago. These new immigrants found the North American continent in ecological turmoil and experiencing a high level of extinction in many of the large assemblages of native ruminants. The earliest fossils of deer in North America are represented by *Eocoileus gentryorum* found in five million-year-old deposits in Florida (Figure 1.5) (Webb, 2000). The antlers of *Eocoileus* rose straight up from the frontal bones and were very similar to present-day roe deer (Figure 1.6). This North America form was probably not far removed from the ancestor of all roe deer, Chinese water deer, and deer of the New World (Webb, 2000; Pitra et al., 2004).

Another very early North American cervid is found in similarly aged deposits (4.8–3.4 million years ago) in Nebraska. *Bretizia pseudalces* was very similar to *Odocoileus*, but differed in that the antlers were strongly palmated and spread laterally much like a moose (*pseudalces* = “fake moose”). This deer was found on the west coast and Great Plains, but disappears from the fossil record at the end of the Pleistocene (Fry and Gustafson, 1974; Gustafson, 1985; Gunnell and Florin, 1994).

Navahoceros was a short-legged, stocky deer found in the Rocky Mountains starting about three million years ago. This animal was built for life in the mountains with a body form similar to other mountain ungulates (Kurten and Anderson, 1980). This deer sported three-tined antlers not unlike white-tailed deer, but had cranial characteristics similar to *Rangifer* (Webb, 1992). By 11,500 years before present, *Navahoceros* falls out of the fossil record (Kurten and Anderson, 1980), although it may live on today in South American descendants (Webb, 2000).



FIGURE 1.5 Sometime prior to five million years ago, an early deer ancestor crossed the Bering Land Bridge and thus true deer were introduced into North America. *Eocoileus gentryorum* fossils from that time unearthed in Florida represents the earliest known cervid in North America. (Illustration by R. Babb.)



FIGURE 1.6 The fossil antlers of *Eocoileus* (UF90400, left) bear a remarkable resemblance to extant European roe deer (right), illustrating the close relationship between the latter and all New World deer. (Photo by J. Heffelfinger.)

The oldest fossils identified as *Odocoileus* are found in Kansas and dated to the middle Pliocene (about four million years ago; Oelrich, 1953). These fossils consisted of large molars that were unmistakably *Odocoileus*, but appeared shorter and wider than the teeth of present day white-tailed and mule deer. Oelrich (1953) named this deer *Odocoileus brachyodontus*, but more recent evaluation of material attributed to this name has shown there are no characteristics to reliably differentiate these molars from those of living *Odocoileus* (Wheatley and Ruez, 2006).

New World Deer Find a New Continent

In the late Pliocene Epoch (2.7 million years ago), a shifting of tectonic plates formed the Isthmus of Panama, which joined South America to North America and facilitated the Great American Biotic Interchange (Webb, 2006). Deer did not occur in South America prior to establishment of this land bridge, but immigrating cervids found abundant resources to exploit and thus began a remarkable evolutionary radiation. From this immigration event, there was an explosive diversification of deer resulting in six genera and at least 13 species of deer currently occupying South America (Webb, 2000; Gilbert et al., 2006).

The extant forms such as pudu, pampas deer, marsh deer, brocket deer, and taruka/huemul represent an amazing diversity of morphology and ecological adaptation resulting from this radiation. White-tailed deer are sometimes cited as the source of all South American deer, but it is more likely they all derived from one or more North American ancestors. The current view is that one or more ancestral deer may have entered South America in the Pliocene.

Morphological similarities and recent genetic analysis indicate that at least two ancestral forms crossed the isthmus into South America. The first clade consists of the diminutive pudu, taruka, and huemul occupying the Andes. Taruka and huemul share morphological affinities to *Navahoceros* in that they have keeled basioccipital bone on the underside of the skull and relatively short legs indicative of mountain dwellers. The fossil record is nearly silent for pudu, but morphology and genetic analysis of both nuclear DNA (nDNA) and mitochondrial DNA (mtDNA) show they are closely aligned with the taruka and huemul meaning they probably share a common immigrating ancestor (Webb, 2000; Gilbert et al., 2006).

Another immigrant closely resembling a primitive *Odocoileus* probably represents a separate cervid to enter South America in the mid-Pliocene. This source stock eventually diversified into marsh deer, pampas deer, and red brocket deer (Webb, 2000). The rest of the brocket species (gray brockets) are genetically

very different (Gilbert et al., 2006; Duarte et al., 2008), which may indicate a Central American origin and several immigrations. The fact that white-tailed deer presently occur in South America indicates they arrived in their present form after the great cervid diversification, or that they immigrated with a more *Eocoileus*-like ancestor that evolved into marsh and pampas deer.

Duarte et al. (2008) proposed a scenario with eight different forms of cervid immigrants in the Pliocene. This analysis was based on mtDNA and sometimes mtDNA lineages do not correspond to true evolutionary lineages (Cronin, 1993). Rapid radiation and diversification in the newly colonized South American continent seems a more plausible scenario given the near lack of large ungulates and associated predators at the time. Additional analysis with nDNA markers will help tell the story of the origin of New World deer.

The Rise of White-tailed Deer

During the late Pliocene, there were at least three recognizable types of deer in North America: *Navahoceros* in the mountains, *Bretzia* in the West, and the widespread, increasingly common *Odocoileus*. Only *Odocoileus* made it out of the Pleistocene alive and emerged as the only medium-sized cervid in North America. Remarkably, fossils indistinguishable from living *Odocoileus* have been found dating back nearly four million years and the subsequent fossil record includes locations throughout most of this species' current geographic range in North America (Kurten and Anderson, 1980). *Odocoileus* had clearly found the environmentally tumultuous Pleistocene and Holocene environment (last two million years) conducive to its incredible success as a species.

White-tailed deer and mule deer are closely related and the product of the same Pliocene *Odocoileus* stock. These two forms probably started to differentiate during the early to mid-Pleistocene. Several recurring glaciation events occurred during the last two million years and produced a complicated and poorly understood pattern of geographic barriers in the northern latitudes of North America. The most likely cause for speciation of mule deer and white-tailed deer is physical isolation due to climate-induced habitat changes. These cyclical changes in the distribution of forests, shrublands, and grasslands occurred through the many glacial/interglacial changes throughout the Pleistocene. Any one of these glacial cycles lasting 10,000–100,000 years could be enough to differentiate the two species. The last Pleistocene glaciation (11,000–20,000 years before present) may have facilitated the subspecific division between mule deer and black-tailed deer, as the latter was isolated in coastal refugia of the Pacific Northwest (Latch et al., 2009).

The current geographic distribution of white-tailed deer overlaps that of mule deer in many places. This overlap represents a secondary contact between the two species after their post-Pleistocene range expansion. Where they are sympatric, hybridization has been documented (Heffelfinger, 2000), but occurs at a low rate and does not represent an ecological problem.

Unravelling the complete story of deer evolution throughout the late Pliocene/early Pleistocene (4 million years to 600,000 years ago), has been hampered by repeated glaciations that scoured the landscape for thousands of years, destroying most evidence of early North American deer evolution (Geist, 1998). Additionally, white-tailed deer and mule deer are difficult to distinguish without lacrymal fossa, certain leg bones (Jacobson, 2004), or antlers from mature males. Most materials designated as one or the other species have been done so based solely on geography or size. Because Pliocene and Pleistocene geographic ranges are not clearly known and body size is variable, most of these species assignments are suspect. A reevaluation is needed of New World deer fossils, particularly *Odocoileus* using all the information currently available (Jacobson, 2004).

With the lack of a strong fossil record, science has turned to genetic analysis to investigate the evolutionary relationships of white-tailed and mule deer. By making assumptions about the rate that a genome accumulates mutations, geneticists can estimate the time since two organisms diverged from a common ancestor (Avise, 1994). These molecular clocks are notoriously sensitive to the assumptions that are used and should be viewed with healthy skepticism. However, molecular clocks provide another way to estimate the evolutionary history of an animal. Various attempts to estimate the time of divergence between white-tailed and mule deer have resulted in a range of 750,000–3.7 million years (Baccus et al., 1983; Carr and Hughes, 1993; Douzery and Randi, 1997).

Distribution

Geographic Variation in White-tailed Deer

White-tailed deer have emerged as the most abundant and widespread of all the New World deer species. With this success and vast geographic distribution, we see phenotypic and genotypic variations throughout their range. Some of these differences are due to genetic changes brought about by isolation of some populations and others are simply examples of the phenotypic plasticity as populations in local areas adapt to habitat, forage, or climatic conditions (Strickland and Demarais, 2000, 2008).

Phenotypic variation of white-tailed deer has been expressed in discrete taxonomic subspecies, complete with multicolored maps showing well-defined distributions. Currently there are 38 subspecies of white-tailed deer commonly recognized, but many more have been described (Table 1.2). Most of these descriptions were based on only a few specimens and have not been evaluated sufficiently to determine whether they are valid. Overlap in characteristics among most deer subspecies is so great that no list of differences can be written to allow biologists to differentiate subspecies. Most authorities simply keep using these names because there is no information available to support or reject their subspecies designation. In the early years of the field of natural history, it took only a single specimen and a polygon on a map to create a subspecies. Science is a process of disproving theories and so we are stuck with our multicolored maps and nebulous descriptions until someone is able to conduct a range-wide comprehensive evaluation of subspecies using genetic, morphological, and perhaps ecological characteristics.

The current geographic distribution and genetic integrity of white-tailed deer has not escaped human influence. In addition to internal and external natural forces shaping the whitetail phenotype, humans have influenced local phenotypes by moving tens of thousands of deer back and forth across the United States. Reviewing the history of white-tailed deer translocation illustrates the folly of our current topological view of subspecies. The state of Virginia was restocked with deer from 11 states (Marchington et al., 1995). Florida, Georgia, Arkansas, Kentucky, Louisiana, Mississippi, North Carolina, Tennessee, Virginia, and West Virginia each received hundreds of deer from Wisconsin. Mississippi received at least 72 deer from Mexico (Handley, 1952). In addition to Wisconsin deer, deer from Texas were released in Florida (437), Louisiana (>167), and Georgia (1058) to restock deer habitat (Marchington et al., 1995). White-tailed deer restoration programs throughout the continent are rightly hailed as a conservation success story, but they have also gone a long way to befuddle an already poor characterization of geographic differentiation (Leberg and Ellsworth, 1999).

The whole concept of subspecies has been under attack for some time (Wilson and Brown, 1953). Subspecies' boundaries, when taken literally (as they usually are), frequently create a nonsensical pattern of geographic differentiation. For example, it is doubtful if Minnesotans find value in differentiating between the three subspecies of white-tailed deer in their state. However, in some cases, recognizing these animals as a different "race" or "ecotype" may be helpful in addressing unique conservation problems facing animals in that area. Recognizing ecotypes can aid the management of those populations by encouraging management actions that are critical, but may not be needed elsewhere. However, when the difference between geographic variants is not well documented and they are given the official status of a scientific name (subspecies), disproportionate legal repercussions may occur (O'Brien and Mayr, 1991; Geist, 1992; Cronin, 1997). For example, the Guatemalan white-tailed deer (*O. v. mayensis*) was placed on Appendix III of the Convention on International Trade in Endangered Species (CITES) in 1981. The CITES "Information Sheet" containing the reasons for listing, distribution, and description of the taxon has never been submitted. This subspecies has enjoyed international legal protection for nearly 30 years and yet it has never been described and appears nowhere in the scientific literature. This CITES designation on a nonexistent subspecies could have serious legal repercussions for anyone hunting or exporting white-tailed deer from Central America.

Increasingly, sophisticated genetic analyses are being employed to identify genetic differences among populations of a species throughout its range, and have yielded useful taxonomic guidance. In most genetic studies of geographical variation, the genetic patterns do not match previously defined subspecies (DeYoung et al., 2003; Latch et al., 2009).

TABLE 1.2
Subspecies Described for White-tailed Deer (*Odocoileus virginianus*)

Subspecies	Common Name of Subspecies	Subspecific Synonyms	Distribution	Source of Designation
<i>O. v. acapulcensis</i>	Acapulco		Pacific coast of southwest Mexico from states of Colima to Oaxaca	Caton (1877), Méndez (1984)
<i>O. v. borealis</i>	Northern woodland		Northeastern United States and southeastern Canada	Miller (1900)
<i>O. v. cariacou</i>	Brazilian		French Guiana and northeastern Brazil, South America	Boddaert (1784), Brokx (1972, 1984)
<i>O. v. carminis</i>	Carmen Mountains	<i>sylvaticus, campestris, spinosus, suacuapara</i>	Sierra del Carmen, northern Coahuila, Mexico; Chisos and surrounding mountains in West Texas	Goldman and Kellogg (1940)
<i>O. v. chiriquensis</i>	Chiriquí		Southern tip of Costa Rica and Panama, Central America	J. A. Allen (1910), Méndez (1984)
<i>O. v. clavium</i>	Florida Key		Florida Keys, Florida	Barbour and Allen (1922)
<i>O. v. couesi</i>	Coues	<i>battyi, baileyi</i>	Arizona, New Mexico, Sonora, Chihuahua, Durango	Coues and Yarrow (1875), Smith (1991)
<i>O. v. curassavicus</i>	Curacao		Curacao Island, Venezuelan Coast, South America	Hummelink (1940), Brokx (1972, 1984)
<i>O. v. dacotensis</i>	Dakota		North Central United States and South Central Canada	Goldman and Kellogg (1940)
<i>O. v. goudotii</i>	Northern Andes	<i>columbicus, lasiotis</i>	Andes Mountains in Colombia and Mérida Andean highlands in western Venezuela, South America	Gay and Gervais (1846), Brokx (1972, 1984)
<i>O. v. gymnotis</i>	Savannah	<i>savannarum, wiegmammi, tumatumari</i>	Savannahs of Venezuela, Guyana and Surinam, eastern llanos of Colombia, South America	Wiegmann (1833), Brokx (1972, 1984)
<i>O. v. hiltonensis</i>	Hilton Head Island		Hilton Head Island, South Carolina Coast	Goldman and Kellogg (1940)
<i>O. v. leucurus</i>	Columbia River		Mouth of the Columbia River, Washington and Oregon	Douglas (1829)
<i>O. v. macrourus</i>	Kansas	<i>louisianae</i>	Iowa south to Louisiana	Rafinesque (1817)
<i>O. v. margaritae</i>	Margarita Island		Isla de Margarita, Venezuelan Coast, South America	Osgood (1910), Brokx (1972, 1984)
<i>O. v. mcilhennyi</i>	Avery Island		Coastal areas of Louisiana and East Texas	Miller (1928)
<i>O. v. mexicanus</i>	Mexican Tableland	<i>lichtensteini</i>	Southcentral Mexico, encompassing Queretaro, Hidalgo, México, Morelos, Tlaxcala, Puebla and portions of surrounding states	Gmelin (1788), Méndez (1984)
<i>O. v. miquihuanensis</i>	Miquihuana		Sierra Madre Oriental in Coahuila, Nuevo Leon, San Luis Potosí and portions of surrounding Mexican states	Goldman and Kellogg (1940), Méndez (1984)
<i>O. v. nelsoni</i>	Chiapas		Highlands from Chiapas, Mexico to Nicaragua, Central America	Merriam (1898), Méndez (1984)
<i>O. v. nemoralis</i>	Nicaragua	<i>truei, costaricensis, mayensis</i>	Lowland areas throughout Central America in Belize, Guatemala, Honduras, San Salvador, Nicaragua and Costa Rica	Hamilton-Smith (1827), Méndez (1984)

continued

TABLE 1.2 (continued)
Subspecies Described for White-tailed Deer (*Odocoileus virginianus*)

Subspecies	Common Name of Subspecies	Subspecific Synonyms	Distribution	Source of Designation
<i>O. v. nigribarbis</i>	Blackbeard Island		Blackbeard Island, Georgia Coast	Goldman and Kellogg (1940)
<i>O. v. oaxacensis</i>	Oaxaca		Central Oaxaca, Mexico	Goldman and Kellogg (1940), Méndez (1984)
<i>O. v. ochrourus</i>	Northwest		Southwestern Canada and northwestern United States	Bailey (1932)
<i>O. v. osceola</i>	Florida Coastal	<i>fraterculus</i>	Northwest Florida	Bangs (1896)
<i>O. v. peruvianus</i>	Peruvian	<i>brachyceros, peruviana, philippii, peruanus</i>	Slopes of the Andes in Peru and possibly Bolivia, South America	Gray (1874), Brokx (1972, 1984)
<i>O. v. rothschildi</i>	Coiba Island		Coiba Island, Panama Coast, Central America	Thomas (1902), Méndez (1984)
<i>O. v. seminolus</i>	Florida		Florida	Goldman and Kellogg (1940)
<i>O. v. sinaloae</i>	Sinaloa		Mexican states of Sinaloa, Nayarit, Jalisco, parts of Michoacan and Guanajuato	Allen (1903), Méndez (1984)
<i>O. v. taurinsulae</i>	Bull Island		Bull Island, South Carolina Coast	Goldman and Kellogg (1940)
<i>O. v. texanus</i>	Texas		Texas north through the Central Plains	Mearns (1898)
<i>O. v. thomasi</i>	Mexican Lowland		Eastern Veracruz and Oaxaca, Villahermosa, portions of Chiapas and Campeche, Mexico	Merriam (1898), Méndez (1984)
<i>O. v. toltecus</i>	Rain Forest		Northern Oaxaca and southern Veracruz, Mexico	Saussure (1860)
<i>O. v. tropicalis</i>	Tumbesian	<i>columbicus, punensis</i>	West of the Andes along the Pacific coast of Ecuador and northern Peru, South America	Cabrera (1918), Brokx (1972, 1984)
<i>O. v. ustus</i>	Ecuador	<i>consul, abeli, gracilis antonii, aequatorialis</i>	The Andes of Ecuador and maybe southern Colombia, South America	Trouessart (1910), Brokx (1972, 1984)
<i>O. v. venatorius</i>	Hunting Island		Hunting Island, South Carolina Coast	Goldman and Kellogg (1940)
<i>O. v. veraecrucis</i>	Northern Veracruz		Southeastern Tamaulipas, Mexico and most of Veracruz, Central America	Goldman and Kellogg (1940), Méndez (1984)
<i>O. v. virginianus</i>	Virginia	<i>wisconsinensis</i>	Southeastern United States	Zimmerman (1780)
<i>O. v. yucatanensis</i>	Yucatan		Throughout Yucatan and the northern half of Campeche and Quintana Roo, Mexico	Hays (1874), Méndez (1984)

Regardless of whether one uses genetic or morphological characteristics to differentiate subspecies, the difficulty lies in delineating categories out of what is usually a continuum of differences. Animals at each end of the continuum may look different, but there is no place in between that offers a clear division. This is the crux of the subspecies dilemma. In some cases, a characteristic will change more abruptly at a point along the continuum, but the question remains, “How different is different enough?” to consider using two names (or 38!) to designate this difference. Unfortunately, there is no answer that is universally applied.

Heffelfinger (2005) and Villarreal et al. (2009) argued that creating categories for trophy record-keeping purposes could improve deer conservation. In some parts of white-tailed deer distribution, deer almost never grow antlers large enough to make the record books. Separating record book categories geographically could encourage conservation interest and funds for deer in otherwise neglected areas of their range. Especially in Central and South America and Mexico, this interest could lead to an economic benefit to local communities, who would then see local deer populations as a resource with high economic benefit to be protected and promoted. As beneficial as these categories may be for conservation, they must not be thought of as taxonomic entities (i.e., subspecies) unless defensible with morphological and genetic data.

North America

In general, the northern extent of the geographic range of white-tailed deer is limited by harsh winter conditions (i.e., deep snow), exacerbated by short growing seasons, and boreal forest that lacks large areas in early successional stages that are nutritionally important to deer (Figure 1.7a). One or two harsh winters can reduce local deer populations by half at the northern periphery of whitetail range. During these events, the remaining deer survive in pockets of the best habitat or agricultural areas and then repopulate

(a)

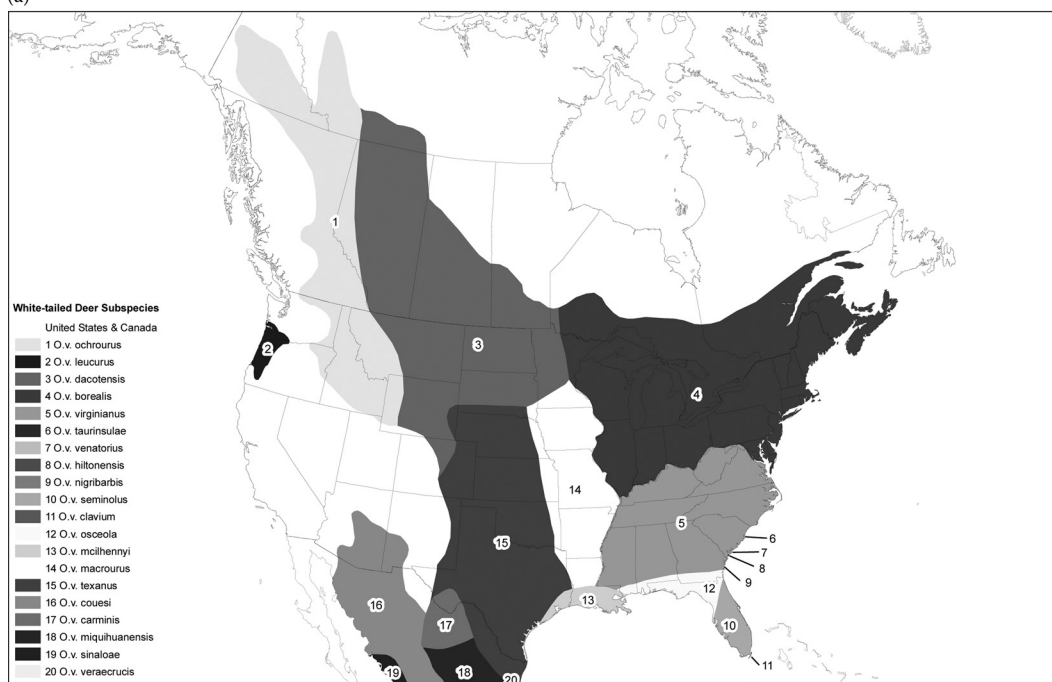


FIGURE 1.7 Distribution of white-tailed deer in the United States and Canada (a), Mexico (b), and Central and South America (c) with general areas representing the subspecies that have been described in the literature. (Cartography by C. Query. With permission.)

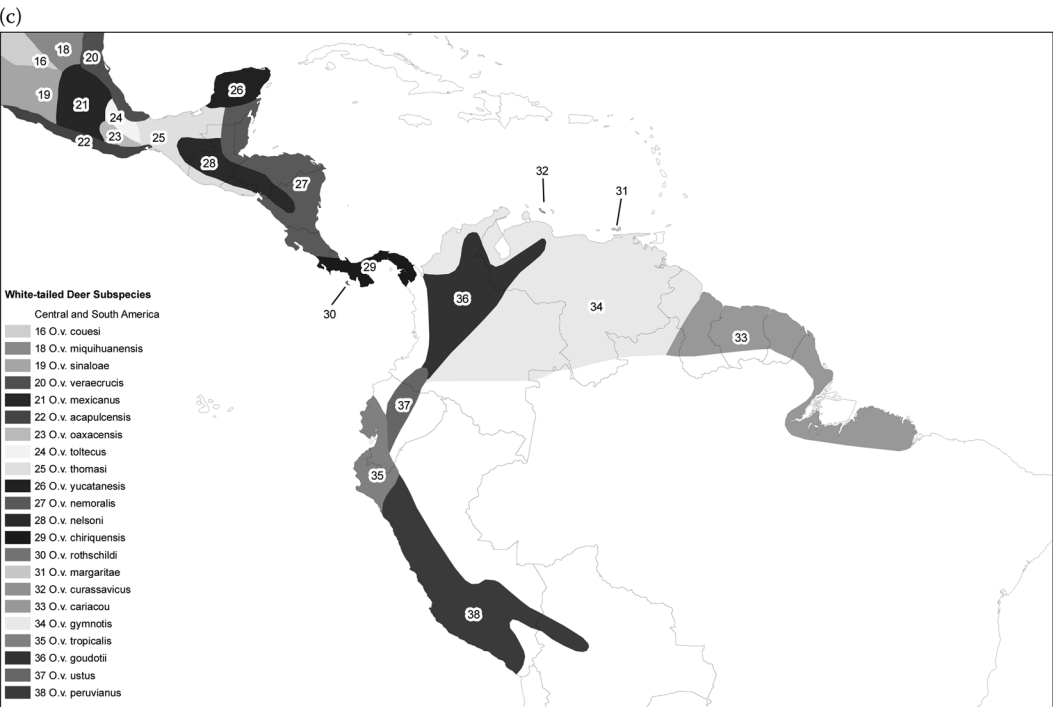
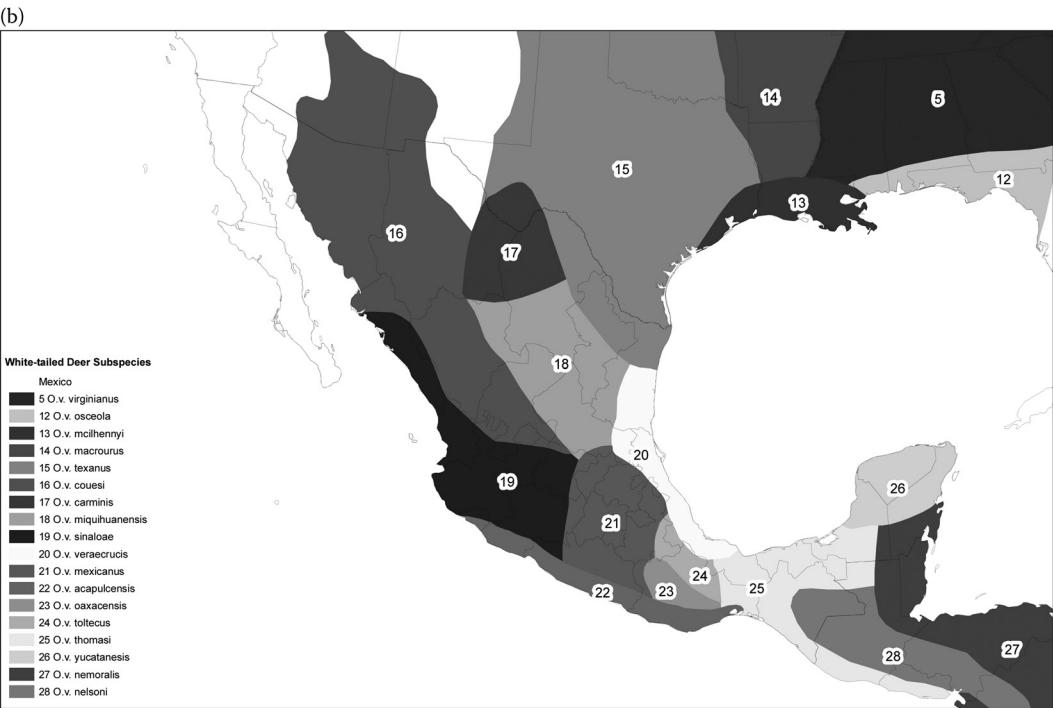


FIGURE 1.7 continued



FIGURE 1.8 White-tailed deer in the northern extent of their geographic range are much larger than their southern counterparts and their distribution is limited primarily by harsh winters. (Photo by T. Daniel. With permission.)

surrounding habitat during mild winters (A. Schmidt, Saskatchewan Ministry of Environment, personal communication). Long, severe winters in the northern latitudes are harder for deer to survive because the summer growing season is relatively short and there is less opportunity to obtain optimum nutrition for reproduction and store fat reserves to survive the winter (Figure 1.8). This combination of short summers and relatively long winters creates an ebb and flow at the northern edge of whitetail distribution and that balance can be influenced by other natural and anthropic factors.

White-tailed deer are expanding northward along their northern boundary, in part as a continuation of the post-Pleistocene range expansion of many plants and animals. However, there are many other potential factors that could be accelerating this increase in distribution in recent decades. Human alteration of forests may increase white-tailed deer survival and reproduction. Thus, timber harvest in the Boreal Forest near the edge of whitetail range could enable deer populations to exist in areas that would otherwise be unsuitable. Also, the establishment of long linear seismic lines through the forest has been implicated as a factor facilitating expansion of white-tailed deer populations (Gainer, 1995). These seismic lines are kept clear of trees and vegetate with shrubs and forbs that favor deer use (K. Morton, Alberta Fish and Wildlife Division, personal communication). Still, the effects of these forest alterations are not consistent across the northern periphery. For example, when clearcuts are replanted with trees, herbicides may be used that eliminate important hardwood browse, making the area unsuitable for deer. Fires can also have a beneficial effect on deer habitat by opening patches of closed forest and encouraging aspen and other valuable early successional plants.

Agricultural production is known to attract and hold white-tailed deer in new areas and is generally considered an important factor promoting range expansion (K. Dawe, University of Alberta, personal communication). Agriculture brings high-energy and high-protein foods that compensate for the shorter growing season. These high-quality, abundant foods allow deer to obtain the nutrients necessary not only to survive winter, but also to have the reproductive capacity for population growth when conditions are favorable. In some cases, open windswept agricultural fields offer areas of limited snow cover where deer can access food during winter and that are free of snow weeks earlier than nearby forest during spring (T. Nette, Nova Scotia Department of Natural Resources, personal communication).

A series of mild winters certainly allow for range expansion to the north because of increased survival in peripheral populations. This leads to speculation of how much of the recent expansion may be due to changes in the global climate. In the Boreal Forest it is not entirely clear whether winter severity has changed significantly during this recent expansion of white-tailed deer. Evaluation of winter severity by decade in British Columbia failed to detect any obvious patterns (Baccante and Woods, 2008). If the overall climate continues to warm significantly for the next 50–100 years, northward expansion of the white-tailed deer's range should continue (Veitch, 2001). In the southwestern United States and northern Mexico, continued warming may cause a reduction in distribution as marginal arid habitat becomes

unsuitable. There is probably little value in speculating about future distribution too much farther into the future than the next update of this book. As is frequently the case, a combination of weather and habitat changes will dictate where we find whitetails in the coming decades.

Whitetails were not a part of the native fauna in the Yukon Territory, but first appeared along the British Columbia border in 1975 and had reached Moose Creek near Stewart Crossing by 1998 (Hoefs, 2001). They remain rare, but stable, and scattered in small pockets rather than a continuous distribution as the map implies (Figure 1.7a). On the east side of the MacKenzie Mountains, in the Northwest Territories, whitetails are expanding northward. White-tailed deer were also not native to the Northwest Territories, but were reported in the early 1900s and documented more frequently beginning in the early 1960s. In 1996, a hunter harvested a healthy doe along the MacKenzie River north of Norman Wells, which is only about 100 km south of the Arctic Circle (Veitch, 2001). This represents the northernmost whitetail record in North America to date. Although still existing in scattered and small populations, whitetails are common in some areas and overall seem to be increasing in abundance (R. Gau, Northwest Territories Department of Environment and Natural Resources, personal communication).

White-tailed deer are native to southern Alberta, but became established in the Peace River Parklands in the northwestern part of the province in the 1980s (Wishart, 1984; Gainer, 1995), and now extend north farther than mule deer (K. Morton, Alberta Fish and Wildlife Division, personal communication). Whitetails do not extend as far to the north in neighboring Saskatchewan, being limited to the southern half of the province. In both Alberta and Saskatchewan, whitetails are not as common in the Boreal Forest, but have expanded in the last 10–15 years to occupy areas with hardwood forest stands or mixed forest with a significant aspen component (A. Schmidt, Saskatchewan Ministry of Environment, personal communication). Whitetails expanded northward with agricultural development, but there are also areas where agriculture stops at the Boreal Forest and whitetail distribution continues about 160 km farther north. This is marginal habitat for whitetails, where arboreal lichen has become an important source of nutrition (Latham, 2009).

To the west in British Columbia, white-tailed deer have expanded northward and westward almost to the Pacific Ocean, with a population near the town of Hope in the extreme southwestern corner of the province (G. Kuzyk, British Columbia Ministry of Environment, personal communication). Most white-tailed deer in British Columbia occur in the southeast corner with highest densities along river corridors (Mowat and Kuzyk, 2009). Extra-limital occurrences have been documented throughout much of the southcentral part of the province connecting with low-density populations in the northeast.

Whitetails are also found across the international boundary in eastern Washington and in northeast Oregon. Along the Pacific coastal area there are two main subpopulations of whitetails that are isolated in distribution from each other and from those to the east. One subpopulation occupies the mouth of the Columbia River at the Washington–Oregon border and the other is about 320 km south near Roseburg in southern Oregon. On February 19, 1806, Lewis and Clark wrote about the deer they encountered at the mouth of the Columbia River by saying “These do not appear to differ essentially from those of our country being about the same size, shape, and appearance in every respect except their length of tail which is more than half as long again as our deer” (Lewis, 1806). These Columbia River white-tailed deer (*O. v. leucurus*) were designated as a different subspecies by Douglas (1829) based on one specimen shot, but not preserved. Because everyone considered these deer to be unique and their range very limited, they were designated as Endangered Species in 1967 (Figure 1.9). Eleven years later the Roseburg population was designated to be the same subspecies as Columbia River whitetails and also became endangered by association (Smith et al., 2003).

Despite the legal designations, no one had evaluated the uniqueness of the Columbia River white-tail until Gavin and May (1988) used early genetic analysis techniques which led them to question the uniqueness of this whitetail subspecies and also identified a low level of hybridization with black-tailed deer. More recent morphological evaluation of cranial variation in these deer showed that these two endangered deer subpopulations differed from one another as much as they differed from the nearby nonendangered whitetail subspecies (Smith et al., 2003). After a robust population recovery to more than 6000 deer and acquisition of more habitat, the Roseburg population was delisted in 2003 and Oregon authorized a hunt in that population beginning in 2005. Piaggio and Hopken (2009) completed a relatively



FIGURE 1.9 Columbia River white-tailed deer have been designated as Endangered Species since 1967, but recent genetic work questions the uniqueness of this population. (Photo by J. David. With permission.)

comprehensive genetic analysis using both mtDNA and nDNA to evaluate the taxonomic status of this endangered subspecies. Their analysis of samples taken from the Roseburg area, mouth of the Columbia River, and northeastern Oregon led them to conclude that the subspecific designation of the Columbia River white-tailed deer is not warranted.

Large, cold-adapted whitetails are found in western Canada, across the prairie-dominated areas of southern Canada and the northcentral United States, into the midwestern farmland, and up through the northeastern forests. The upper Midwest is one of the most fertile areas in North America and likewise produces the most record book bucks. The four leading states for the production of bucks qualifying for the Boone and Crockett record book are: Iowa, Minnesota, Wisconsin, and Illinois, with those four states representing 39% of the top 100 entries (Boone and Crockett Club, 2005). This geographic pattern of the largest number of trophy bucks from the most fertile soils is not a coincidence.

In the northeast, white-tailed deer are distributed throughout southern Ontario, Quebec, and the northeastern United States. Whitetail distribution in parts of the northeast has shifted northward in recent years, but is probably stable at present (C. Curley, Ontario Ministry of Natural Resources, personal communication). Deer are found throughout Nova Scotia (including Cape Breton Island), and New Brunswick, but do not occur on Isles de la Madeleine or Newfoundland. Whitetails were absent on Prince Edward Island until very recently when a few whitetails appeared unexpectedly. It is not clear how they navigated the 16 km of icy waters and strong currents of the Northumberland Strait between the mainland and the island. It is not likely they walked the 12-km Confederation Bridge on to the island, but possible some were transported to the island by well-meaning people as fawns. Dispersal atop floating ice would be unusual, but this has been observed in the area (Figure 1.10). Regardless of their mode of arrival, deep snows and very little remaining forest will limit the permanent establishment of a large deer population on Prince Edward Island (T. Nette, Nova Scotia Department of Natural Resources, personal communication). Whitetails occur on Anticosti Island (Quebec), but were not native there and they did not arrive through natural dispersal. Henri Menier released about 200 deer onto the island in 1896–1897 and their population has grown to exceed 120,000 deer (Plante et al., 2004).

From a taxonomic standpoint, there is probably little physical difference among white-tailed deer across the northern portion of their range. Each population adapts to local conditions and nutrition levels, but in a broad sense, are exposed to similar environmental stresses. Minnesotans do not spend much time thinking about the three different whitetail subspecies designated in their state, nor should they.

White-tailed deer become somewhat smaller as one moves into the southeastern United States. However, Barbour and Allen (1922) evaluated skull size and pelage variation and had difficulty separating specimens of northeastern deer from others collected along the eastern seaboard as far south as the Florida peninsula. They concluded the characters used to describe these subspecies were “hardly diagnostic.”



FIGURE 1.10 White-tailed deer are occasionally seen on ice floes off the coast of New Brunswick, Canada which may play a role in dispersal to islands. (Photo by J. Mundle. With permission.)

Several studies in the southeastern United States have evaluated patterns of genetic diversity. Some early work was contradictory (Ellsworth et al., 1994; Leberg et al., 1994), but a combined and more comprehensive effort showed that deer translocations had substantial and long-lasting effects on the genetic composition of populations receiving deer (Leberg and Ellsworth, 1999). Other nearby populations were not significantly affected due to limited dispersal of translocated deer and their offspring. Early genetic work with allozymes at the Savannah River Ecology Laboratory found no significant genetic differentiation among six subspecies covering the northeast, Blackbeard Island, Florida, Texas, and Virginia (Smith et al., 1984). Other studies have found some regional differentiation among whitetails in the southeastern United States, but the genetic divisions do not match described subspecies ranges (Ellsworth et al., 1994; Leberg and Ellsworth, 1999; DeYoung et al., 2003).

On the coast of Georgia and South Carolina there are four “island” populations that have been designated as unique subspecies (Blackbeard/Sapelo, Hilton Head, Hunting, and Bull islands). Most authors have considered these valid subspecies as they are island forms and assumed to be isolated from other deer populations. However, upon closer inspection one sees that these are not discrete and completely isolated islands, but simply coastal areas separated from the mainland by a river or marshy area. These subspecies have not been evaluated comprehensively using modern genetic analyses. Leberg and Ellsworth (1999) analyzed samples from one of these four insular subspecies (*O. v. nigribarbis*) in a comparison of mtDNA among whitetails from the southeastern United States, including other islands where populations were not designated as unique. They concluded that coastal island whitetail populations retained the ancestral genetic variation lost from many southeastern deer populations because of translocations and genetic bottlenecks during times of low deer abundance. Deer on these islands are smaller than deer on the mainland (Klimstra et al., 1991), but Leberg and Ellsworth (1999) found that the islands were not genetically isolated from the mainland, which is consistent with reports that deer swim between the mainland and some of these barrier islands. These four coastal populations are worthy of conservation, but if they represent valid taxonomic subspecies, then there are potentially hundreds more undescribed subspecies up and down the Atlantic Coast.

The subspecific status of white-tailed deer inhabiting the Florida Keys (*O. v. clavium*) is unquestionable, being geographically, phenotypically, and genetically differentiated. In the 1940s, it was thought there were fewer than 50 Key deer remaining (Dickson, 1955), but their population has increased in recent decades. About 600 Key deer now occupy 20–25 islands in a 40-km stretch between Johnson and Saddlebunch Keys (Figure 1.11). Historic reports indicate they may have been distributed as far as Key West (Dickson, 1955), but most deer are now found on Big Pine Key ($n = 400$), No Name Key ($n = 100$), Big Torch, Little Torch, Cudjo, and Sugarloaf ($n = 100$) (P. Hughes, National Key Deer Refuge, personal



FIGURE 1.11 The diminutive Key deer represents a classic example of an island phenotype that has become smaller to cope with reduced forage availability inherent in an isolated existence. (Photo by M. Averette. With permission.)

communication). The northernmost Key deer are separated from the mainland by at least 48 km of open water and an even longer string of uninhabited (by deer) islands. Key deer were placed on the endangered species list in 1967 and restoration efforts are ongoing (U.S. Fish and Wildlife Service, 2008). As part of the recovery plan, a few dozen deer have been translocated from Big Pine Key to Upper Sugarloaf and Cudjo keys in an effort to assist natural dispersal.

Early studies with relatively small sample sizes documented that Key deer were smaller than other whitetails (Barbour and Allen, 1922; Dickson, 1955). They typically stand about 61 cm at the shoulder with an average weight of 30 and 40 kg for does and bucks, respectively. A more recent study by Maffei et al. (1988) using 20 measurements of about 400 Key deer skulls and mandibles showed that this population was clearly smaller from those on the Florida mainland. Analysis by age class of antlers from 501 male Key deer and 601 of their mainland counterparts in the Everglades (*O. v. seminolus*) showed Key deer antlers to be significantly smaller (Folk and Klimstra, 1991). It is not surprising that these island deer would be smaller because insular mammals, following a well-documented ecological pattern, typically adapt to a more efficient body size in response to chronically inadequate resources (Case, 1978; Brisbin and Lenarz, 1984). Few genetic studies have been done on Key deer. Small insular gene pools would be expected to have low genetic diversity and change rapidly due to their isolation, founder effect during colonization, periodic genetic bottlenecks, and genetic drift. When Ellsworth et al. (1994) analyzed mtDNA variation in 142 deer from the southeastern United States; they found that all 15 Key deer in their sample had the same haplotype that was not shared with any deer sampled from the mainland.

Deer throughout the Florida peninsula and westward along the Gulf coast to Texas have been described as three different subspecies, but none have characteristics that would clearly distinguish them as unique from other deer in the southeastern United States. One of these subspecies was first collected near Avery Island, Louisiana (*O. v. mcilhennyi*) and named after the family (McIlhenny) that produced Tabasco hot sauce there (Miller, 1928).

Three forms of white-tailed deer have geographic ranges straddling the United States–Mexico border. The Coues white-tailed deer (*O. v. couesi*; pronounced “cows”) are found in scattered populations throughout most of the southwestern United States in central and southeastern Arizona and southwestern New Mexico, and also in the Mexican states of Sonora, Chihuahua, Durango, and Zacatecas (Heffelfinger, 2006). Coues whitetails prefer oak woodland habitat between 1220 and 2440 m in elevation (Figure 1.12). This is the only form of whitetail that is recognized with a separate category in the Boone and Crockett Club record book because it is morphologically different and geographically isolated from other whitetail subspecies, except to the south where it blends into other recognized forms in Sinaloa and Central Mexico. Mature bucks of this diminutive race commonly have field dressed weights around 45 kg.



FIGURE 1.12 Coues white-tailed deer of the southwestern oak woodlands are the only whitetail subspecies recognized as a separate category in the Boone and Crockett scoring system. (Photo by G. Andrejko. With permission.)

Preliminary investigation into the genetic uniqueness of Coues whitetails has begun using a suite of microsatellite markers and early results are promising (D. Paetkau, Wildlife Genetics International, unpublished data). Because of partial geographic isolation, further analyses may reveal molecular markers that differentiate this small southwestern race from other North American subspecies.

The Texas white-tailed deer (*O. v. texanus*) occur throughout that state, but has become famous for the large-antlered bucks produced in South Texas under conservative harvest and sometimes intensive management. This deer is smaller than northern whitetails, but larger than other southwestern races with body size increasing to the north in the southern Great Plains. Texas white-tailed deer in the Great Plains have no recognizable physical differences from other adjacent mid-continent subspecies. In Mexico, the Texas whitetail occupies northeastern Coahuila, Nuevo Leon, and Tamaulipas before fading off to the West into the scattered mountain ranges occupied by the Carmen Mountains whitetail or merging into other ill-defined subspecies to the south.

The Carmen Mountains white-tailed deer (*O. v. carminis*) was first described in 1940 as being different from Texas whitetails because they were smaller and had antlers with shorter tines (Goldman and Kellogg, 1940). The original description placed them in the Sierra del Carmen in northern Coahuila and the Chisos Mountains in the Big Bend Region of Texas (Figure 1.13). Later authors and local biologists have noted that smaller whitetails also occupy other isolated mountain ranges on both sides of the international boundary (Baker, 1956; Krausman and Ables, 1981). The smaller Carmen Mountains phenotype is believed to inhabit the Chisos, Sierra Quemada, Sierra del Caballo Muerto, Chinati, and Sierra Vieja in West Texas (B. Tarrant, Texas Parks and Wildlife Department, personal communication). They have occurred in the Christmas and Rosillos mountains in the past, but apparently not in recent years. The Del Norte and Glass mountains are also reported to have Carmen Mountains whitetails at higher elevations, but larger deer resembling the Texas whitetail in the lower surrounding desert scrub. Whitetails



FIGURE 1.13 Carmen Mountains white-tailed deer occupying a cluster of small, isolated mountains in northern Coahuila, Mexico, and West Texas appear to be an intermediate form between the diminutive Coues whitetail and those in Texas. (Photo by T. Fulbright. With permission.)

are found throughout the Davis Mountains, but many of them are more similar to Texas whitetail in size (Krausman et al., 1978).

South of the border, the Carmen Mountains deer are said to occur in the Serranias del Burro, Sierra del Carmen, Sierra Encantada, Hechiceros, Sierra Santa Rosa, and Sierra Santa Fe del Pino in northern Coahuila and Chihuahua (Krausman and Ables, 1981; B. McKinney, CEMEX, personal communication). Whitetails resembling the Carmen Mountains phenotype occur in other scattered mountains to the south as far as Jaral, Coahuila (Baker, 1956), but very little work has been done to evaluate phenotypic or genetic variation in that portion of their range.

Krausman et al. (1978) recorded 15 measurements from 167 skulls and antlers representing Texas, Carmen Mountains, and Coues whitetails. Their measurements clearly showed a clinal change in skull morphology from small Coues to larger deer in the Sierra del Carmen and then a gradual increase in size northward and eastward through West Texas to the range of the Texas whitetail. Carmen and Coues whitetails were more similar to each other than to the Texas whitetail, but intergradation of body size through the region was evident. Carmen Mountains whitetails give way to the larger Texas whitetail north and east of Alpine, Texas and in Coahuila on the east side of the Serranias del Burro (Baker, 1956) and the foothills of the Sierra de Santa Rosa (C. Sellers, Rancho la Escondida, personal communication). This body size cline was recognized by Goldman and Kellogg (1940, p. 82) in the original description of the subspecies when they wrote “that complete intergradation of the two must occur along the basal slopes of the mountains.”

Most of the current geographic range of white-tailed deer in the southwestern United States and northern Mexico was pine–juniper–oak woodland until about 8000–9000 years ago when a change in climate brought in desert scrub communities and pushed the mesic woodlands to remnant “islands” in higher elevations (Van Devender, 1977). This shift occurred throughout the present ranges of Coues and Carmen Mountains whitetails, thereby isolating them across a fragmented landscape and allowing selective processes to operate on these populations independently. Today the Coues deer have a fairly continuous distribution in the Sierra Madres and the Texas whitetail has a continuous distribution in northeastern Mexico. Between these distributions is an area where an intermediate white-tailed deer occurs sparsely in a few scattered, isolated mountain ranges in eastern Chihuahua and western Coahuila. Considering geographic distribution and morphology of the deer referred to as Carmen Mountains whitetails, it seems that this is simply a series of isolated populations from a formerly continuous cline between the smaller Coues whitetail to the west and the larger Texas whitetail to the east.

In addition to the three aforementioned deer, Mexico has had no less than 11 designated subspecies, many with relatively small geographic ranges and without characteristics that are unique to deer in that area (Figure 1.7b). Mexican white-tailed deer inhabit an incredible variety of habitat conditions

throughout the country from dry deserts to mixed conifer forest to tropical rainforest with annual precipitation ranging from 25 to 280 cm/year (Mendez, 1984). Because of the great diversity of elevations and vegetation associations, white-tailed deer vary in a myriad of ways throughout the country, tending to be larger in more mesic forested conditions and smaller where nutrition is limited and a more efficient body size is advantageous. In general, deer continue the clinal body size reduction as one moves south into central and southern Mexico (Goldman and Kellogg, 1940).

Unfortunately, there have been few studies of white-tailed deer in central and southern Mexico and almost no work to clarify subspecific taxonomy (Mandujano, 2004). Mandujano et al. (2008) presented a sensible approach to recognizing geographical differences in white-tailed deer in Mexico by grouping regions of the country together into ecotypes based on vegetation associations. This approach has been used successfully in mule deer (Heffelfinger et al., 2003) and represents a logical way to improve management and conservation without relying on weakly supported subspecies taxonomy.

Central and South America

White-tailed deer distribution continues southeasterly through the Central American countries of Guatemala, Belize, El Salvador, Honduras, Nicaragua, Costa Rica, and Panama. These countries provide diverse vegetation communities from tropical forest to open savanna, but whitetails reach their highest densities in the thorn scrub and forest-savanna ecotones (Mendez, 1984). The unbroken tropical forests such as those on the Caribbean side and eastern Panama are not considered ideal for white-tailed deer and in these areas brocket deer are the more common cervid (J. Barrio, Centro de Ornitología y Biodiversidad-Peru, personal communication).

Almost no taxonomic work has been done in Central America (Gallina et al., 2010). These deer are very much like those occupying similar habitats in southern Mexico, although a higher percentage of specimens lack a metatarsal gland (Lydekker, 1898). Indeed when describing the white-tailed deer in Honduras, Hershkovitz (1951, p. 568) wrote: "Whatever the characters, the British Honduran Virginia Deer could be assigned indifferently to any one of a half dozen forms described from southern Mexico." One general trend that is evident in whitetails throughout their range is a trend toward more compressed breeding seasons in the northern extent of their range due to high seasonality. In Central America and locations further south, this breeding synchrony weakens because seasonal fluctuations are less evident (Klein, 1982; Branen and Marchington, 1987).

Whitetails are native to the 673-km² island of Coiba situated 24 km off the Pacific Coast of Panama. Now a national park, the island has been separated from the mainland for about 15,000 years. This island form of whitetail is considered a separate subspecies (*O. v. rothschildi*) and is demonstrably smaller than other Central American whitetails, rivaling the Key deer in south Florida (Halls, 1978). Whitetails are also abundant on Contadora Island, 48 km off Panama's Pacific Coast; however, this island population is the result of escapes (or liberations) from a captive herd brought from the mainland.

White-tailed deer in South America are present throughout the northern and northwestern portions of the continent (Figure 1.7c) in diverse environmental conditions ranging from islands and marshy savannas near sea level to 4200 m in the Andes Mountains. Body size of these deer is generally a little larger than those of Central America and southern Mexico (Brokx, 1984). A higher incidence of maxillary canine teeth, proportionately larger molars, and shorter tails are also characteristics that have been associated with whitetails in South America (Gallina et al., 2010). Whitetails in South America also universally lack a metatarsal gland although some may have a remnant tuft of hair in a slightly different location than North American white-tailed deer (Husson, 1960; Brokx, 1972).

Several authors have noted that all the different whitetail subspecies in South America seem to group into two ecotypes based mostly on pelage similarities shaped by environmental pressures (Hershkovitz, 1958; Brokx, 1984). One ecotype consists of the deer found in the High Andes or temperate zone and the other inhabits the lowlands. The difference between the two forms is mostly in appearance of the pelage. The temperate ecotype is sometimes referred to by the locals as Venado Gris (Gray Deer) because it has a gray coat year-round (Brokx, 1984). The lowland whitetail ecotype appears reddish-brown throughout the year.

Of the lowland ecotype, there are two island deer populations that are isolated from the mainland and have their own unique subspecies designations. Deer on Isla de Margarita (*O. v. margaritae*) off

the Venezuelan Caribbean coast are the smallest whitetails in South America and have support as a valid subspecies because of geographic isolation and demonstrated genetic (Moscarella et al., 2003) and morphological (Molina and Molinari, 1999) differentiation. Curiously, one sample from the mainland adjacent to Isla de Margarita included in the analysis by Moscarella et al. (2003) clustered with all other Margarita Island deer and not with mainland deer.

The other island population is not as clearly defined as a subspecies. White-tailed deer on the island of Curacao, 60 km off Venezuela's northwest coast, have not been evaluated taxonomically (*O. v. curassavicus*). Hummelinck (1940) described this subspecies as also occurring on the mainland on the Guajira Peninsula in Colombia. White-tailed deer remains are not present in the island's archaeological sites from Archaic Age inhabitants (prior to 500 AD), but only appear after the arrival of Caquetio immigrants sometime after 500 AD (Hooijer, 1960; Havier, 1987). By the time the Spaniards arrived on the island (1499 AD), white-tailed deer were common. Hernandez de Alba (1963) notes that Caquetios traded venison and live deer between Venezuela and the islands prior to Spanish contact. This strongly suggests white-tailed deer were not native to the island, but were introduced by this immigrating culture from the South American mainland (Husson, 1960). Caquetios transporting live deer in wooden canoes across 60 km of ocean represents the earliest known deer translocation. The population now numbers a few hundred deer and has been protected since 1931. Most of the deer are currently found on the northwest end of the island in protected areas, such as Christoffel Park. Their habitat is currently being dramatically altered by rapid housing development to support the tourism industry (J. de Freitas, CARMABI, personal communication).

The lowland ecotypes on the mainland extend from the dry deciduous forests on the northwest (coastal Peru and Ecuador) around to the northeast (Colombia through Brazil) in the more extensive open marshes and grassland savannas (llanos). These lowland deer have a thin reddish-brown summer coat similar to North American white-tailed deer, but their "winter" pelage has almost no insulative underfur. Interestingly, Brokx (1972) reported that after moving a lowland deer to colder elevations, it grew thick wooly underfur which provides some insight into the problems of using pelage as a taxonomic character.

Brokx (1972, 1984) advocated a new subspecies from the llanos of eastern Colombia and the Apure Region in western Venezuela (*O. v. apurensis*) (Figure 1.14). Deer in this region appear to have several phenotypic characteristics that differ from other lowland whitetails in northern Venezuela such as a yellow-tan pelage (due to a different banding pattern on the hairs), smaller body size, and skull characteristics (Brokx, 1972; Molinari, 2007). Interestingly, recent genetic analysis included only two samples from and adjacent to the Apure Region, but both shared a unique haplotype that was not found in any of the other samples (Moscarella et al., 2003). Even though whitetails in this area show some differentiation, it makes little sense to establish a 39th white-tailed deer subspecies without a more comprehensive taxonomic evaluation of all South American forms.



FIGURE 1.14 White-tailed deer in the Apure Region of the Venezuelan llanos face dramatically different conditions and yet are unmistakably whitetails. (Photo by W. Atkinson. With permission.)



FIGURE 1.15 The dry deciduous Tumbesian Forest on the west side of the Andes Mountains are home to a race of white-tailed deer that was originally described as having a short tail and a short brown coat year-round. (Photo by J. Barrio. With permission.)

Along the Pacific Coast, west of the Andes in Ecuador and northern Peru exists the dry, deciduous Tumbesian Forest. Another lowland form of whitetail occurs here and is characterized by short brown pelage year round and a short tail (*O. v. tropicalis*) (Figure 1.15). These whitetails are reportedly smaller than those of the llanos in Colombia and Venezuela (Brokx, 1984).

The temperate ecotype inhabits extremely high-elevation habitat in the Andes Mountains up to at least 4200 m in Colombia, Ecuador, Peru, and Bolivia (J. Barrio, Centro de Ornitología y Biodiversidad–Peru, personal communication). Separate subspecies have been designated for Colombia (*O. v. goudotii*), Ecuador (*O. v. ustus*), and Peru (*O. v. peruvianus*), but no genetic or phenotypic characteristics differentiate them. No compelling data suggest there is more than one form of white-tailed deer throughout the Andes Mountains in these countries (Brokx, 1972). White-tailed deer in the Colombian Andes do not come into contact with those in the lowlands to the east and are thus isolated (Moscarella et al., 2003). Deer in these high-elevation ranges have a more synchronous breeding season, an obvious thick gray winter coat with underfur on their body, and thicker pelage on the ears. They have a shorter summer coat, but even that appears gray. High-elevation deer weigh 52–57 kg (Molinari, 2007), which is slightly larger than lowland deer.

Distribution of white-tailed deer in the Andes is not limited by elevation per se, but by steep and arid habitat above and thick rainforest on mountain slopes below (Brokx, 1984). The extreme southern distribution of white-tailed deer is represented by an extension from southern Peru into Bolivia along a portion of the Andes. In Bolivia, white-tailed deer are found at least as far south as the village of Pelechuco, and maybe somewhat farther based on habitat (Jungius, 1974). At elevations around and above 4000 m in Peru and Bolivia, whitetails share the range with taruka (Jungius, 1974; Tarifa et al., 2001; Barrio, 2006).

Molina and Molinari (1999) compared skull and mandible characteristics of 140 Venezuelan white-tailed deer to similar published information from North America (Rees, 1969). The analysis found

substantial diversity in skull and mandible characters within Venezuela, with the Isla de Margarita and the Andes subspecies differentiated from each other and from the lowland ecotype. This is probably not surprising for a sample of skulls ranging from the small insular race to the temperate ecotype at 3650 m elevation. They also found differences between white-tailed deer in Venezuela and North America which led them to suggest that North and South American whitetails were different species. The suggestion to split whitetails at the species level was based on the presence/absence of a metatarsal gland, 13 discrete cranial–mandibular characters, and principle component analysis of mandible measurements. The metatarsal gland has been long recognized as being of little value as a taxonomic character (Lydekker, 1898; Brokx, 1972) as it is sometimes absent in Central American whitetails and has even been documented missing from Coues white-tailed deer in Arizona (Arizona Game and Fish Department, unpublished data). While the cranial–mandibular analysis illustrated a Venezuela–North America difference, data were not complete nor compelling enough for establishing three new *Odocoileus* species in South America.

Moscarella et al. (2003) compared mtDNA sequences from 26 samples representing three subspecies from Venezuela to help clarify taxonomic discussions. They confirmed a remarkable divergence among haplotypes in Venezuela and North America and genetic support for differentiation of deer from Isla de Margarita and the temperate ecotype in the Andes. However, Moscarella et al. (2003) argue that genetic differentiation was within the range of other subspecies and splitting whitetails in Venezuela into three species is not supported by the genetic data. The original analysis of Molina and Molinari (1999) was revisited by Molinari (2007) and expanded to incorporate the genetic information from Moscarella et al. (2003). However, the expanded discussion did not add substantively new information that would make a compelling case for three new species of Venezuelan white-tailed deer.

Although others have reported differences between the continents (Smith et al., 1986), a separation of *Odocoileus virginianus* at the species level with the information currently on hand would be incongruent with the level of differentiation seen in other ungulate species. Only a comprehensive analysis that includes specimens representing all recognized subspecies (not just those in Venezuela) will help answer this question. As phylogenies inferred with mtDNA can be misleading (Cronin, 1991, 1993), especially with the *Odocoileus* complex, the analysis will have to include nDNA and possibly a Y chromosome marker to be able to tell the whole story (Gallina et al., 2010). Much of the good work of Moscarella et al. (2003) and Molinari (2007) will be helpful in coming to a final resolution once additional data are available.

Extra Limital Distribution

New Zealand

Three species of bats were the only mammals native to New Zealand before human intervention. Since the arrival of Captain Cook in 1769, at least 50 mammal species have been introduced into New Zealand and of these eight nonnative deer species have become established (Harris, 1984). White-tailed deer were first introduced with two bucks and two does from Kansas in the Takaka Valley in 1901 (Whitehead, 1972). Four years later, 19 more from New Hampshire were released with two bucks and seven does going to Cook's Arm on Stewart Island, and nine more (three bucks, six does) released on the north end of Lake Wakatipu on South Island (Harris, 1984). One buck was also released in the Takaka Valley in 1905 in an unsuccessful attempt to maintain the original release.

From these releases both the Lake Wakatipu and the Stewart Island population have become established. Under protection from 1905 through 1919, they increased steadily before a hunting season was established. By 1926 it was apparent that hunting was not going to limit the population and all restrictions on harvest were lifted. The Lake Wakatipu population occupies only about 350 km² north of the lake and has been plagued by diseases and low productivity (King, 2005). It is hunted on a small portion of Aspiring National Park and on a few large properties in the area (S. Laing, New Zealand Hunting Info, personal communication).

The release on the 1720-km² Stewart Island was much more successful and deer quickly spread throughout the island. The island consists of steep slopes and ridges covered by thick forest and scrub



FIGURE 1.16 New Zealand white-tailed deer were not native to that country, but have adapted to the new environment as illustrated by these deer eating kelp on Stewart Island. (Photo by P. Peychers. With permission.)

habitat. This, and a lack of predators, provided conditions for rapid population growth and by 1926 not only were protections lifted, but a bounty was paid for every deer tail brought in. Because whitetails were not distributed completely throughout the island until the 1950s, there is some question how much damage by red deer was being wrongly attributed to whitetails. Throughout the 1930s and 1940s, government shooters killed thousands of white-tailed deer (Harris, 1984). Today Stewart Island is a popular whitetail hunting destination with 50 hunting blocks around the perimeter of the island and unlimited hunting in the central area where deer are much less common. White-tailed deer are strong swimmers and occasionally swim to some of the nearby islands such as Earnest, Pearl, Bravo, Owen, and Noble islands (King, 2005; Harper, 2006). Two other populations were established briefly in the 1990s in Canterbury, but none persist as wild populations (King, 2005; J. DeLury, Stewart Island Whitetail Research Group, personal communication).

New Zealand white-tailed deer are smaller than their source stock in New Hampshire with weights averaging 54 kg for bucks and 40 kg for does (Davidson and Challies, 1990). Interestingly, because these northern hemisphere deer are living in the southern hemisphere, their annual cycles have adjusted to be exactly the opposite of their homeland. The peak of rut is April–May and fawns are born during December–January, with twin births rare (Harris, 1984). The ever-adaptable whitetail in New Zealand has found seaweed such as kelp to be an important source of nutrition (Figure 1.16).

Finland

Wanting to present a gift to their motherland, Minnesotans of Finnish descent captured and donated three male and four female fawns to the Public Finnish Hunters Association. These seven “Virginia deer” were sent by train from (ironically enough) Virginia, Minnesota to the east coast where they were loaded on a ship during August 1934 (Kairikko and Ruola, 2005). Only one male and four female fawns survived the two-week voyage to Helsinki, Finland and the sole buck fawn was near death upon arrival. After some nurturing he recovered and was released with the does into a 3-hectare enclosure on the Laukko Estate, 170 km north of Helsinki. One of the females was blind, never produced a fawn, and was killed by a golden eagle in 1937. The other does successfully reproduced and so began the Finnish white-tailed deer herd.

Four additional deer (two males, two females) were sent from New York State in 1937 and upon arriving in autumn were placed in the Korkeasaari Zoo to be released into the wild the next spring (Kairikko and Ruola, 2005). Records are sketchy, but it does not appear any of these deer were ever released into the wild. All deer from the original translocation escaped from the Laukko enclosure in March of 1938.



FIGURE 1.17 White-tailed deer translocated to Finland in the 1930s have been tremendously successful despite originating from less than 10 founding members. Finnish white-tailed deer have distinctively dark, long noses and golden foreheads, perhaps due to this genetic bottleneck. (Photo by H. Mikkola. With permission.)

The does were enticed back in, but the buck stayed out and roamed close by until they were all released in May of that year (one buck, three does, and two male fawns). The population grew steadily in the Laukko Estate area, but authorities were concerned that all deer born in Finland were sired by the same male with only three maternal lines.

Late in 1948, six white-tailed deer (three male, three female) were flown from Minnesota to Helsinki and placed in the Laukko enclosure where two males quickly died (Kairikko and Ruola, 2005). The next spring, one buck and three does were released to join the growing population in the vicinity (about 100 deer). The population continued to grow and expand each year until the first hunting season was established in 1960 when nine bucks were harvested. The current license allows the harvest of one adult and two fawns (the latter for population control). By 2008, more than 25,000 deer were harvested annually in Finland (S. Laaksonen, Finnish Fish and Wildlife Health Research Unit, personal communication). White-tailed deer are now abundant in the southern half of Finland (Figure 1.17). To the northwest, they have reached the Swedish border, but have not become established in this area. Some white-tailed deer are even being reported just over the Russian border on the Karelian Isthmus and north near Ladoga Lake (K. Nygren, Game and Fisheries Research Institute—Finland, personal communication).

In the late 1960s and early 1970s, nearly 100 deer were translocated over several years to other areas in Finland in an attempt to expand the population. Some of these were successful, including those near the eastern border with Russia (Kairikko and Ruola, 2005). During this effort, 10 whitetails were also translocated to Russia and split between the Moscow Zoo and other locations. Some of these may have gone to the Zavidovo wildlife management area 100 km northwest of Moscow (K. Nygren, Game and Fisheries Research Institute—Finland, personal communication).

British Isles

One vague reference to white-tailed deer being released on the Scottish Isle of Arran in 1832 marks the earliest release of this species into a wild setting in Europe (Fitter, 1959). These deer are said to have thrived for a time before dying out sometime after 1872.

Woburn Park in northern England has a long history of captive deer and deer conservation. It was the 11th Duke of Bedford who saved the Peré David's deer from extinction in the 1880s by holding and propagating them in his park. Meticulous inventory records were kept of the deer at Woburn since the late 1800s. Several scientific names were used for white-tailed deer throughout the period of record-keeping, but they were universally referred to as “Virginia Deer” in the records. An entry in *A record of the collection of animals kept in Woburn Park, the property of the Duke of Bedford 1892–1905*, states “Virginian

deer *Mazama Americana* [sic] imported=140, born=44, died=145, killed=1. Present total [in 1905] 38. Date of importation=1894" (A. Mitchell, Woburn Enterprises Limited, personal communication).

For some reason the highly adaptable white-tailed deer did not fare well in Woburn Park, but when released out of the enclosure sometime before 1905 and allowed to roam free in the nearby forest, the small nucleus of animals became more numerous. In 1913, personal records kept by the Duchess of Bedford recorded only nine whitetails at Woburn Park, but noted that those outside the fence could not be counted (A. Mitchell, Woburn Enterprises Limited, personal communication). Whitehead (1950, p. 121) writes that the last white-tailed deer were seen at the beginning of World War II and since they were free-ranging in the nearby woods, "the troops occupying those areas soon exterminated them." No records of deer inventory survived the period from 1914 to 1946, but records from 1947 to the present make no mention of the white-tailed "Virginia" deer.

Since very early times there have been hundreds of deer parks and zoological gardens scattered across the United Kingdom that have exchanged deer. Many of these parks did not keep records that survived the ages so a complete reconstruction of all white-tailed deer held in captivity is not possible. An inventory of zoological gardens in 1949 recorded two male white-tailed deer in Whipsnade Park and four does (one from South America) in Regent's Park (Whitehead, 1950). As of the end of 2008, the three largest zoological parks in Great Britain: Whipsnade, Woburn Park, and the London Zoo held no white-tailed deer. There are currently no free-ranging whitetails in the British Isles.

Austria

In 1870, some white-tailed deer were translocated from the United States to the Grafenegg Castle in lower Austria. Five years later, some of those deer were then moved to an enclosure near Weidlingau and then to Vienna in 1910 (Bojović and Halls, 1984; Kairikko and Ruola, 2005). There are few details of these early translocations, but all deer seemed to disappear during the turmoil of World War I.

Czech Republic and Slovakia

Some records place the earliest releases of white-tailed deer in the Czech Republic around 1840, but no details are available (Bartoš, 1994). In 1853, seven whitetails were released in then Czechoslovakia, but it was probably not until 15 more deer, mostly from Canada, were released in 1892 and 1893 when the population really became established (Bojović and Halls, 1984; Bartoš, 1994). These deer were released into an enclosure within the Dobris forest about 30 km southwest of Prague (Czech Republic) between the Vltava and Berounka rivers. Sixteen more deer were added to this population in 1906 to bolster numbers. During the turmoil of World War I, the Dobris forest enclosure was destroyed and the deer escaped their confinement, with most remaining in the area.

To help spread white-tailed deer to other parts of the country, eight deer were translocated to a 17-hectare enclosure in Holovous (northern Czech Republic) and two others to a small pen near Košice in Slovakia. The deer at Holovous were accidentally released into the wild in 1965 (Bartoš, 1994). The main population still localized in the Dobris forest is considered well established and stable at about 700 deer (L. Bartoš, Research Institute of Animal Production, personal communication).

Poor reproduction has been typical of this population from the beginning (Bartoš et al., 2002), which has limited its ability to increase and expand as white-tailed deer have in Finland. Unfortunately, introduction of white-tailed deer inadvertently also introduced the large liver fluke to Europe. These parasites have now infected other native cervids such as red deer and are considered a major management problem (Bojović and Halls, 1984).

Serbia and Croatia

Establishment of white-tailed deer in the former Yugoslavia is a more recent accomplishment. Twenty-one deer from eastern and southern United States formed the nucleus of this effort. Seven deer were translocated from Virginia and Maryland between 1970 and 1971 and released into a 5-hectare enclosure about 15 km from Belgrade, Serbia. In 1973, two shipments from Pennsylvania and Louisiana totalling 14 white-tailed

deer arrived and were placed in an enclosure near Karadjordjeve along the Danube River in northwestern Serbia, about 120 km west of Belgrade (Bojović and Halls, 1984). Several deer escaped the enclosure and were seen in the area for many years, but no wild population persisted there (Paunovic et al., 2010).

In spring 1975, the captive populations were doing well and so they were used as source stock to increase their distribution in the region. One buck and two does were moved to the Deliblato forest east of Belgrade near the Serbian–Romanian border. Another two bucks and three does were moved to Brać, a large island on the Croatian coast of the Adriatic Sea (Bojović and Halls, 1984). In both of these new areas the deer were confined to small enclosures for at least three years and then released. A hunting season was established in 1980, an indication of the deer's success. The population at Karadjordjeve increased to at least 150 deer by 1983, but only about 40 remained in 2007. This fenced population is hunted, but annual legal harvest is only about two deer with another 10 poached annually (Paunovic et al., 2010). The current hunting season for white-tailed deer opens on September 16 for bucks, and on October 1 for does. The season closes for both sexes January 31 (Paunovic et al., 2010). Persistence of deer at the other release sites in Serbia and Croatia is unknown, but it is thought that Karadjordjeve holds the only white-tailed deer in the country. War and economic turmoil with the break-up of Yugoslavia in the 1990s diverted attention away from wildlife management.

Bulgaria

The Finnish white-tailed deer population was so productive, they sold six does and four bucks to Bulgaria in 1977. These deer were placed in the Kozy Rog area near the Greek border. After growing to 20–30 animals that population appears to be in decline or already extirpated (Whitehead, 1993).

Caribbean Islands

Cuba

White-tailed deer were introduced to Cuba around 1850. The source of these animals is not clear, but originally thought to be Mexico or the southeastern United States (DeVos et al., 1956). Emerging genetic information indicates Cuban whitetails are not from the nearby Florida Keys nor the Southeastern United States (D. Reed, personal communication). Whitetails occupy many of the forested and mountainous areas throughout Cuba (Borroto-Páez, 2009), but are more common in the eastern and western portions and a few locations in the center such as Cienaga de Zapata, Sierra Najasa, and the Escambray Mountains. There is no open hunting season for whitetails, but poaching and widespread forest clearing have caused populations to decline (R. Borroto-Páez, Instituto de Ecología y Sistemática, personal communication). White-tailed deer are strong swimmers and have populated peripheral islands such as Cayo Sabinal, Cayo Romano, Isla de la Juventud, and the Camaguey Archipelago (Borroto-Páez, 2009) (Figure 1.18).

Jamaica

When Christopher Columbus landed on Jamaica in 1494, he did not find white-tailed deer among the native fauna. Whitetails became established by accident on this 11,396-km² island. Hurricanes Allen in 1980 and Gilbert in 1988 damaged a captive facility near Sommerset Falls on the island's northeastern coast and freed the captive deer. It is not known how many escaped in 1980, but it is thought that three bucks and three does were liberated in 1988 (Chai, 2003).

Jamaica is dominated by mountains rising to more than 2134 m and covered with lush forest full of endemic species so there is great concern that white-tailed deer will overpopulate the island and cause damage to native flora and small independent farms. Some local farmers are organizing deer hunts to reduce crop damage and one community leader reports that more than 300 whitetails were killed during a three- to four-year period (Chai, 2003).

United States Virgin Islands

The U.S. Virgin Islands consist of four main islands (St. Thomas, St. John, St. Croix, Water Island) and dozens of smaller islands that are considered part of a group called the Leeward Islands. Christopher

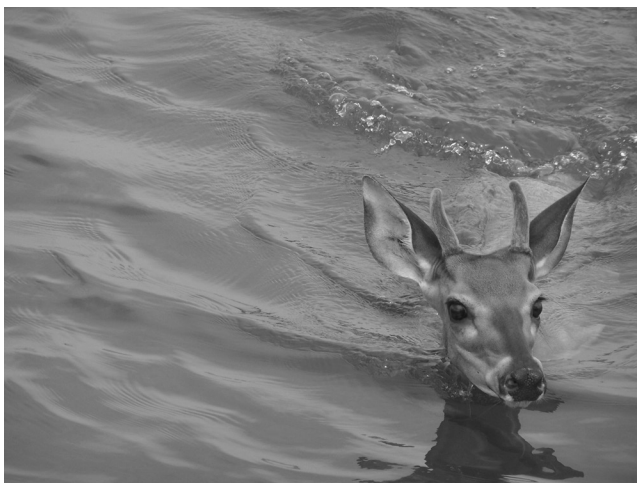


FIGURE 1.18 White-tailed deer are strong swimmers and can swim from the Cuban mainland to nearby islands and back again. (Photo by Christopher Creighton, U.S. Naval Station, Guantanamo Bay, Cuba. With permission.)

Columbus documented and named the Virgin Islands and brought them into the written record of history in 1493. Through time, the islands were claimed by many nations, but eventually became a Dutch colony in the mid-1700s. It is through an early colonial document that we first learn about white-tailed deer in this region. There is a Danish record by a ship captain that mentions five white-tailed deer being released on St. Croix during or before 1790. The nucleus of this population may have included more than the five deer mentioned, but we know that they proliferated on the island and in 1840 were said to “inhabit the mountainous parts of the island” (Seaman, 1966).

By the time the United States purchased the Virgin Islands from the Danish in 1917, there was an estimated 3000 deer well distributed throughout the 212 km² St. Croix Island (Seaman, 1966). This was probably the peak in that population because shortly after that time, commercial venison hunters started to use spotlights and buckshot at night to shoot whitetails indiscriminately. To stop the slaughter and conserve deer on the island, Governor Paul Pearson established a restrictive open season and made it illegal to kill deer outside of that season. This era of conservation was short-lived, however, with the 1938 initiation of a cattle-fever tick eradication program. In support of this program, the Governor approved a bill to eradicate all deer from the island of St. Croix (Seaman, 1966). This program only lasted until 1941 and hundreds of deer remained and persist on the island today.

In 1854, some of the St. Croix deer were moved across 56 km of open sea to St. Thomas Island. Later a few of those deer swam 6.4 km to populate St. John Island. More deer were reportedly brought from Texas and the Carolinas until there were 1000 deer estimated to be living on St. Croix and 600 on St. Thomas in 1979 (Baker, 1984).

White-tailed deer on St. John (52 km²) are found over most of the island and increasing in abundance as evidenced by recent trends in vehicle collisions and anecdotal sightings (C. Stengel, Virgin Islands NP, personal communication) (Figure 1.19). There are currently no deer on Water Island, the fourth largest of the Virgin Island complex.

St. Thomas (83 km²) is also home to white-tailed deer where they are found in pockets where there is little development. They occur in highest densities in undisturbed areas on the west end, north side, and some residential areas on the east end of the island. They swim to nearby islands and have been seen recently on St. James, Thatch, Congo, and other small islands (R. Platenberg, Virgin Islands NP, personal communication).

True to its long-term island existence, whitetails on the island weigh less than their assumed parent population in the southeastern United States. Seaman (1966) reports St. Croix bucks weighing 41–50 kg and does ranging 32–41 kg. White-tailed deer are not established on any of the British Virgin Islands (C. Petrovic, Econcerns, personal communication), but individuals may periodically swim there from St. John.

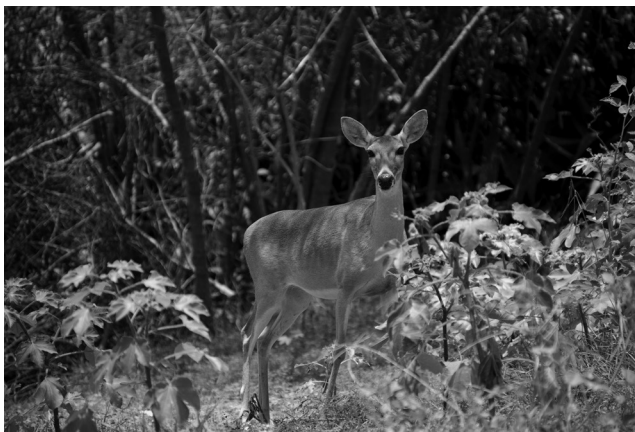


FIGURE 1.19 Despite more than 220 years of island isolation, white-tailed deer in the U.S. Virgin Islands could be mistaken for their conspecifics in the southeastern United States. (Photo by C. Stengel. With permission.)

Puerto Rico

White-tailed deer were introduced to the Puerto Rican island of Culebra in 1966. This island is only 20 km west of St. Thomas Island (U.S. Virgin Islands) and 27 km east of Puerto Rico (Philibosian and Yntema, 1977). Whitetails are still present on Culebra (mostly on the east end of the island) and on the small islands of Luis Peña and Cayo Norte (Long, 2003).

Other Islands

There are other reported translocations of white-tailed deer to various islands of the West Indies, but very few details are available. Records indicate whitetails and fallow deer were released on the islands of Antigua and Barbuda (Leeward Islands) in the seventeenth century, but today only fallow deer remain and those are on Barbuda and the small island of Guiana north of Antigua (Lever, 1985; Long, 2003). Other vague reports mention Dominica, Grenada, and the Dominican Republic as receiving white-tailed deer at some point. There is no evidence of free-ranging whitetail herds at any of these locations (Whitehead, 1993).

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Part II

Biology



2

Anatomy and Physiology

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The white-tailed deer exhibits considerable variation in anatomy and physiology across its range. Factors such as latitude, climate, and habitat influence morphological characteristics, as well as physiological adaptations that allow white-tailed deer to thrive across North and South America. In all cases, these adaptations have evolved over thousands of years in response to local selective pressures to enhance survival and productivity of the species. Detailed knowledge and understanding of anatomy and physiology is critical to the management and research of white-tailed deer. Most behavioral aspects (e.g., reproduction, foraging, predator avoidance, social interactions) of white-tailed deer are physiologically driven, and a thorough understanding of these processes requires intimate knowledge of their

physiological basis. Anatomical attributes of many internal and external structures in white-tailed deer strongly influence function (e.g., digestion, vision), and so it is also critical that managers and researchers understand anatomy as well. Finally, hunters and others who interact with white-tailed deer from a recreational perspective could increase their enjoyment of this renewable resource by understanding anatomy and physiology.

Anatomy and physiology generally correspond to local conditions and are highly predictable. However, wide-scale translocations and reintroductions have resulted in a mosaic of genetic strains across North America. For example, in the early and mid-1900s, many states across the Southeast began restocking programs to revitalize populations that had been extirpated or driven to rarity. Sources of deer used in these restocking programs were highly variable, and often translocated deer had substantially different physical or physiological characteristics than local deer. For example, from 1926 to 1998 there were 44 documented translocations of white-tailed deer in the state of Alabama (McDonald and Miller, 2004). While about 85% of these deer were relocated from populations within the state, 579 deer were moved to Alabama from Arkansas, Georgia, Michigan, Ohio, North Carolina, Texas, and Wisconsin. In all, these restocking programs involved deer from six subspecies. Deer from northern regions were larger than those translocated from instate populations. Additionally, the Alabama stock used during these restocking efforts had a traditionally late breeding season (January), which has resulted in a mosaic of physiologically driven breeding dates across the state (Causey, 1990; Gray et al., 2002). Similar patterns of varying physiology and physical characteristics are found in other states where white-tailed deer populations have become a mosaic of highly variable genetic strains. As a result, white-tailed deer anatomy and physiology may not always be predictable based solely on geography.

Physical Characteristics

Pelage

The pelage of an adult white-tailed deer is normally a uniform reddish-brown to gray on the head, back, sides, and legs. During summer, the coat thickness is light with little underfur, and typically the coloration is red or rust. However, as cold weather sets in, white-tailed deer grow their winter pelage which is brown intermixed with gray, is generally thicker than the summer coat, and has a well-developed underfur layer. White fur is found on the abdomen and chest, the inside of the legs, around the chin, inside the ears, and on the underside and edges of the tail. Some adult deer have a defined white throat patch that may be continuous with white fur under the chin. Markings on the neck and face may vary considerably among deer. Most deer have some black hair immediately posterior to the nose pad, and then a patch of white hair immediately posterior to the black. Both the black and white hair posterior to the nose pad may continue onto the lower jaw. There is normally some white hair around the eyes, with the remainder of the hair on the head and neck being brown. Variation in facial markings can often be used to uniquely identify individual deer. Other areas on the body that may exhibit unique color patterns are the back of the ears and tail. Some deer will carry the prototypical red-brown color on the back of the ears and tail, while others will have black.

Fawns are born with a cryptic, camouflage coloration. The base color is red or brown with white spots 1–2 cm in diameter along the back and sides. There is normally a line of white spots from the neck to the base of the tail on each side of the spine. This coloration enables the bedded fawn to blend into its surroundings because spots break up the fawn's outline and mimic patches of sunlight filtering through vegetation. The spots begin to fade after about two months of age and normally are not visible after four months. In many cases, fawns will retain a reddish hue during winter, as opposed to adults that replace their reddish summer pelage with brown or gray fur. Observant sportsmen can sometimes use this difference in coloration to help classify deer during the hunting season.

While most white-tailed deer exhibit the pelage coloration pattern described above, occasionally individual deer are found to be all, or partially, white (Newsom, 1937; Taylor, 1956; Ryel, 1963; Hesselton, 1969; Martin and Rasmussen, 1981). Albinism is a rare recessive trait in which individuals exhibit white pelage and pink eyes because of a lack of pigmentation in the eyes, skin, and hair. Although very rare



FIGURE 2.1 A white-tailed deer buck with melanistic pelage. Notice the lack of white hairs around the head, neck, chest, and legs. Compare the coloration to that of a normal white-tailed deer on the right. (Photo by J. T. Baccus. With permission.)

in natural populations, the frequency of albinism in a population can increase due to inbreeding (Smith et al., 1984) or laws that protect white animals from harvest (Martin and Rasmussen, 1981). More common than albinos are partially white or piebald deer. These deer have variable amounts of white pelage across the body but lack the pink eyes that are a defining characteristic of true albinos. Smith et al. (1984) reported that less than 1% of deer in hunted populations are piebald. The low frequency of white, or partially white, deer in natural populations has been attributed to increased susceptibility to predators and to such deer having a greater incidence of physical deformities such as dorsal bowing of the nose, short legs, scoliosis, or short mandibles that increase the likelihood of death at an early age (Davidson and Nettles, 1997).

Even rarer than albinos are melanistic white-tailed deer (Rue, 1978). Melanistic animals lack distinctive variations in color such as brown or white pelage and are dark or even black across the majority of the body (Figure 2.1). In white-tailed deer, melanistic individuals normally are black across the entire body, with the exception of white hairs on the ventral surface of the tail extending onto the anal region and on the tarsal and metatarsal glands (Baccus and Posey, 1999). Melanistic deer may have a distinctive darker mid-dorsal stripe that extends from the head to the tail. Baccus and Posey (1999) described semimelanistic deer as those who retain the typical white pelage patterns (e.g., face, neck, tail, and ventral surface) of nonmelanistic deer, but black hairs have replaced the reddish-brown to gray hues that normally cover the rest of the body. Melanistic deer have been documented in Texas (Smith et al., 1984; Baccus and Posey, 1999), Wisconsin (Wozencraft, 1979), South Carolina, Michigan (Rue, 1978), Pennsylvania (D'Angelo and Baccus, 2007), Idaho (Severinghaus and Cheatum, 1956), and New York (Townsend and Smith, 1933). Melanism is a genetic morphism that coexists with typical color morphs in temporary or permanent balance such that this condition may occur in the same locale on a semiregular basis (Ford, 1945). Although melanism is extremely rare, Baccus and Posey (1999) reported an incidence of 8.5% of melanistic white-tailed deer in eight counties in central Texas.

Fetal Development

Gestation in white-tailed deer is approximately 200 days, although gestation lengths have been reported as short as 187 days (Haugen, 1959) and as long as 213 days (Verme, 1969). By about 37 days of gestation, the period of tissue differentiation and organ development is complete, and what was once considered an embryo is now a fetus (Armstrong, 1950). External pinnae become apparent between 58 and 65 days of gestation and pigmentation of the skin first becomes apparent between 79 and 95 days. Spots appear on

the fetus at about 145 days, pigmentation and hair patterns are complete by 160 days, and by 180 days the fetus has all the appearances of a neonate (Short, 1970). Fetal development is curvilinear, such that 75–80% of fetal growth occurs during the last trimester (Armstrong, 1950). Peak energetic costs of gestation during the third trimester are 84% greater than fasting metabolic rate (Pekins et al., 1998). This pattern of fetal growth is referred to as delayed development, which ensures that the greatest nutrient demands of gestation generally occur when forage availability is adequate, rather than during winter (Robbins et al., 1975). From about 40 days after conception until parturition, fetal growth is highly predictable (Soprovich, 1992), and measures of fetal development such as forehead-rump measurements can be used to accurately estimate age, and consequently conception dates (Hamilton et al., 1985).

Neonates and Fawns

At birth, white-tailed deer weigh from 1.8 to 4.1 kg (Trodd, 1962; Verme, 1989) depending on litter size, geographic region, and maternal nutrition. Small neonates have a difficult time suckling due to less physical strength and endurance, and many studies have documented positive relationships between birth mass and survival in ungulates (Clutton-Brock et al., 1982; Fairbanks, 1993; Sams et al., 1996).

Litter size in white-tailed deer is normally one or two, and the average litter size of adult deer in a healthy population ranges from 1.6 to 1.8 (Roseberry and Klimstra, 1970; Wilson and Sealander, 1971; Haugen, 1975; Johns et al., 1977; Jacobson et al., 1979; Kie and White, 1985; Rhodes et al., 1985; Ozoga, 1987; Verme, 1989). Triplets are not uncommon in white-tailed deer and litter sizes of four and even five have been reported (Trodd, 1962; Van Deelen et al., 2007). Litter size is associated positively with female age (Table 2.1). Younger does tend to have smaller litter sizes because of the competing demands of growth and reproduction, and normally, fawns do not reproduce unless they are in exceptional nutritional condition. The high nutritional demands of producing twin fawns normally results in lower birth mass per fawn compared to singleton litters (Verme, 1963). For example, male and female singleton fawns in Michigan averaged 4.1 and 3.9 kg, respectively, while twin males and twin females averaged 3.7 and 3.5 kg each, respectively (Verme, 1989). Male and female fawns from mixed-sex litters averaged 3.6 and 3.4 kg, respectively. In most ungulate species females differentially invest in male fetuses, which results in greater birth weight of male offspring (Clutton-Brock et al., 1982; San José et al., 1999; Adams, 2005). Clutton-Brock et al. (1981) speculated that females in polygynous mammals invest greater resources in sons than daughters during gestation because of the greater potential reproductive success of sons relative to daughters, and the influence that birth mass has on lifetime reproductive success in sons.

Gestation is a productive process that requires nutritional resources beyond those needed for maintenance of the body. Therefore, females in better condition or on a higher nutritional plane will have greater resources available for investment in productive processes, and the result will be larger fawns at birth. Verme (1963) found during experimental trials that does with adequate nutrition and in good condition produced fawns that were 11% greater in mass on average than does that had experienced

TABLE 2.1

Litter Size of Female White-tailed Deer in Relation to Age at the Time of Breeding

State	Doe Age at the Time of Breeding				References
	0.5	1.5	2.5	≥3.5	
Illinois	1.00	1.76	1.90	1.93	Roseberry and Klimstra (1970)
Manitoba	1.14	1.34	1.91 ^a		Ransom (1967)
Minnesota		1.30	1.80 ^a		DelGiudice et al. (2007)
Mississippi	1.00	1.40	1.66 ^a		Jacobson et al. (1979)
New York	1.26	1.58	1.84 ^a		Hesselton and Jackson (1974)
South Carolina	1.06	1.56	1.73	1.76	Rhodes et al. (1985)

^a Mean number of fetuses is for does that are ≥2.5 years of age.

nutritional restriction during gestation. A variety of factors including climate, deer density, habitat quality, doe age, and prior reproductive output can influence the nutritional status of gravid does. Climatic factors such as extreme winter can negatively influence resources available to does and result in lower birth weights (Verme, 1965). Mech et al. (1987) speculated that climatic influences on maternal condition can be cumulative over a number of years, and periods of nutritional restriction that occurred several years previously may still negatively influence reproduction. Additionally, Mech et al. (1991) surmised that climatic influences can be multigenerational and reported that fawns born to does whose mothers experienced harsh winters during gestation had greater probability of mortality due to wolf predation. Low birth weights of mothers that had experienced reduced prenatal growth due to harsh climatic conditions during gestation negatively influenced prenatal and/or postnatal growth of their offspring.

Population density (Kie and White, 1985) and habitat quality (Rhodes et al., 1985) strongly influence food availability and reproduction in white-tailed deer. Young females (fawns or yearlings) normally produce fewer fawns or fawns with lower birth mass than prime-aged does (Roseberry and Klimstra, 1970; Jacobson et al., 1979; Rhodes et al., 1985; Verme, 1989). Younger deer must balance the competing nutritional demands of reproduction and growth, and cannot invest the same resources in reproduction as older does (Rhodes et al., 1985). Reproductive expenditures (e.g., gestation, lactation) during the previous year can also negatively influence the condition of a doe and result in reduced productivity (Cheatum and Severinghaus, 1950; Verme, 1967).

Postnatal growth of fawns is a function of maternal nutrition and milk production. Lactation is probably the most costly activity among any mammalian species; the nutritional demands of lactation far exceed those of gestation (Moen, 1973; Robbins, 1993). Postnatal growth of fawns will be influenced by litter size (e.g., competition with siblings for milk), milk production of the dam, and, like all other aspects of reproduction, by population density, habitat quality, and climatic factors. Verme (1989) reported that by three months of age, singleton fawns could weigh up to 5 kg more than twin fawns. This trend was particularly apparent among fawns born to 2-year-old does; older does seemed better able to obtain nutrients required to sustain lactation for twin fawns. These data suggest, like birth weights, that nutrient demands of growth in young does compete with lactation and thereby negatively influence fawn growth. In cases where poor maternal condition negatively influences birth weight and one fawn of a pair dies shortly after parturition, the remaining fawn may exhibit a growth rate greater than twin fawns of does in better condition because of greater availability of milk (Verme, 1963). Male fawns exhibit greater growth rates than female fawns (Verme, 1989), which is partly a function of greater milk consumption because of more and longer suckling bouts relative to females (Clutton-Brock et al., 1981).

Subadults and Adults

Body mass and size vary considerably in both subadults and adults across the range of white-tailed deer. Body size in white-tailed deer tends to be associated positively with latitude. This general tendency holds true for adult males and females, yearlings, and even fawns. For example, body mass of yearling bucks ranges from less than 30 kg in parts of Texas to over 50 kg in many northern states (Table 2.2). Adult body mass follows similar patterns. Mature, male white-tailed deer in northern regions may exceed 180 kg, but body mass commonly ranges from 60 kg to over 100 kg across most of their range (Sauer, 1984). Subspecies, habitat quality, age, season, genetic quality, and other factors may also influence body size in adult deer. The smallest subspecies of white-tailed deer is the Key deer, found only on a group of small islands off the southern coast of Florida. At one year of age, bucks weigh only 19.1 kg and does weigh only 16.7 kg (Hardin et al., 1984). Geographic isolation to islands and the resulting ecological and evolutionary pressures associated with island populations have likely influenced the body size of this subspecies.

The body size of adult deer is generally attributed to effects of genetics, nutrition, and other factors such as disease and injury. However, a recent study has suggested that other less obvious factors may influence adult body size. Mech et al. (1991) originally proposed that nutritional effects can be multigenerational in white-tailed deer, and found that regardless of nutrition through life, the nutritional conditions experienced by the grandmother of a deer may influence life-history traits throughout that individual's life. Recently, Monteith et al. (2009) reported convincing evidence that multigenerational

TABLE 2.2

Eviscerated Carcass Mass (kg) of Yearling Male and Female White-tailed Deer in North America

Location	Males		Females		References
	n	Mass	n	Mass	
Texas					
Edwards Plateau	101	25.7	36	23.8	Teer et al. (1965)
Llano Basin	43	24.4	146	23.0	
Florida	253	41.5 ^a			Shea et al. (1992)
Georgia	18	31.4	8	27.1	Wentworth et al. (1992)
Mississippi					
Coastal Flatwoods	138	34.9	199	28.5	Strickland et al. (2008)
MS River Delta	4164	47.5	6104	37.5	
South Carolina	131	43.9 ^a	372	37.3 ^a	Ditchkoff et al., unpublished data
Oklahoma	250	36.8	94	32.0	Ditchkoff et al. (1997)
Tennessee	NA	42.6 ^c	NA	35.6 ^c	Jenks et al. (2002)
Kentucky					
Central	NA	50.5	NA	40.3	Dechert (1967)
Western	235	43.6	60	37.0	Feldhammer et al. (1989)
Missouri					
Northeast			214	44.3	Stoll and Parker (1986)
Southern			34	34.1	
Illinois	88	44.8 ^b	114	36.6 ^b	Roseberry and Klimstra (1975)
West Virginia					
Eastern	451	35.9	295	32.7	Gill (1956)
Western	436	47.7	417	41.3	
Ohio					
Northwest	531	56.1	244	47.1	Tonkovich et al. (2004)
Southeast	824	48.3	468	42.2	
Michigan	42	61.2 ^a	50	54.3 ^a	Ozoga and Verme (1982)
New York	166	37.9	144	35.9	Severinghaus (1955)
			71	43.5	Hesselton and Sauer (1973)
Minnesota	278	50.2	55	44.0	Fuller et al. (1989)

^a Whole-body mass.^b Eviscerated carcass mass was calculated from whole-body mass using regression equations from Roseberry and Klimstra (1975).^c Reported figures are an estimate of data described in graphical format in the literature.

nutritional effects influence the body size of white-tailed deer. In the wild, deer from southwestern South Dakota are about 30% smaller than their counterparts in agricultural areas of eastern South Dakota; antler size is also smaller in these animals. In captivity, first-generation animals from these same genetic stocks showed these same patterns in body size, even though they were all raised on high-quality food in similar conditions. However, second-generation males from southwestern South Dakota attained body mass and antler size approaching that of second-generation captive males from the eastern part of the state (Figure 6.7). These data suggest that nutritional restriction takes several generations to overcome, and body size of individual deer may be strongly influenced by nutritional conditions during that deer's life time and the nutritional plane of its mother and perhaps grandmother.

Adult male and female white-tailed deer display different patterns of growth into adulthood. By two to four years of age, females normally attain maximum body size, while males increase in body size well past this age (Figure 2.2). This general pattern is apparent across the white-tailed deer's range. Growth patterns differ between males and females because of differences in reproductive strategies

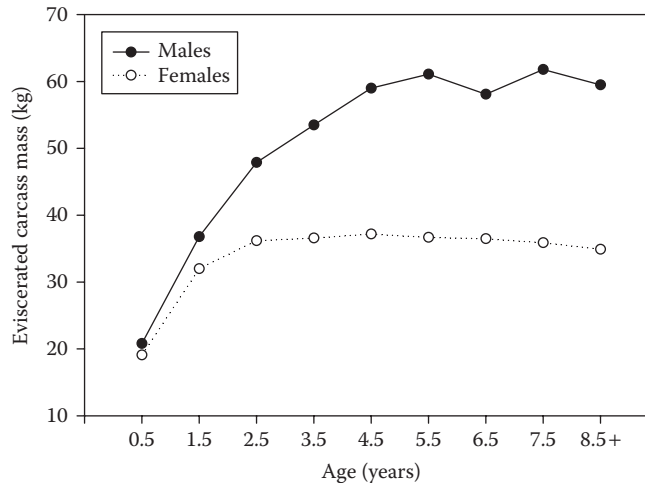


FIGURE 2.2 Eviscerated carcass mass of adult male and female white-tailed deer harvested at the McAlester Army Ammunition Plant in southeast Oklahoma during a period of quality management from 1989 to 1996. (Data from deer in Ditchkoff, S. S. et al. 1997. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 51:389–399.)

and patterns of reproductive success between the sexes. In white-tailed deer and other polygynous species, female body size does not influence breeding opportunity: small females will be bred just as readily as large females. Thus, there is little advantage, from a reproductive perspective, for a female to invest resources to increase body size. Instead, reproductive success of female deer and survival and reproductive success of their offspring benefit from resources invested in offspring during gestation and lactation. Because fawn birth mass is associated positively with survival (Sams et al., 1996), resources diverted by a doe from adult growth to fetal development improve the chance her fawns will survive. The energetic costs of gestation are 16.4% greater than the energetic requirements for non-pregnant does (Pekins et al., 1998), and thus pregnant females cannot afford to put resources toward adult growth if reproduction is a priority. Reproductively active females also need to cope with the cost of lactation. In terms of energy and nutrients, lactation is two to three times more costly than gestation (Robbins, 1993). Moen (1973) reported that the energetic cost to a female with twins at the end of gestation was 1.64 times the basal metabolic rate (BMR), and at the peak of lactation was 2.3 times the BMR. Reproduction is a long-term investment for females, and lifetime reproductive success will ultimately be a function of resource investment. Because a doe's ability to acquire nutrients and support reproduction is partially a function of body size, young does are forced to balance the costs of growth with those of reproduction, and litter sizes are reduced in younger does. When nutrient availability is limited, females will adopt a strategy that favors their own survival, reproductive potential, and growth over that of their offspring (Therrien et al., 2007). In these cases, fawn growth rates and survival will be less than normal.

In contrast to females, males continue to increase in body size until five years of age or older. Reproductive success in males is a function of their ability to acquire breeding opportunities. Male breeding success will be a function of dominance, and dominance is at least partially driven by body size. In short, larger males will acquire more breeding opportunities than smaller-bodied males, and hence have greater reproductive success. In contrast to females, males have the luxury of being able to divert resources to growth without compromising reproduction. In fact, their reproductive success is dependent upon this allocation of resources. Those males who are more efficient at or are better able to allocate resources to growth will achieve greater lifetime reproductive success than their counterparts. Additionally, larger males may benefit by being able to store greater energy reserves, enabling them to spend more time searching for and tending mates and less time searching for food during the breeding season. Because large males already possess a body size that allows them to effectively compete for

breeding opportunities, they have the luxury of diverting resources to energy stores. In contrast, younger, smaller males must continue to invest in body growth at the expense of fat deposition because they do not yet possess a body size that enables them to effectively compete for potential mates. As a result, their effort during the breeding season will be limited by competing demands of feeding and searching for mates.

Senescence

Declines in productivity, body mass, antler size, or physical and physiological condition with advancing age are evidence of senescence, and it is generally believed that white-tailed deer begin to senesce by 10 years of age. Although understanding senescence is important for predicting population dynamics in herds with low adult mortality, few studies have examined senescence in white-tailed deer. DelGiudice et al. (2007) examined fertility in free-ranging female white-tailed deer through 15 years of age and found no measurable reduction in the number of young produced per female. Similarly, Masters and Mathews (1990) found that does greater than 10 years of age exhibited little evidence of reproductive senescence. Mech and McRoberts (1990) reported no evidence of declines in body mass of female deer up to 12 years of age. There are few data available for male body mass at older ages. The probability of mortality increased after six years of age in female deer (DelGiudice et al., 2002, 2006) and at a similar age in male deer (Ditchkoff et al., 2001c; Webb et al., 2007). Increased mortality at older ages is likely a function of nutritional decline due to dentition wear and the subsequent increase in susceptibility to other mortality factors. Misrepresentation of productivity or the presence of extremely old deer in population models likely has little measurable impact for most populations because very few animals live past 10 years of age. However, in populations that have older age structures because hunting is either tightly controlled or absent, old individuals could influence population productivity (Masters and Mathews, 1990).

Exocrine Glands

Seven glands or regions of enhanced glandular activity have been identified in white-tailed deer (Figure 10.4). Glands in white-tailed deer are important during olfactory communication, and may communicate information such as sex, social status, reproductive status, individual identity, genetic characteristics, and condition (see Chapter 10). Tarsal glands are located on the medial surface of the hind legs at the tarsal joint. Metatarsal glands are located on the outside of each hind leg 10–15 cm above the hoof. Quay (1971) noted regional variation in the development of metatarsal glands. North of the Mexican border, almost all deer exhibit fully developed metatarsal glands, whereas the frequency of deer exhibiting metatarsal gland development in populations south of the United States ranges from 0% to 94%. Interdigital glands are located on both the front and rear legs between the hooves. Substances secreted by the interdigital, tarsal, and metatarsal glands are believed to serve as kairomones to some tick species (Carroll et al., 1998; Carroll, 2001). The presence of these secretions on the ground and vegetation may assist ticks in identifying ambush sites and locating deer hosts. Additionally, Wood et al. (1995) found that interdigital gland secretions in mule deer have antimicrobial properties and speculated that these secretions may serve as a defense mechanism against microorganisms.

Preorbital glands are found on the lower-front portion of the eye (Sauer, 1984). The forehead region of deer contains large numbers of apocrine glands. Activity of and secretions by these glands appear to be greater in males than females, and greater in dominant than subordinate males (Atkeson and Marchinton, 1982). Preputial glands are located on the ventral surface of the prepuce, and have been described by Odend'hal et al. (1992) as enlarged sebaceous glands that are normally associated with a hair follicle. Nasal glands are located within the haired skin of the lateral wall of the nostrils (Atkeson et al., 1988). Nasal glands, unlike the other glands described here, do not appear to function in chemical communication. The chemical composition of some deer glands and the association of these compounds with age and sex have been reported (Gassett et al., 1996, 1997).

Reproductive Physiology

Females

Endocrinology

White-tailed deer are seasonal polyestrous breeders, with a breeding season during autumn to early winter across most of their range. Timing of the breeding season is linked to photoperiod, and as such, there is a general continuum in breeding season timing associated with latitude. Deer in more northern regions tend to breed in November, whereas the breeding season in southern regions may be as late as January or February (Verme and Ullrey, 1984) (Figure 16.1). Melatonin serves as a physiological calendar for white-tailed deer and other mammals. Melatonin is produced during periods of darkness by the pineal gland, and as the day length decreases from summer to autumn, production and circulating levels of melatonin gradually increase. When melatonin levels reach a critical concentration, a series of hormonal events ensue.

Hormonal control of estrus is governed by the hypothalamus, the anterior lobe of the pituitary, and ovaries (Figure 2.3). A few days prior to ovulation, melatonin stimulates the hypothalamus to release gonadotropin-releasing hormone (GnRH). This surge of GnRH causes a sharp increase in the production of luteinizing hormone (LH) by the anterior pituitary, which is responsible for stimulating ovulation. Plotka et al. (1980) noted that serum LH was no more than 1.0 ng/mL, except for the day of ovulation when the mean concentration was 26.4 ng/mL. Knox et al. (1992) found that LH levels ranged from 35.0 to 60.1 ng/mL on the day of ovulation, but also noted that LH concentrations were slightly elevated in the days preceding ovulation and, in some study animals, were elevated prior to entering estrus. They described these LH surges as pre-estrus peaks associated with the termination of seasonal anestrus. Following ovulation, corpora lutea develop and produce progesterone, which is essential for the development and maintenance of the uterine environment during pregnancy. Prior to ovulation, serum progesterone is normally less than 2 ng/mL, but increases to more than 5 ng/mL following ovulation (Plotka et al., 1977).

Estrogen is produced by the ovaries, and its role in reproduction is multifaceted. The rise in estrogen during the days prior to estrus serves to stimulate breeding behavior and development of the uterine environment for receipt of a fertilized embryo. Estrogen levels are normally 5–30 pg/mL during the month preceding estrus (Plotka et al., 1980; Knox et al., 1992), and peak at or near the day of estrus. Following estrus, estrogen concentrations decline, but slowly rise throughout gestation and peak at parturition (Plotka et al., 1977), serving as a signal to the female body that parturition is approaching.

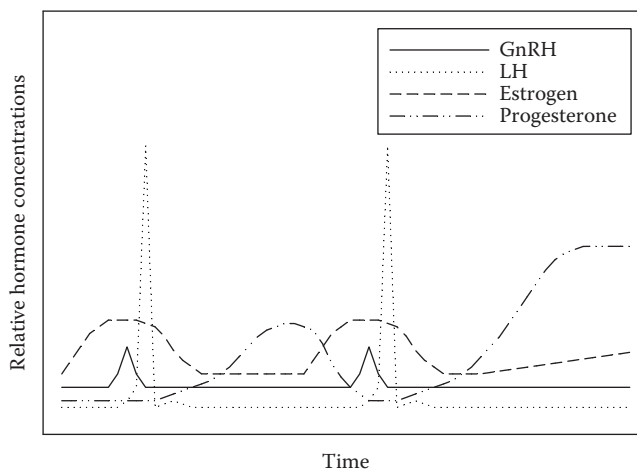


FIGURE 2.3 Timing and pattern of hormone production in adult, female white-tailed deer during the estrous cycle. Peaks in LH concentration occur at ovulation, and sustained elevated concentrations of progesterone following the second ovulation are representative of pregnancy.

If a female fails to become pregnant during an estrous cycle, she will enter estrus again 21–30 days later. This cycle of recurrent estrus in deer may repeat up to seven times before the female stops cycling and enters anestrus (Knox et al., 1988). If pregnancy does not occur, the corpora lutea will decrease in size, and progesterone concentrations will decline about seven days prior to the next ovulation (Plotka et al., 1980). When the ratio of progesterone to estrogen reaches a critical level, GnRH will once again trigger a surge in LH, which will lead to ovulation.

Fertility control in white-tailed deer is based largely on understanding the endocrine control of the reproductive cycle. The three primary approaches to reducing fertility in deer include hormonal implants, contragestational agents, and contraceptive vaccines. Norgestomet and levonorgestrel, synthetic derivatives of progesterone, have both been studied for use in white-tailed deer. These compounds simulate hormonal conditions of pregnancy and prevent ovulation. DeNicola et al. (1997a) reported that norgestomet could be effective at reducing fertility rates in white-tailed deer, while White et al. (1994) had limited success in reducing the fertility of deer with levonorgestrel implants. Prostaglandin $F_{2\alpha}$, a contragestational agent that acts on the corpus luteum to cause luteolysis, can also reduce pregnancy rates in deer (DeNicola et al., 1997b; Waddell et al., 2001). Another approach to reduce fertility is by blocking the GnRH pathway. GnRH agonists prevent GnRH from binding to receptors in the anterior pituitary and subsequently stop production of LH and other hormones essential for ovulation. GnRH agonists are effective at reducing pregnancy rates in deer (Miller et al., 2000; Baker et al., 2004), but may also cause behavioral changes because GnRH is the initial hormone responsible for stimulation of the behavior and physiology of reproduction.

Porcine zona pellucida (PZP) has received the most attention as an immunocontraceptive in recent years (Turner et al., 1996; Miller et al., 2001; Walter et al., 2002; Locke et al., 2007). The zona pellucida is a glycoprotein coating that surrounds the cell membrane of an oocyte and is involved in sperm binding. When PZP is injected into a female, her immune system mounts an immunological defense against the foreign material and, concurrently, against her own zona pellucida, thereby preventing pregnancy. The greatest advantage of immunocontraceptives compared to other approaches to fertility control is that they do not alter hormonal balance, and thus cause associated negative side effects. While many feel that these forms of fertility control show promise as tools to reduce overpopulated herds of white-tailed deer, inherent limitations associated with remotely delivering these compounds to enough deer to have a measurable impact on herd productivity preclude use in most areas (Warren, 1995; Muller et al., 1997). The greatest limitation of these compounds is that they are not effective if delivered orally, and thus require much time and money to administer.

Lactation

Near the end of gestation, the anterior pituitary produces prolactin, which signals the mammary tissue to begin development. This stage in the reproductive cycle is a critical, yet often overlooked aspect of deer population productivity. Production of milk is a defining characteristic of a mammal and a critical stage in the development of young. Neonatal development and survival is largely a function of milk consumption, and fawns that consume inadequate quantities of milk have reduced growth rates and survival. The first few days of a neonate's life are critical with regard to milk consumption. Additionally, immune system health is dependent upon adequate milk consumption during the first 24 hours because colostrum is present in the milk during this period. Colostrum is comprised of large numbers of immunoglobulins representing antibodies present in the maternal blood at the time of birth. This passive transfer of immunity from doe to fawn is the fawn's first line of immunological defense. Immunity to additional pathogens will be acquired as the fawn is exposed to novel immune challenges. When colostrum transfer is compromised, gamma globulin levels in neonate serum are generally lower, and the probability of mortality is elevated during the first 21 days of life (Sams et al., 1996). When the immune system is compromised in neonates, they are more susceptible to parasitic infection, and levels of tumor necrosis factor- α (TNF- α) may be elevated (Ditchkoff et al., 2001a). Elevated TNF- α stimulates the mobilization of peripheral energy reserves in support of metabolic demands associated with an inflammatory response. Thus, inefficient nursing during the time of colostrum transfer in fawns with low birth mass may lead to immune system deficiencies (Sams et al., 1996; Ditchkoff et al., 2001a).

Milk production is often limited by the high nutritional demands placed on the lactating female. As a result, there is considerable variation in the quantity of milk produced as a function of a female's condition and ability to acquire the necessary nutritional resources. White-tailed deer milk ranges in water content from 66.5% to 77.8%, in protein from 10.1% to 11.5%, in sugar from 2.2% to 3.0%, and in ash from 1.6% to 1.8% (Silver, 1961). Fat content varies from 7.5% to 18.0% and is greatest near weaning. Undernutrition of the female during lactation has a greater impact on milk production than milk composition. In most cases, milk composition is not affected.

Secondary Sex Ratios

At birth, the sex ratio of fawns is approximately 1:1, and yet several theories that describe differential investment of mothers in sons and daughters have been put forth. Trivers and Willard (1973) suggested that females in good condition should invest in sons, whereas females in below average condition should produce daughters. The differential cost of producing sons and daughters, and variation in potential lifetime reproductive success of well-nourished and undernourished sons and daughters is the basis of this theory. Verme (1983) reported that the opposite holds true in white-tailed deer. More male offspring tend to be produced by younger females, females in poor condition, and females in poor-quality habitat, the opposite of what would be expected according to Trivers and Willard (1973). Observations of females in good condition producing more daughters than sons have been explained by the local resource competition hypothesis (Clark, 1978), the advantaged daughter hypothesis (Hiraiwa-Hasegawa, 1993), and the advantaged matriline hypothesis (Leimar, 1996). The local resource competition hypothesis suggests that a female should produce the dispersing sex when in poor condition to reduce competition for resources. The advantaged daughter and advantaged matriline hypotheses suggest that mothers are better able to influence reproductive success in daughters than sons, and thus should invest in daughters when in good condition. Date of conception may also influence the sex of offspring and further complicate interpretations of fawn sex ratio data. For example, the ratio of male versus female offspring varied throughout the birthing period in Michigan (Saalfeld et al., 2007) (Figure 2.4), and females in Alabama produced 54–55% male offspring during the first half of the birthing season and only 47% males after the peak of birth (Ditchkoff et al., 2009; Figure 2.5). Early-born males have a developmental advantage over late-born males that could translate into variation in lifetime reproductive success; the effect of this developmental advantage on lifetime reproductive success of females would not be as dramatic.

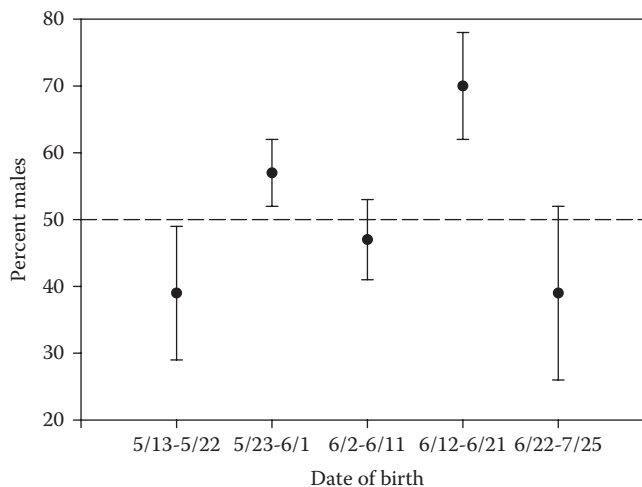


FIGURE 2.4 Fetal sex ratios of white-tailed deer from the Cusino enclosure, Michigan from 1973 to 1984. (Data from Saalfeld, S. T. et al. 2007. *Canadian Field-Naturalist* 121:412–419.)