

## Moose

*Alces alces*

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## NOMENCLATURE

COMMON NAME. Moose in North America, elk in Eurasia

SCIENTIFIC NAME. *Alces alces*

SUBSPECIES. Moose are in the suborder Ruminantia, infraorder Pecora, family Cervidae, subfamily Odocoileinae, and tribe Alcini. *Alces* (Gray 1821) is a monotypic genus with four subspecies recognized in North America (Peterson 1952, 1955; Hundertmark et al. 2003). The Alaskan moose (*A. a. gigas*) occupies Alaska, United States, and western Yukon Territory, Canada. Moose in southeastern Alaska appear distinct from other subspecies based on their mitochondrial DNA, but traditionally have been classified with *A. a. gigas* (Hundertmark et al. 2003). The northwestern moose (*A. a. andersoni*) occurs from British Columbia to Ontario in Canada and into the northern tier of the lower United States. Shiras moose (*A. a. shirasi*) inhabits mostly mountainous areas of southern British Columbia, northeastern Washington, Idaho, Montana, and Wyoming, and now also occurs in Colorado and Utah. The eastern moose (*A. a. americana*) occurs from Ontario eastward to the Atlantic seaboard (Fig. 45.1). Franzmann (1981) provided a complete taxonomic account of *Alces*, including synonyms.

## EVOLUTION AND DISTRIBUTION

*Alces* likely evolved in Eurasia during the early Pleistocene (about 1.5 million years ago) with a direct lineage from *A. gallicus* to *A. latifrons* to *A. alces* (Lister 1993). Although *A. alces* may have existed in Europe as early as 100,000–150,000 years ago (Lister 1993), remains of *A. latifrons* from Beringia may be as recent as 35,000 years old (Guthrie 1990, 1995). Thus, *A. latifrons* may have been isolated from *A. alces* and persisted for much longer in Beringia than in Eurasia.

*Cervalces* (= *Alces*) *scotti* occurred in North America from as early as 100,000–200,000 to 11,000 years ago. Those mooselike cervids (stag moose) are not thought to be progenitors of modern moose (Lister 1993), and likely diverged from *A. latifrons* during the Wisconsinan glaciation. The earliest remains of modern moose (*A. alces*) in Alaska date from only about 9700 years ago (Guthrie 1990). Thus, *A. alces* colonized the New World via the Bering land bridge during the late Pleistocene. Moose then likely dispersed down an ice-free corridor between the Cordilleran and Laurentide ice shields into suitable habitat south of the ice, which still covered much of the north (Bowyer et al. 1991; Hundertmark et al. 2003). Glaciation clearly played an important role in the evolution of moose in North America, but not in the manner previously proposed. Several hypotheses forwarded to explain differences in subspecies of moose in North America require that *A. a. gigas* be separated from the other subspecies by the Wisconsinan glaciation (Peterson 1955; Kelsall and Telfer 1974; Bubenik 1998; Geist 1998). Those hypotheses, however, are not consistent with the late dates for *A. alces* in Alaska and their absence south of the ice sheet, and, consequently, do not provide an adequate explanation for subspeciation of moose in the New World (Bowyer et al. 1991; Hundertmark et al. 2002, 2003).

Systematics of moose are complicated further by European moose possessing a karyotype of  $2n=68$  (Gustavsson and Sundt 1968),

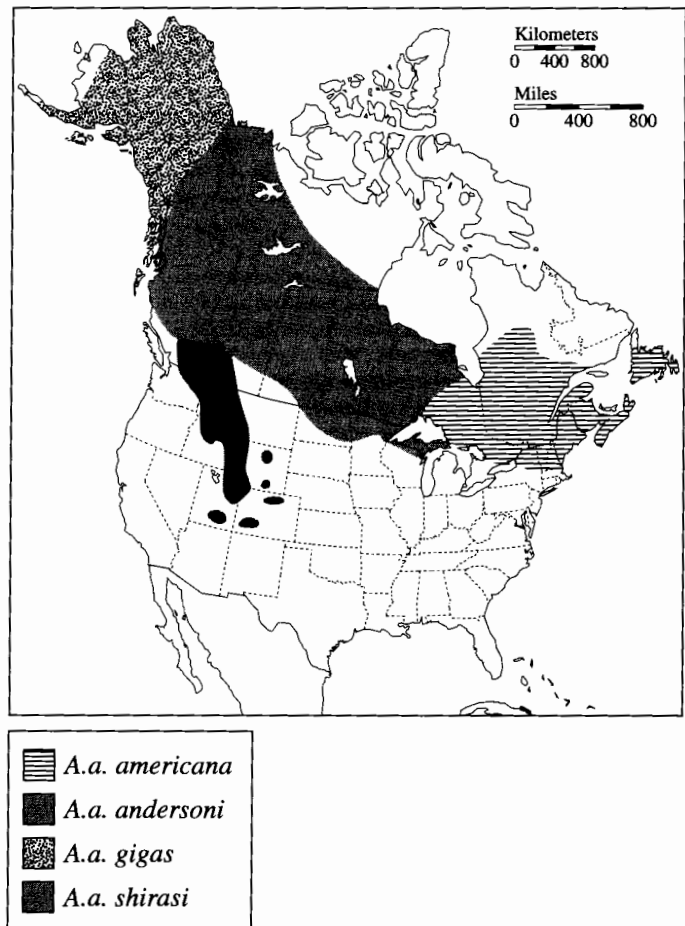


FIGURE 45.1. Distributions of subspecies of moose (*Alces alces*). Intergradation is common along zones of contact between subspecies. SOURCE: Data from Hall and Kelson (1959), Hall (1981), Peek and Morris (1998), and Franzmann (2000).

whereas moose from North America are typified by  $2n = 70$  (Hsu and Benirschke 1973). Moreover, North American moose have a 75-base pair indel in their mitochondrial control region thought to be lacking in European moose (Mikko and Andersson 1995). Those differences have led to speculation that a back-colonization occurred in moose from North America to the Russian Far East (Coady 1982), or that moose on opposite sides of the Bering Strait were separate species (Boeskorov 1997). Recently, however, the North American indel was documented for moose inhabiting eastern Asia (Boeskorov 1993, 1997; Udina et al. 2002; Hundertmark et al. 2002), indicating that moose colonizing the New World were a subset of the races occurring in Asia. Thus, moose occupying opposite sides of the Bering Strait are best characterized

as distinct subspecies, which are not closely related; morphological similarities between those subspecies are the result of convergent evolution (Hundertmark et al. 2002, 2003). Moreover, the hypothesis that a double migration of the New World occurred from Asia (Bubenik 1998) is not supported by genetic relationships among subspecies of moose (Hundertmark et al. 2002, 2003). Evidence indicates, however, that moose colonizing the New World across the Bering land bridge underwent extremely rapid evolution, with differences in morphology and behavior evident among subspecies developing in about 10,000 years (Bowyer et al. 1991). Moose in the Alexander Archipelago in southeastern Alaska probably colonized that area via movements down major river corridors from interior British Columbia, Canada (Hundertmark et al. 2003), rather than from the south following retreat of the ice sheet, as did many other mammals (Klein 1965). Those moose are genetically distinct from *A. a. gigas* in Alaska and *A. a. shirasi* and *A. a. andersoni* in British Columbia; indeed, mitochondrial DNA indicates differences among all subspecies of moose (Hundertmark et al. 2002, 2003).

Moose are a prominent component of boreal landscapes throughout the Holarctic. In North America, these large herbivores are associated with forests dominated by spruce (*Picea*), fir (*Abies*), and pine (*Pinus*) (Telfer 1984; Karns 1998). Likewise, moose may occupy tundra where suitable forage is plentiful or occur in mountain zones with a more open overstory than in dense taiga. Fire plays a crucial role in the ecology of moose, with populations tracking forest succession in many areas (Peek 1974a; Bangs and Bailey 1980; Loranger et al. 1991; Weixelman et al. 1998). Forage and snow cover likely influence the northern distribution of moose, whereas a hot climate may limit their distribution to the south (Kelsall and Telfer 1974; Renecker and Hudson 1986; Karns 1998).

Moose populations are stable or increasing throughout North America; estimates compiled by Karns (1998) indicate about 939,000 moose in 1960 and 975,000 moose in 1990. Timmermann (In press) estimated about 973,000 moose in 2001. Their geographic range recently has expanded southward down the Rocky Mountains (Smith 1985) as well as down the east coast of the United States (Peek and Morris 1998). Historical records on the distribution of moose are summarized in Seton (1927) and Peterson (1955). Translocations have aided the expansion of moose in some areas (Pimlott 1961; Burris and McKnight 1973; Dodds 1974; Duvall and Schoonveld 1988; Aho and Hendrickson 1989; Franzmann 1998; Olterman and Kenvin 1998).

## DESCRIPTION

Numerous accounts describing the biology of moose are available (Murie 1934; Peterson 1955; Houston 1968; Krefting 1974a; Franzmann 1978, 1981; Coady 1982; Bowyer et al. 1997; Franzmann and Schwartz 1998; Franzmann 2000). Moreover, the journal *Alces* is dedicated to understanding the biology and management of moose. Those sources, as well as other publications referenced in this chapter, provide additional information and relevant citations for this unique mammal.

The moose is the largest extant member of the Cervidae. Adult males have massive palmate antlers, which typically are absent in females. Indeed, like many polygynous ruminants (Weckerly 1998; Loison et al. 1999a), moose exhibit extreme sexual dimorphism, with males being >40% heavier than females (Schwartz et al. 1987). *A. a. gigas* is the largest subspecies of moose (including subspecies in Eurasia). In North America, *A. a. andersoni* is next largest, followed by *A. a. americana*, and *A. a. shirasi*.

Adult moose have long legs supporting massive bodies with a pronounced shoulder hump. Their nose is disproportionately long and slightly pendulous compared with that of other cervids, and they have an overhanging upper lip with a small, inverted triangular area of bare skin. Moose have long ears (250 mm) and short tails (80–120 mm). Moose also have a long dewlap of hair-covered skin, termed the bell, which hangs beneath their neck (Bubenik 1983; Miquelle and Van Ballenberghe 1985). Among adults, bells become shorter with age. Especially long bells may freeze off during winter (Franzmann 1981; Timmermann et al. 1985, 1988). Unlike those of most other cervids,

the ears of male moose are positioned above the main beam of the antlers. The neck of male moose swells markedly in preparation for the mating season (rut). Moose may appear awkward and ungainly until they are observed negotiating tussock tundra or deep snow; their gait and smooth movement attest to their unique adaptations to a northern environment.

Moose have a suborbital (lacrimal) gland below each eye and, compared with other cervids, have small tarsal glands on the inside of their hind legs. They lack metatarsal glands on the outside of their legs (Franzmann 2000). Moose have four mammae. Contrary to most published accounts, however, moose have interdigital glands (Chapman 1985). Unlike *Odocoileus* and *Rangifer*, moose lack nasal glands (Atkinson et al. 1988). Sokolov and Chernova (1987) described the morphology of the skin.

**Pelage.** Young are born with a reddish-brown pelage, which lacks spots or other markings more typical of adults. Coloration of pelage for adult moose varies among subspecies, with *A. a. gigas* possessing a shiny black rump patch, which extends forward toward the withers. Legs are black with white "stockings"; pelage across the back and down the sides can be dark gray to grizzled brown (Bowyer et al. 1991). Adult males have darker facial hair than do females (Timmermann 1993). Adult females possess a line of white hair around the vulva, which can be used to identify them during aerial surveys (Mitchell 1970; Roussel 1975). A white color morph of moose that is not an albino has been described (Franzmann 1981). White moose may give birth to normal-colored young (Armstrong and Brown 1986). Moose molt in spring and acquire a coat of short, shiny hair. They grow their winter pelage by late September. Winter pelage is characterized by long (20 cm), hollow guard hairs and a substantial undercoat, which provides excellent insulation (Franzmann 1981). The pelage becomes gradually lighter during winter as hairs become bleached and broken. *A. a. shirasi* and *A. a. americana* are much darker and less distinctly marked than *A. a. gigas*, with *A. a. andersoni* possessing intermediate pelage characteristics. Franzmann et al. (1977) discussed mineral composition of moose hair.

**Weight and Measurements.** Male *A. a. gigas* may attain >770 kg and females >570 kg in body weight when mature. Males achieve asymptotic body weight by 8 years old, whereas females typically do so by 4 years of age (Schwartz et al. 1987). Other subspecies are smaller (Breckenridge 1946; Blood et al. 1967; Doult 1970; Schladwieler and Stevens 1973; Peterson 1974; Sæther 1985; Quinn and Aho 1989; Lynch et al. 1995). Substantial annual variation occurs in body weight, especially for males, which may lose 12–18% of their weight during rut (Schwartz et al. 1987), when they become hypophagic for about 18 days (Miquelle 1990). Moose may lose 20–55% of their maximal body weight attained in autumn by late winter (Franzmann et al. 1978); a maintenance diet cannot be obtained by feeding on browse in winter (Schwartz and Renecker 1998; Spalinger 2000). Karns (1976) and Haigh et al. (1980) correlated body measurements with weights of moose. Hundertmark and Schwartz (1998) provided equations for predicting body weight from body measurements and indices of condition, and Hundertmark and Schwartz (2002) predicted body fat from bioelectrical impedance. Adult female *A. a. gigas* averaged 302 cm in body length and 201 cm in chest girth, and were 182 cm high at the shoulder (Franzmann et al. 1978). Sexual dimorphism also occurs in the morphology of phalanges and the metapodials (Iregren 1985). Regional variation can occur in skeletal measurements of moose even within the same subspecies (Crête 1988).

Mean birth weight for male *A. a. gigas* was 18 kg, with females weighing about 2 kg less. Average weight of twins was 3–4 kg less than singletons (Keech et al. 2000). By 10 months of age, female Alaskan moose had attained a mean body weight of 148.9 kg (Keech et al. 1999). Mean total body length was 205.7 cm and mean metatarsus length reached 50.3 cm. Neonates with low body weight at birth remained among the smallest individuals in their cohort 10 months later (Keech et al. 1999).

**Skull and Dentition.** Facial bones of moose skulls are elongated in comparison with those of other cervids (Fig. 45.2). Frontal bones, which support antler pedicles in males, are anchored to the parietal with an unusually strong suture, which likely helps support massive antlers and strenuous forces placed on the skull during rutting activities (Bubenik 1998). The orbits protrude from the skull and possess a pronounced supraorbital rim; moose undoubtedly have a wide-ranging view of their surroundings. Nasals are relatively short with a space between those bones and the anterior edge of the premaxillae, which likely was associated with the development of a muscular and somewhat prehensile nose (Bubenik 1998). The maxilla is long and slender; the vomer is V-shaped and separates the nasal cavity into two chambers. Turbinate

bones are well developed, and probably indicate enhanced olfactory capabilities (Bubenik 1998). The lower mandible narrows distally toward the front teeth and possesses a distinct diastema, which separates the front teeth from premolars and molars. Diastema length is correlated with the total length of the skull (Peterson 1955). Moose exhibit sexual dimorphism in their cranial development (Bartowskiwicz 1987).

Moose possess hypsodont cheek teeth, with enamel and dentin interfolded to help reduce wear from browsing on woody vegetation; premolars and molars are broad. The typical dentition of moose is I 0/3, C 0/1, P 3/3, M 3/3. Moose normally lack upper incisors and canines. Supernumerary incisiform teeth have been reported (Peterson 1955; Steele and Parana 1979), as have rudimentary upper canines (Bubenik 1998), though both are rare. The lower incisors and incisiform canines bite against a callous pad in the upper jaw. Breadth of incisiform teeth reaches an asymptote at about 4 years of age in males and females. Moose have a much narrower muzzle relative to their body weight than do other ruminants, which likely relates to their feeding selectively on browse (Spaeth et al. 2001). Tooth eruption and replacement of deciduous teeth (incisors, canines, and premolars) have been used to determine age in moose (Peterson 1955; Peterson et al. 1983; Hindelang and Peterson 1993). The first permanent incisors may erupt by 6 months of age, the first molars emerge at 4–6 months, second molars at 10–13 months, and the third molars by 16–19 months of age. By 16–19 months, all premolars have been replaced and full permanent dentition has been attained (Peterson 1955). Thereafter, tooth wear may be used to estimate age of moose. Nonetheless, tooth wear and breakage of incisiform teeth (Smith 1992) can be exacerbated in populations at high density feeding on coarse foods, leading to early senescence (Young and Marty 1986; Hindelang and Peterson 1994; Bowyer et al. 1999a). Counts of cementum annuli are thought to provide a more accurate estimate of age than patterns of tooth wear and eruption (Sergeant and Pimlott 1959; Wolfe 1969; Gasaway et al. 1978; Haagenrud 1978), but also may be influenced by effects of population density on physical condition in cervids (McCullough 1996).

**Antlers.** Male moose possess the largest antlers of any living cervid, attaining weights of up to 35 kg (Bubenik 1998); antlered females are rare (Wishart 1990). Antler growth, size, and conformation are dependent on a combination of genetics, age, and nutrition (Goss 1983). Antler abnormalities can be caused by injury to growing antlers or to other parts of the body during antlerogenesis, as well as by abnormal hormone levels (Bubenik 1998). Accessory antlers occasionally occur in moose (Bubenik and Hundertmark 2002). Antlers of moose in North America are strongly palmate (palmicorn), with *A. a. gigas* possessing a “butterfly” configuration involving the main palm and brow palm, which is absent or less evident in other subspecies (Gasaway et al. 1987). Antler size and body weight are correlated among cervids (McCullough 1982; Sæther and Haagenrud 1985; Bowyer 1986; Solberg and Sæther 1994; Stewart et al. 2000). Accordingly, size of antlers at maturity generally follows patterns of body size noted for subspecies of moose in North America, with *A. a. gigas* possessing the largest antlers and *A. a. shirasi* the smallest. Although nutrition affects the size and confirmation of moose antlers, clear differences in the size of antlers exist among subspecies of moose (Gasaway et al. 1987; Bowyer et al. In press).

Antlers are regrown and cast each year. During antler growth, which may begin as early as March in large males, antlers are covered with skin and short, fine hair referred to as “velvet,” and are highly vascularized and innervated—paths of blood vessels can be seen in the hardened antler following shedding of velvet in late August. Antlers are among the fastest growing of all vertebrate tissues and during June and July, when most growth occurs, may increase in length by nearly 2.5 cm each day (Van Ballenberghe 1983a). Antler thrashing of trees and shrubs coincides with velvet shedding, and strips of velvet may be removed during that dominance display (Fig. 45.3); sometimes males consume the shed velvet (Van Ballenberghe and Miquelle 1996). Hardened antlers are composed of an outer layer of compact bone and an inner core of cancellous bone. Growth and ultimately mineralization occur as osteoblasts build on a cartilaginous matrix. Demands for calcium

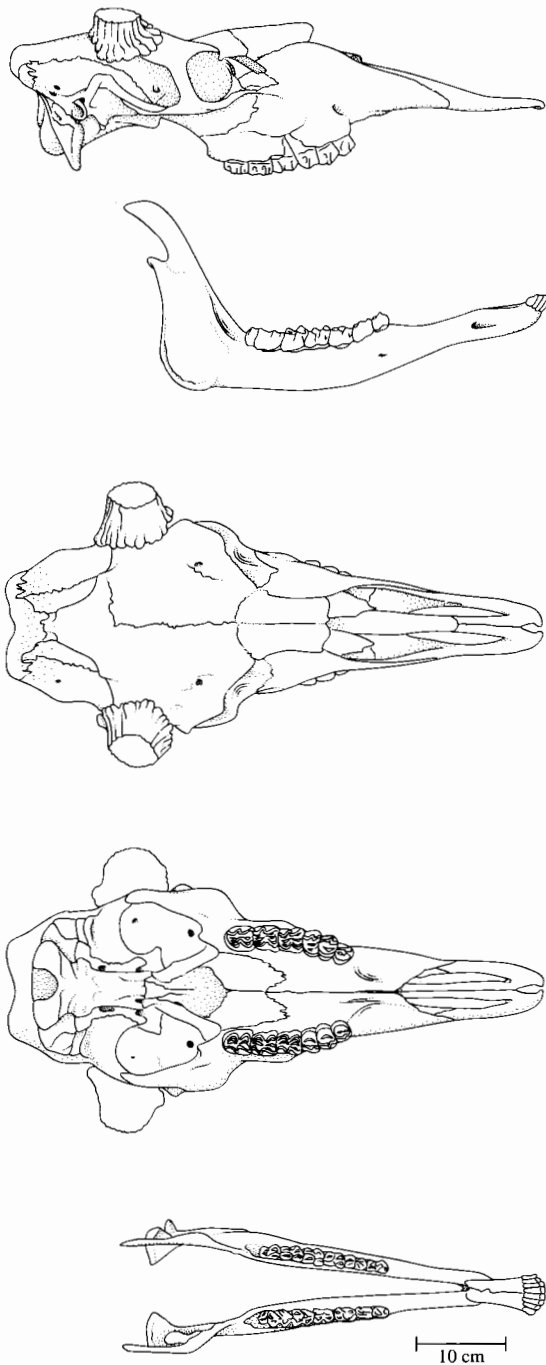


FIGURE 45.2. Skull of a male moose (*Alces alces andersoni*). From top to bottom: lateral view of cranium, lateral view of mandible, dorsal view of cranium, ventral view of cranium, dorsal view of mandible.



FIGURE 45.3. Antler thrashing by a male moose (*Alces alces gigas*). This behavior is a dominance display used to intimidate rivals. The primary function of antler thrashing is not shedding of velvet; although velvet may be stripped away during this aggressive activity, antler thrashing continues long after velvet shedding is completed. SOURCE: Photo by V. Van Ballenberghe.

and phosphorus (deposited in a ratio of about 2:1) are high during mineralization of antlers (Moen and Pastor 1998), and may be provided by temporary decalcification of the skeleton (Hillman et al. 1973). Such high demands for those minerals may result in osteoporosis in moose (Hindelang and Peterson 1996, 2000; Hindelang et al. 1998).

Following the mating season (rut), large males may begin antler casting as early as late November, with most large males having completed that process by early January. The phenology of the antler cycle in moose differs by age class, with larger, older males typically growing, shedding velvet, and casting antlers earlier than their smaller, younger counterparts (Table 45.1).

Casting of antlers likely is achieved by osteoclasts demineralizing bone at the distal ends of the pedicles, thereby allowing the antlers to drop off. Blood sometimes is observed on the pedicle immediately following casting. Antler pedicles usually are obvious in young moose by their first autumn, and some males may produce a small, mineralized area at the tip of the antler (Bubenik 1998). Thereafter, sets of antlers grow rapidly in size each year until maximal size is attained at 7–11 years old, with a subsequent senescence in antler size through about 18 years of age (Bubenik et al. 1978; Gasaway et al. 1978; Bowyer et al.

TABLE 45.1. Generalized phenology of the moose antler cycle in Alaska

Time Period	Phenological Event
Late March	Initiation of antler growth by mature males
Mid-April	Last casting of antlers by small-antlered males
Late April	Mature males with antlers in stalk plus bulb stage; up to 25 cm of new growth evident
Mid-May	Some nonyearling males with no obvious new growth; mature males with small palms forming
Early June	Midpoint of growth period for mature males; antlers about 25% grown
Late June	Some yearling males with about 15 cm of new growth
Early July	Antlers of mature males about 75% grown
Late July	Some yearling males still in stalk plus bulb stage
Early August	Antlers of mature males 90–95% grown
Mid-August	Termination of antler growth by mature males
Late August	Velvet shedding begins
Mid-September	Velvet shedding complete
Late November	Antler casting begins
Early January	Most mature males antlerless
Late January	Antler castings virtually complete; a few small-antlered males retain antlers for 60–80 additional days

SOURCE: Van Ballenberghe (1983a).

2001a) (Fig. 45.4). Moose invest differentially in antler grow relative to their body weight, with maximal investment occurring after body growth is complete at about 8 years of age (Fig. 45.5), but declining slightly in senescent individuals (Stewart et al. 2000).

Moose possess slightly more tines on left than right antlers (directional asymmetry), but the functional significance of that difference is unknown (Bowyer et al. 2001a). Likewise, moose exhibit fluctuating asymmetry (small random departures from perfect bilateral symmetry) in palm length and width, but not in circumference of antler beams. That finding is contrary to research on fluctuating asymmetry based solely on counts of antler tines (Solberg and Sæther 1993; Nygrén 2000). Moreover, an inverse relation exists between overall size of antlers and relative fluctuating asymmetry, an outcome expected for a secondary sexual characteristic such as antlers. Consequently, antler size may serve as an index to male quality in moose both among and within age cohorts (Bowyer et al. 2001a).

## PHYSIOLOGY

Moose are uniquely adapted to northern environments (Kelsall and Telfer 1974; Schwartz 1992; Van Ballenberghe 1992; Bowyer et al. 1997). Their massive body size and the insulating properties of their pelage buffer them against cold temperatures. The lower limit of the thermal-neutral zone of a moose (the temperature below which energy must be expended beyond basal metabolism to maintain body heat) has never been measured, but lies below  $-30^{\circ}\text{C}$  (Renecker and Hudson 1986). Likewise, their long legs help them negotiate deep snow; only depths  $> 70$  cm hinder movements of moose (Coady 1974, 1982). Travel through deep snow is energetically costly (Telfer and Kelsall 1979), and snow of sufficient depth or with a crusty surface that will not support moose may increase energetic expenditures markedly or curtail movements during winter. Moose are susceptible to heat stress (Renecker and Hudson 1990). In winter pelage, heat stress may begin when temperatures reach  $-5^{\circ}\text{C}$ . In summer coats, heat stress begins at  $14^{\circ}\text{C}$ , and panting occurs at  $20^{\circ}\text{C}$  (Renecker and Hudson 1990). Thus, high temperatures may limit the use of some habitats by moose in summer or even influence the extent of their southern distribution.

Moose inhabit boreal environments with extreme seasonal variation in climate as well as forage abundance and quality. The growing season is short and winter typically is long and severe; snow may persist for up to 9 months at the northern limit of their distribution. Consequently, moose accumulate large stores of fat during the brief growing season, which they rely on to meet their energetic needs during the long winter (Fong 1981; Ballard and Whitman 1987; Cederlund et al. 1989; Schwartz 1992). Digestibility and crude-protein content of the diet vary seasonally, with the highest values occurring from May to August (Regelin et al. 1987). Moose may consume aquatic plants that are high in sodium during spring and summer to replenish mineral reserves depleted in winter and meet requirements for lactation (Belovsky and Jordan 1981; Jordan 1987). Moose do occur in areas without substantial amounts of aquatic plants, where they often consume a diet high in willows (*Salix*) (Van Ballenberghe et al. 1989), which also are higher in sodium content than many other terrestrial plants (Staal and White 2001). Moose also may obtain sodium from natural mineral licks, especially in spring and early summer (Jordan et al. 1973; Fraser and Hristienko 1981; Fraser et al. 1982; Tankersley and Gasaway 1983; Risenhoover and Peterson 1986). Moose also will use roadside salt licks where sodium has been applied to hasten melting of snow and ice from highways (Miller and Litvaitis 1992a); placement of salt blocks can affect patterns of browsing by moose (Risto and Harkonen 1998).

Beeler et al. (1959), Flynn and Franzmann (1987), and Treble and Thompson (1998) discussed minerals in moose; copper (Flynn et al. 1977; Frank et al. 1994; Galgan and Petersson 1994; Barboza and Blake 2001; O'Hara et al. 2001) and chromium (Frank et al. 1994; Galgan and Petersson 1994) deficiencies have been reported. Cadmium also has been reported in kidneys, liver, and muscles of moose, with the highest concentrations occurring in kidneys (Scanlon et al. 1986; Glooschenko et al. 1988; Brazil and Ferguson 1989; Paré et al. 1999; Crichton and

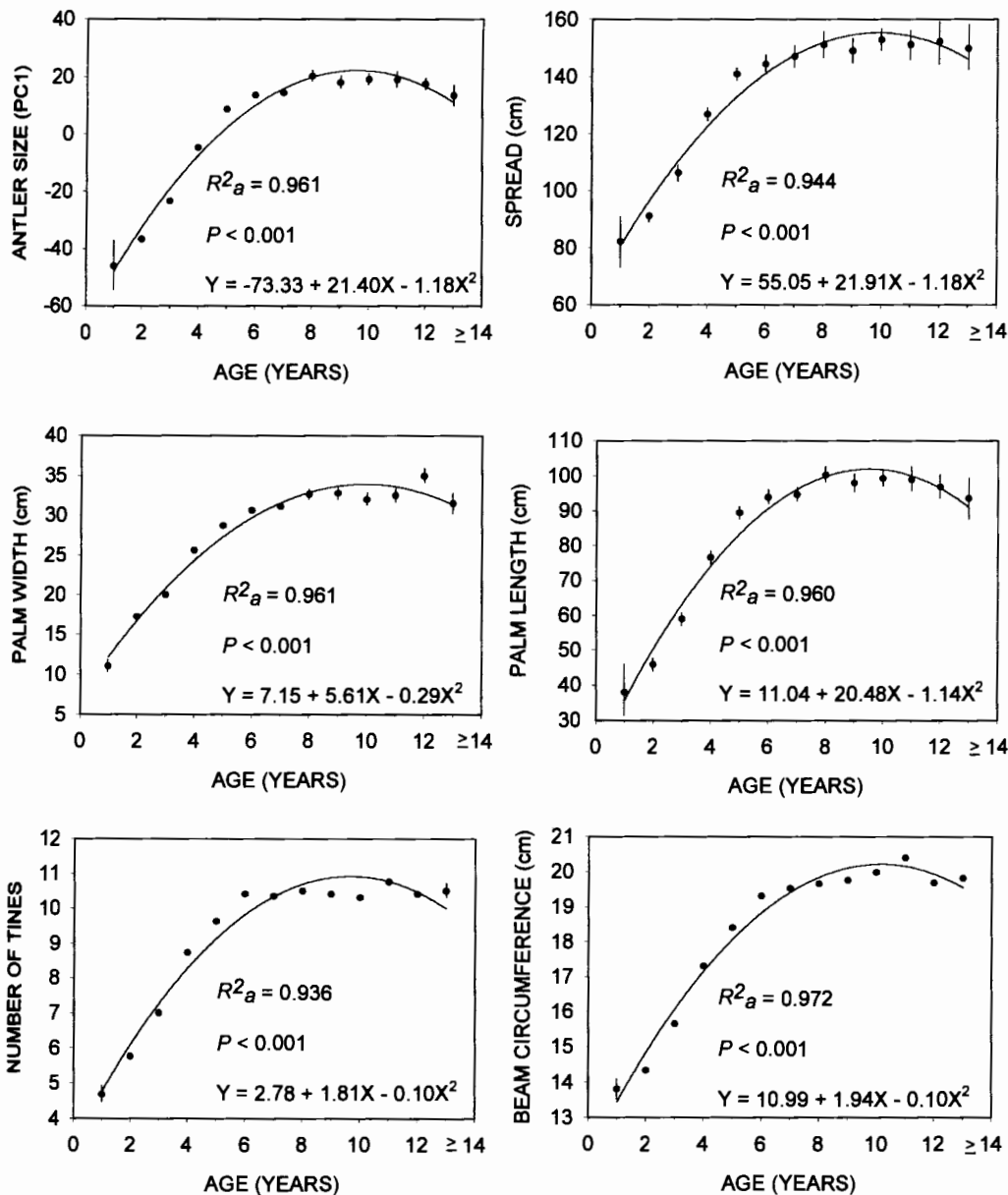


FIGURE 45.4. Changes in size of antler characteristics of male moose (*Alces alces gigas*) with increasing age. Note that senescence occurs in antlers of older moose, producing a curvilinear relation; PC1 (principal component 1) provides an overall index to antler size. SOURCE: Bowyer et al. (2001a). Reproduced with permission from Alliance Communications Group.

Paquet 2000; Gustafson et al. 2000). Contamination may be from either anthropogenic or natural sources. In some areas, concentrations of cadmium in kidneys and liver are sufficiently high that hunters are warned against eating those organs too frequently (Crichton 1998b). Lead, mercury, and nickel have been reported in other northern ungulates (Duffy et al. 2001).

Females must meet the high costs of lactation and recover and replenish body reserves necessary to ovulate and to survive harsh winter conditions. Sufficient fat reserves in females near the end of winter and in early spring are a necessity for successfully bearing and provisioning young (Keech et al. 2000). Males must accumulate resources in spring and summer necessary to support intense rutting activities in autumn and likewise survive winter. The diet of moose in winter is mostly woody browse with a low content of crude protein (5–7%), which will not meet maintenance requirements (Schwartz 1992). In addition, moose reduce their metabolic rate and food intake during winter as an adaptation to conserve energy (Schwartz et al. 1988c). Energy metabolism and expenditure in moose has been studied extensively

(Belovsky and Jordan 1978; Regelin et al. 1985, 1986; Renecker and Hudson 1986; Schwartz et al. 1988c, 1991; Hjeljord et al. 1994, 1996). Studies of fat reserves in moose have benefited from recent developments in ultrasonography (Stephenson et al. 1998a). DelGiudice et al. (1991) described urine chemistry and its relation to physical condition of moose during winter.

Milk of moose contains about 1.5 kcal/g (Franzmann et al. 1976a; Renecker 1987). Peak production of milk occurs from 21 to 31 days following birth, with a maximal output of 5.5 kg/day; twins receive 67% more milk than a singleton (Schwartz and Renecker 1998). Energetic costs of lactation far outweigh other components of maternal investment (White and Luick 1984). Cook et al. (1970) described the composition, fatty acids, and mineral constitution of milk from moose. Reese and Robbins (1994) further characterized lactation and neonatal growth in moose.

Moose are ruminants. Unlike mammals with simple digestive systems, moose have a specialized four-chambered structure, which allows them to feed on vegetation high in structural carbohydrates that

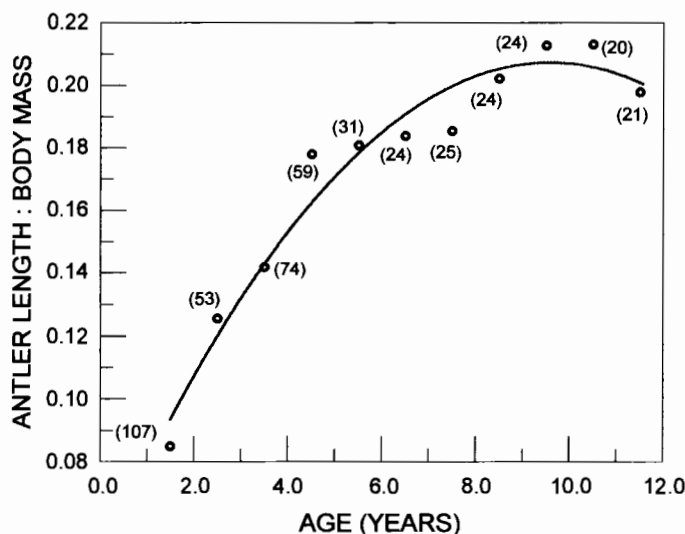


FIGURE 45.5. Antler length:body mass in relation to age in male moose (*Alces alces*). Sample size in parentheses. Note that maximal investment in antlers does not occur until about 8 years of age, when males complete body growth. SOURCE: Stewart et al. (2000).

monogastric mammals cannot digest in their stomach (Schwartz and Renecker 1998). The rumen and reticulum (the first two chambers) form an interconnected compartment where anaerobic conditions coupled with nitrogen and other nutrients recycled in saliva promote microbial fermentation of cellulose and hemicellulose. Moose further aid the digestive process by accumulating coarse vegetation into a bolus (cud) and eructing it from the rumenoreticular complex into the mouth for additional mastication, which reduces particle size. Moose re Chew coarser foods with high cell-wall content longer than more succulent vegetation (Schwartz and Renecker 1998). Microbial breakdown of structural carbohydrates results in production of volatile fatty acids, which are absorbed mostly by papillae on the rumen surface (Hofmann and Nygren 1992; Pehrson et al. 1997), and constitute the primary energy source for moose and other ruminants (Russell and Rychlik 2001). Gasaway and Coady (1974) discussed composition of volatile fatty acids in moose, and Dehority (1974) listed the ciliate fauna of the rumen. Moose also benefit by digesting rumen microbes (bacteria, protozoans, and fungi). The omasum (the third chamber) removes water and prevents passage of large particles of vegetation into the abomasum (the fourth chamber and true stomach), where gastric digestion occurs.

Generally, shorter rumination times are associated with higher-quality diets, and longer retention times with foods of lower quality (Schwartz et al. 1988b). Soluble sugars and other contents within the plant cell (cell-solubles) are fermented rapidly by rumen microbes, whereas cell walls require much longer fermentation times (Spalinger 2000). Lignin content also reduces digestibility of forages, as can tannins and other plant secondary compounds (Danell et al. 1990; Bryant et al. 1991, 1992). Moose, however, possess tannin-binding proteins in their saliva (Hagerman and Robbins 1993; Juntheikki 1996).

The longer forages remain in the rumen, the more completely they are digested, but increasing rumination time reduces the amount of forage that can be processed. Hence, moose face a tradeoff between turnover (and hence digestion) of forage and its rate of passage; those parameters must be optimized for maximal extraction of energy from the diet. Consequently, moose and other ruminants do not technically die from starvation even in winters with extremely deep snow and limited access to forage. Instead, they die from malnutrition with their rumens filled with large and mostly indigestible stems of winter browse (Coady 1982).

Sexual dimorphism (Weckerly 1998; Loison et al. 1999a) coupled with the needs of the sexes to follow different life-history strategies (Bowyer 1984; Bleich et al. 1997; Kie and Bowyer 1999) have led

TABLE 45.2. Summary statistics for variables used to examine the relationship between rump fat and blood-serum components from 38 pregnant, adult moose from the Tanana Flats, Alaska, March 1996

Variable	$\bar{X}$	SD	CV (%)	Range
Maximum depth of rump fat (cm)	1.54	1.01	65.6	0–3.8
Sodium (meq/L)	134.53	4.78	3.6	123–147
Potassium (meq/L)	8.29	1.4	16.9	5.7–10.9
Chlorine (meq/L)	95.42	3.91	4.1	87–103
Glucose (mg/dl)	97.87	19.53	20.0	64–153
Blood urea nitrogen (mg/dl)	3.38	1.15	34.0	2–5
Creatinine (mg/dl)	2.08	0.26	12.5	1.4–2.6
Blood urea nitrogen:creatinine (ratio)	1.55	0.40	25.8	0.8–3.3
Calcium (mg/dl)	11.07	1.09	9.9	8.2–13.4
Phosphorus (mg/dl)	4.77	1.13	23.7	2.5–8.5
Cholesterol (mg/dl)	72.27	11.39	15.8	54–117
Total bilirubin (mg/dl)	0.29	0.07	24.1	0.2–0.6
Protein (gm/dl)	6.87	0.47	6.8	5.4–7.6
Albumin (gm/dl)	3.78	0.36	9.5	2.8–4.5
Globulin (gm/dl)	3.09	0.24	7.8	2.5–3.8
Albumin:globulin (ratio)	1.23	0.13	10.6	0.9–1.5
Aspartate aminotransferase (U/L)	79.11	13.61	17.2	52–107
Alanine aminotransferase (U/L)	71.55	17.62	24.6	43–124
Total lactate dehydrogenase (U/L)	626.29	118.92	19.0	343–907
Creatine kinase (U/L)	50.82	28.87	56.8	20–122
Glutamyl transferase (U/L)	21.18	4.30	19.7	16–39
Alkaline phosphate (U/L)	43.87	19.07	43.5	25–135

CV, Coefficient of variation.

to allometric differences in the digestive systems of moose and other cervids, which promote spatial segregation of the sexes (Barboza and Bowyer 2000, 2001). Thus, the sexes of moose exhibit differences in diet selection or habitat requirements outside the mating season to satisfy their respective nutrient demands during periods of segregation (Miller and Litvaitis 1992b; Miquelle et al. 1992; Bowyer et al. 2001b), a point we return to later.

Mean body temperature of moose exhibiting no or slight excitability was 38.7°C; heart rate was 76.5 beats/min and respiratory rate was 19 respirations/min (Franzmann et al. 1984). Excitability affected those physiological values, as did season and the drug used to immobilize moose. Values that were considered sufficiently high to require intervention and corrective actions for immobilized moose were body temperature  $\geq 40.2^\circ\text{C}$ , heart rate  $\geq 102$  beats/min, and respiratory rate  $\geq 40$  respirations/min (Franzmann et al. 1984). Numerous authors have provided data on blood values of moose (Houston 1969; Franzmann and LeResche 1978; Crête et al. 1982; Franzmann et al. 1987; Ballard et al. 1996; Addison et al. 1998b). A suite of blood-serum values for pregnant females reported by Keech et al. (1998) is provided in Table 45.2. Ballard et al. (1996) noted that some blood variables differed between severe winters and mild ones, and Franzmann et al. (1987) reported differences in blood characteristics between moose populations on differing nutritional planes. Keech et al. (1998) related blood parameters to depth of rump fat and, hence, physical condition. They noted, however, that those results should be used with caution because of potential variability caused by differences in sex, age, season, reproductive status, and the effects of handling on individual moose.

## REPRODUCTION

**Estrous Cycle and Gestation.** Although differences in length of the estrous cycle and gestation for moose have been reported (reviewed by Schwartz 1998), the most reliable data are from Schwartz and Hundertmark (1993). Those authors reported that estrus in captive female moose ranged from 28 September to 12 October. Moose are polyestrous and females will recycle if not bred in their first estrus (Edwards and Ritecy 1958; Markgren 1969). Indeed, Schwartz and Hundertmark (1993) observed a second period of estrus from 19 October to 5 November. The estrous cycle ranged from 22 to 28 days, with females typically being receptive for 15–26 hr (Schwartz and Hundertmark 1993). Females

usually mate only once; observations of copulations with more than one male are uncommon (Van Ballenberghe and Miquelle 1996). Gestation length was 231 days and ranged from 216 to 240 days, with most fetal growth occurring during the last one third of gestation (Schwartz and Hundertmark 1993). Second-estrus females shortened length of gestation markedly (Schwartz and Hundertmark 1993), likely to have sufficient time during the short summer at high latitudes to provision young (Bowyer et al. 1998; Keech et al. 2000). Female ungulates altering length of gestation to cope with an unpredictable environment or short growing season may be more common than previously thought (Rachlow and Bowyer 1991; Berger 1992).

**Productivity and Age at First Reproduction.** Female moose on a high nutritional plane typically mate as yearlings and give birth near their second birthday (Schwartz 1998). Although ovulation by young (<1 year old) moose has been reported (Simkin 1965; Addison 1975), mating and conception does not occur (Schwartz 1998). Most moose have ovulated by either 16 or 28 months of age (Sand and Cederlund 1996; Schwartz 1998), but females in poor physical condition may delay ovulation until they are 40 months old (Albright and Keith 1987). Boer (1992) noted that pregnancy rates for yearlings were affected by the relationship of the population to carrying capacity of the habitat ( $K$ ), with female yearlings from populations well below  $K$  reaching rates as high as 64%. Female yearlings from populations beyond  $K$  had low rates of pregnancy. Pregnant yearlings typically give birth to a single young (near their second birthday), although twins occur rarely (Pimlott 1959; Blood 1974). The proportion of yearlings pregnant in a population is positively correlated with the proportion of adult females giving birth to twins (Boer 1992).

Pregnancy rates among adult females are high (>70%), and adult moose typically give birth to either a single young or twins (for review Schwartz 1998). Some females in poor physical condition, however, may not reproduce in consecutive years (Albright and Keith 1987). Indeed, the energetic costs of successfully provisioning young may affect reproduction in the following year (Testa 1998). Twinning rates for moose are variable and depend on good physical condition of females as affected by the relation of the population to  $K$  (Gasaway et al. 1992; Sand 1996; Heard et al. 1997; Nygrén and Kojola 1997; Testa and Adams 1998; Keech et al. 2000). Twinning rate for a particular population of moose provides an index to their physical condition (Franzmann and Schwartz 1985; Keech et al. 2000). Triplets occur occasionally (Hosley and Glaser 1952; Peterson 1955; Franzmann and Schwartz 1985; Bowyer et al. 1998), and the possibility of quadruplets exists (Martin 1989). Physical condition of maternal females affects litter size, weight of neonates, and date of birth, all of which can influence survivorship of young (Keech et al. 2000). Reproductive senescence occurs from about 12 years of age onward in female moose (Ericsson et al. 2001), ostensibly as a result of tooth wear (Ericsson and Wallin 2001); senescence is typical in other ungulates (Loison et al. 1999b).

The sex ratio at birth tends toward parity in moose, but substantial variation may occur (39–62% male; Boer 1992). Several authors have reported more males (Reuterwall 1981; Albright and Keith 1987; Ballard et al. 1991), others more females (Boer 1987; Larsen et al. 1989), and some no difference in sex ratios of neonates (Schwartz and Hundertmark 1993; Keech et al. 2000). Crichton (1992) noted that the sex ratio of fetuses conceived before the peak of rut were predominantly (66%) females, whereas males were more common (55%) in adult females bred later in the mating season.

Male moose become sexually mature as yearlings (Schwartz et al. 1982). Nonetheless, yearlings seldom gain an opportunity to mate because of their small body and antler size (Van Ballenberghe and Miquelle 1993, 1996; Stewart et al. 2000; Bowyer et al. 2001a). Asymptotic body weight is not reached in males until about 8 years of age, and maximal antler size is attained between 7 and 11 years old. Hence, age at first reproduction tends to be delayed for male moose because of their polygynous mating system, and the inability of small males to compete successfully for mates.

**Timing and Synchrony of Parturition.** Moose give birth in an extremely synchronous manner in late May (Gasaway et al. 1983; Schwartz and Hundertmark 1993; Bowyer et al. 1998; Keech et al. 2000). The median date of birth in interior Alaska was 25 May (Fig. 45.6); 85% of births occurred during an 11-day period and 95% of births during a 16-day period (Bowyer et al. 1998). Remarkably, there is little variation in timing of births by moose across a latitudinal gradient in North America (Sigouin et al. 1997; Bowyer et al. 1998; Schwartz 1998), a pattern that is much different in Fennoscandia, where parturition at far northern latitudes is delayed (Sæther et al. 1996). Predation is not the primary factor promoting synchrony in parturition among moose (Bowyer et al. 1998; Keech et al. 2000). The need to give birth early so there is sufficient time during the short growing season for young to acquire body reserves necessary to survive a harsh and long winter determines their timing and synchrony of parturition (Bowyer et al. 1998; Keech et al. 2000). Young moose born too late in spring have very high rates of mortality compared with others in their cohort (Keech et al. 2000). Moose did not alter timing of births in response to marked variability in winter or spring weather, and may be susceptible to climate change (Bowyer et al. 1998), a topic of increasing interest to those studying northern ungulates (Post and Stenseth 1998, 1999; Lenart et al. 2002).

## BEHAVIOR

**Rutting Dynamics and Mating Systems.** The mating season (rut) in moose peaks in late September and early October and is highly synchronized (Lent 1974; Schwartz and Hundertmark 1993; Van Ballenberghe and Miquelle 1993, 1996). Group size increases as rut approaches (Dodds 1958; Molvar and Bowyer 1994), with aggregations being

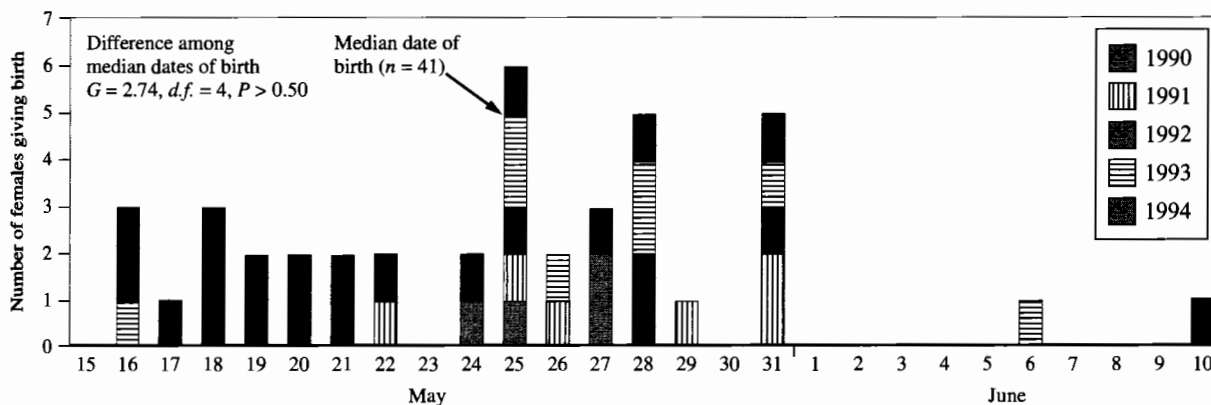


FIGURE 45.6. Timing of parturition in 41 moose (*Alces alces gigas*) from interior Alaska. Note the extremely synchronous nature of parturition for an ungulate that does not congregate to give birth. No differences occurred in timing or synchrony of births among years. SOURCE: Data from Bowyer et al. (1998).

largest at peak of rut, and then declining again late in the mating season (Van Ballenberghe and Miquelle 1996). Among polygynous, sexually dimorphic cervids, the largest males with the largest antlers typically mate most often (Hirth 1977; McCullough 1982; Bowyer 1986; Weckerly 1998), a generalization that also holds for moose (Peek et al. 1986; Van Ballenberghe and Miquelle 1993; Stewart et al. 2000). Aggregations of rutting moose occupy more open habitat in Alaska than elsewhere (Molvar and Bowyer 1994), and *A. a. gigas* tends to occur in larger groups than other subspecies (Peek et al. 1974).

Moose throughout most of North America exhibit a tending-bond system of mating similar to that of white-tailed deer (*Odocoileus virginianus*; Hirth 1977), wherein a dominant male defends an estrous female until he mates with her, and then moves on in search of additional mates (Altmann 1959; Geist 1963). Moose are not territorial (Peterson 1955). Moose in Alaska, however, exhibit a harem mating system more typical of North American elk (*Cervus elaphus*; Bowyer 1981). A dominant male herds and defends a group of females without regard to their state of estrus and does not permit sexually mature males in his rutting group. Harem masters court females as they come into estrus (Van Ballenberghe and Miquelle 1993; Molvar and Bowyer 1994; Van Ballenberghe and Miquelle 1996). In Alaska, a second bout of rutting behavior occurs in late October and early November, ostensibly for mating with females that were not bred in their first estrus or came into estrus late. During that second rut, the mating system reverts to a tending bond, probably because there are too few estrous females to form sufficiently large groups to make harem mating a worthwhile strategy. Only about 11% of females are bred in their second estrus (Schwartz and Hundertmark 1993).

**Aggressive Behavior by Males.** General accounts of the social behavior of moose during rut are provided by Altmann (1959), Geist (1963), de Vos et al. (1967), Lent (1974), Peek et al. (1986), Van Ballenberghe and Miquelle (1993, 1996), and Bubenik (1998). In addition, other authors have considered particular behaviors or focused on time periods surrounding rut (Dodds 1958; Houston 1974; Miquelle and Van Ballenberghe 1985; Miquelle 1990, 1991; Bowyer et al. 1994; Molvar and Bowyer 1994; Whittle et al. 2000). Our descriptions of rut-related behaviors rely on all those publications, but draw most heavily from Van Ballenberghe and Miquelle (1993, 1996).

Sparring (ritualized fighting) occurs mostly before and after the peak of rut and often involves opponents of different size and dominance status, and sometimes more than two individuals (Fig. 45.7). Antlers are presented to solicit sparring, and participants carefully position the antlers together; the ears are not held back and downward as in more serious encounters. Such interactions are of low intensity, and antler positioning and pushing are done gently. Subordinate individuals



FIGURE 45.7. Three bachelor male moose (*Alces alces gigas*) about to engage in sparring. Sparring is a low-key behavior, and differs markedly in intensity from serious fights among older males during the peak of rut. SOURCE: Photo by V. Van Ballenberghe.

may give a submissive whine if the level of aggression escalates. That vocalization often lowers the level of aggression or terminates the interaction.

Antler thrashing, which is a dominance display between males, does not function principally to remove velvet; thrashing behavior continues long after all velvet has been removed in moose as well as other cervids (Bowyer 1986; Van Ballenberghe and Miquelle 1993). Once velvet shedding begins, antlers no longer are innervated or supplied with blood—they are dead bone that function primarily as weapons for male–male combat (Geist 1966). Consequently, hardened antlers lack feeling; cervids do not thrash their antlers to masturbate (Bowyer and Kitchen 1987). Large males may antler thrash to intimidate small opponents, or antler thrashing may precede more serious encounters between opponents of more equal size and dominance status. In contrast to North American elk (Bowyer and Kitchen 1987), moose do not release urine when antler thrashing.

Large males often exhibit a swaying gait in which the antlers are rocked from side to side as they approach or challenge each other during rut. That behavior may be followed by broadside displays of the body or lateral displays of the antlers. If one opponent does not retreat, such dominance displays may lead to a serious fight. Fighting typically occurs over access to estrous females. Male moose may antler thrash, direct antler threats at opponents, or threaten them by approaching with their head below the level of the withers and their ears held downward; hair along the dorsal midline also may be piloerected. Males also may rush or charge a rival with the antlers being lowered and tines tipped downward as the opponent is approached. Males seldom kick toward each other with a stiff foreleg during rut.

Serious fighting usually occurs between large males of near-equal dominance around the peak of rut. Fighting is dangerous and smaller individuals typically flee dominant males, thereby avoiding violent and risky encounters. Fighting often is initiated by two large males presenting their antlers with their ears held back and downward. Lateral displays of antlers, accomplished by turning the head sideways rather than by repositioning the body, and pawing the ground often accompany this behavior. Males may engage in jousting, whereby they place their antlers together without pushing, ostensibly so an individual can gain a more favorable positioning of his tines relative to the shield provided by the antler palms of an opponent. Violent clashes occur after males take several quick steps together, or thrust forward following jousting; antler tines may be broken during these fierce encounters. Males attempt to gore each other during combat, either by twisting the neck of an opponent sideways, thereby breaking antler contact, and then thrusting tines into the side of an opponent's body, or by driving antlers into the rump of an adversary as he turns to flee. Males that are being gored in the side may whirl in a tight circle to break contact with opponents, and then slam their antlers back into those of rivals to regain a more favorable position and continue the fight. Losers of fights typically flee, often with the victor in close pursuit attempting to gore the retreating opponent. If opponents are equally matched, fights can last for hours with bouts of displaying and jousting intermixed with vigorous pushing.

Fighting is hazardous and males may be killed outright or die later from wounds sustained during combat. Rarely, moose will perish with antlers locked (Peterson 1955). In addition, rut-related injuries may make males more vulnerable to predators or impair their ability to survive harsh winter conditions. Large male moose cease feeding (i.e., become hypophagic) for about 18 days during the peak of rut (Miquelle 1990), which may further compromise their energy reserves and their ability to endure winter. Sex ratios among adult polygynous ungulates that strongly favor females may result, in part, from increased mortality among males associated with strenuous and hazardous rutting activities (Bowyer 1981, 1991; Berger and Gompper 1999).

**Scent Marking.** Scent marking by moose during rut is typified by two behaviors: digging of rutting pits (Miquelle 1991; Van Ballenberghe and Miquelle 1996; Whittle et al. 2000) and rubbing of trees (Bowyer et al. 1994). Scent urination is widespread among ungulates (McCullough 1969), and in moose, digging and wallowing in rutting pits characterizes



FIGURE 45.8. Pit-digging behavior in moose (*Alces alces gigas*). The dominant male has just dug a rutting pit by pawing a depression in the ground with his forefeet, and is squatting and urinating in the pit. The urine of dominant males is odiferous and highly attractive to females, which are approaching the pit. This strong-smelling urine likely contains a pheromone that primes estrus in females. SOURCE: Photo by V. Van Ballenberghe.

this behavior. A large number of old pits may be observed on traditional rutting grounds of moose (Woodin 1956). Large males paw a shallow depression (pit) in the ground with their forefoot and then squat and urinate into the pit (Fig. 45.8). The urine of large males has a pungent odor during rut and can be smelled by humans at great distances. Males then stomp with a forefoot, splashing the mixture of mud and urine onto the underside of their face, neck, and antlers. Males often bed (wallow) in the pit, and sometimes rock from side to side to impregnate the pelage on their underside with the aromatic urine; they do not roll onto their backs when wallowing. Males also may slap their antlers into the pit, further spreading urine over their forequarters and darkening and discoloring the underside of their antlers. Scent urination in ungulates may serve either a male–male or male–female function (Bowyer and Kitchen 1987); in moose, this behavior clearly is directed toward females (Miquelle 1991). Indeed, females respond immediately to pit-digging behavior by males and rapidly approach the pit. Females then attempt to gain access to the urine, sometime interfering with the male, which can lead to an aggressive response by the male. Females then wallow, often engaging in aggressive interactions to gain access to the pit. Urine of large males undoubtedly contains a pheromone that is attractive to females, which likely helps prime estrus (Whittle et al. 2000). Smaller but sexually mature males do not become hypophagic during rut and do not possess strong-smelling urine or dig rutting pits. Moreover, large males begin feeding again before the second rutting period in late October and early November, and do not engage in pit-digging behavior during that period. Catabolism of body reserves during hypophagia and subsequent elimination of metabolites in urine of males offer a suite of substances that may contain the pheromone involved, but more research is needed (Whittle et al. 2000).

Moose also scent mark small trees and shrubs by stripping away the bark, which is not eaten, with their lower incisors or antlers and rubbing their forehead and preorbital glands into the mark (i.e., sign posting), a behavior common to many ungulates (Bowyer et al. 1994). This behavior is unrelated to territoriality in moose (Weckerly 1992; Bowyer et al. 1994); many mammals that engage in scent marking are not territorial (Ralls 1971). Both sexes of moose rub trees. Females rub during the peak of rut and males rub mostly during the second rutting period in late October and early November. The rubbed tree may be a visual and olfactory cue that indicates the presence of an estrous female at the peak of rut (Bowyer et al. 1994). Trees rubbed by males are attractive to females during the brief second rutting period, and may serve a function similar to rutting pits with odiferous urine—priming of estrus (Bowyer et al. 1994). Rubbing of trees (scent marking) should

not be confused with bark stripping of trees and shrubs for feeding during winter (Bowyer et al. 1994).

**Courtship.** Males repeat a soft croak or grunt when courting females. This same vocalization may be given more forcefully when males are traveling alone or sometimes in response to other males (Van Ballenberghe and Miquelle 1996). Courtship is characterized by tongue flicking as the male approaches the female, sometimes in a low-stretch posture. Large males salivate copiously during rut, and their saliva is high in androsthenones (Schwartz et al. 1990). Females often give plaintive moans in response to male courtship, especially if the male is small. Males typically smell and may lick the perianal region of females they are courting and often exhibit flehmen. This behavior involves the vomeronasal organ, which likely allows the male to determine the state of estrus in the female (Estes 1973). Males also may flehmen after smelling or licking urine of a female from the ground (Fig. 45.9). If the female does not move away, the male places his chin over her rump and moves his head up and down or from side to side. Females may respond by rubbing their head along the flanks of the male. Males mount females by rising on their rear legs and clasping the female with their forelegs; females can terminate such encounters by walking forward. Successful copulation can be accomplished in one pelvic thrust; ejaculation coincides with penile intromission. Females rarely have been observed to accept copulations from more than one male. In Alaskan moose, large

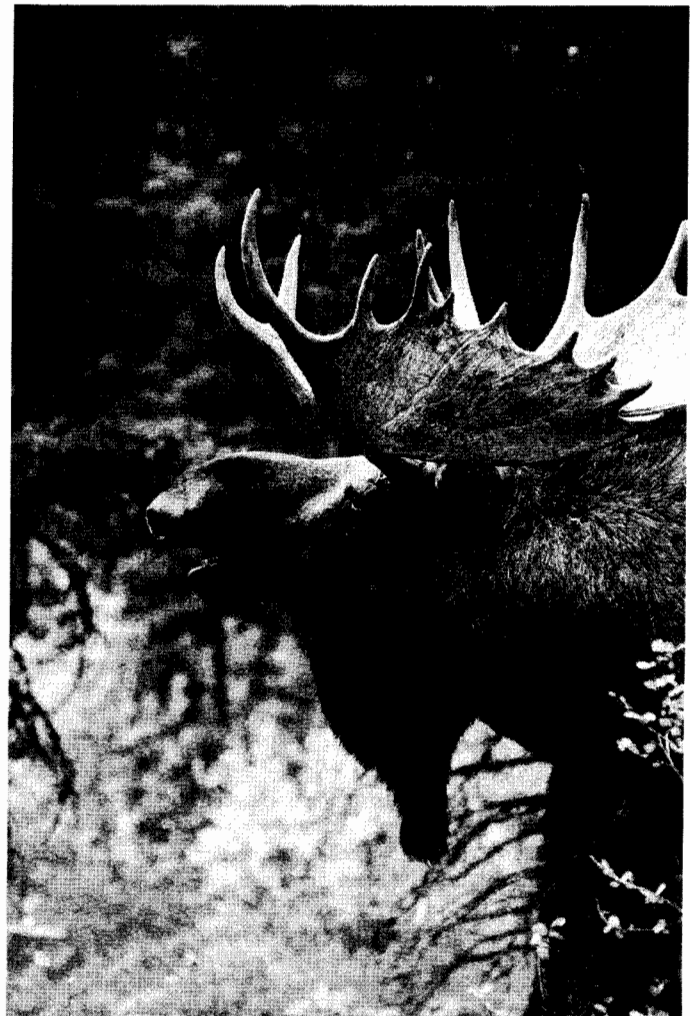


FIGURE 45.9. Flehmen behavior by a male moose (*Alces alces gigas*). This display involves the vomeronasal organ, which likely allows a male to assess the state of estrus in a female from metabolic by-products in her urine. SOURCE: Photo by V. Van Ballenberghe.

males herd females to block their departure from the harem. Males may give a herding vocalization, an explosive, short "oh-wah," which induces females to form a tight group. Under extreme stress, moose may emit a loud growling roar, which is not limited to the mating season (Franzmann 1981).

**Other Behaviors.** Other aggressive behaviors performed by females, or sometimes by males outside the mating season, include a direct stare. This behavior often is accompanied by the dominant individual dropping its ears and aversion of the head by the subordinate. Likewise, females will intimidate opponents with a head-high threat in which the nose is lifted upward and the ears are laid down and backward against the neck. If the opponent does not withdraw, the dominant female may rush toward an opponent and deliver a kick with a stiff foreleg, or rear onto her hind legs and flail with her forelegs. Play in moose often involves exaggerated aggressive behaviors, chases, and running through and splashing in water. Indeed, most play activities involved running (Geist 1963). Comfort behaviors of moose are similar to those of other cervids and were described by Geist (1963).

**Parturition and Maternal Behavior.** Behavior associated with parturition and care of young has been described by several authors (Altmann 1958, 1963; Stringham 1974; Cederlund 1987; Addison et al. 1993; Bubenik 1998). Maternal females become asocial and drive their yearlings away several weeks before giving birth (Peterson 1955). Indeed, as the birthing season approaches, group size declines (Molvar and Bowyer 1994), and the sexes remain spatially segregated (Miquelle et al. 1992). Immediately before parturition, some females may make long, erratic movements, which presumably are an adaptation to hinder predators in locating their birth sites (Bowyer et al. 1999b). Nonetheless, moose use traditional areas for giving birth (Addison et al. 1990; Bowyer et al. 1999b). Females seek secluded sites for parturition. Observations of births are rare, but in several instances young were dropped within 15–20 min of the initiation of labor; twins were born about 30 min apart (Bubenik 1998). Parturition is accomplished either standing or more commonly by laying down. Females lick the neonate clean and eat the afterbirth. Young may begin nursing 1.5 hr following birth. Length of nursing bouts averaged 6.6 min for neonates, but about 42 sec for older infants (Stringham 1974). Nursing is initiated by the neonate bunting the udder of the female, which causes milk letdown. Females remain close to the birth site for several weeks or longer (Addison et al. 1990; Bowyer et al. 1999b). Females and their young communicate with cohesion calls, but young attempt to avoid predators by behaving cryptically at the birth site. Weaning typically occurs between September and early December (Denniston 1956; Altmann 1958), but Molvar (1993) reported nursing by a yearling.

**Activity Patterns.** Moose are crepuscular for much of the year, with peaks of activity occurring around sunrise and sunset (McMillian 1954; deVos 1958; Best et al. 1978; Belovsky 1981a; Cederlund 1989; Renecker and Hudson 1989; Bevins et al. 1990). This pattern tends to be less pronounced during winter, especially at high latitude, where hours of daylight are limited (Risenhoover 1986; Gillingham and Klein 1992). Furthermore, summer activity patterns in the far north may exhibit little synchrony and become free running (Van Ballenberghe and Miquelle 1990). Marked differences in activity occur between the sexes, especially during the mating season, when males engage in strenuous rutting activities (Miquelle 1990; Van Ballenberghe and Miquelle 1996).

## FEEDING HABITS

Moose are browsers, eating mostly the stems and twigs of woody plants in winter and the leaves and succulent shoots of those shrubs and trees during the remainder of the year. Peek (1974b) and Renecker and Schwartz (1998) reviewed plant species consumed by moose. More than 220 different plant genera or species were eaten, with willows (*Salix*), birch (*Betula*), and alder (*Alnus*) predominating in diets of moose across North America where those species were available. Willows are preferred forage for moose (Peek 1974b; Pierce 1984; Renecker

and Schwartz 1998). During winter, however, moose in eastern North America consume large amounts of conifers. Ludewig and Bowyer (1985) reported 73% of winter diet of moose in Maine was composed of conifers, mostly balsam fir (*Abies balsamea*), but also including white spruce (*Picea glauca*). Moose living in the midcontinent select hardwoods, but also consumed balsam fir during winter (Peek 1974b; Crête and Bedard 1975; Thompson and Vukelich 1981; Risenhoover and Maass 1987). Moose also will eat fallen leaves of deciduous trees in winter where the boreal forest has a strong component of hardwoods (Renecker and Schwartz 1998). In Alaska, white spruce is common within the distribution of moose, but spruce or other conifers seldom are consumed (Oldemeyer 1983; Risenhoover 1989; Van Ballenberghe et al. 1989; Weixelman et al. 1998). This east-west gradient in the willingness of moose to eat conifers likely relates to potent secondary metabolites in trees and shrubs (Palo 1991; Sunnerheim-Sjoberg and Hamalainen 1992) in some western species that help deter feeding by moose and other herbivores (Bryant et al. 1994; Bowyer et al. 1997). Population density of moose, however, affects availability of forage and can alter diets (Risenhoover and Maass 1987; Brandner et al. 1990). At sufficiently high density relative to  $K$ , resource depletion occurs (Edenius 1991), and under such circumstances even Alaskan moose may consume white spruce (Bowyer et al. 1999a). Low-quality or limited food resources can affect body condition and consequently population status of moose (Messier and Crête 1984; Ferguson et al. 2000). Moose at lower density relative to  $K$ , however, may have less effect on their food supply (Crête and Jordan 1982a).

During winter, moose may break main stems of shrubs or smaller branches on trees by biting them with their premolars and molars or by using their body to bend and break stems. They then feed on the more nutritious twigs of current and second-year growth that are then within their reach (Telfer and Cairns 1978). Moose also strip bark from trees and shrubs for feeding during winter (Miquelle and Van Ballenberghe 1989; Risenhoover 1989; Faber and Edenius 1998; Scharf and Hirth 2000) and also strip bark of woody species around birth sites in early spring (Miquelle and Van Ballenberghe 1989; Bowyer et al. 1999b).

In spring and summer, moose often consume aquatic vegetation where it is available (Murie 1934; Peterson 1955; Peek et al. 1976; Fraser et al. 1980, 1982, 1984; Timmermann and Racey 1989; MacCracken et al. 1993). Aquatic vegetation provides sodium (Jordan 1987), but moose also may forage on aquatic plants because of the substantial biomass available in some areas and the high digestibility of aquatic vegetation compared with many terrestrial species (MacCracken et al. 1993). Aquatic plants, however, are not necessary for productive moose populations; moose endure where they feed principally on browse in summer with little access to aquatic vegetation (Van Ballenberghe et al. 1989).

Belovsky (1978, 1981b) employed an optimal-foraging approach to predict selection of forage classes by moose. Other mechanistic approaches also have been valuable in understanding use of vegetation patches, intake rates, and diet optimization by moose (Danell et al. 1991; Shipley and Spalinger 1992, 1995; Shipley et al. 1998, 1999). Moreover, substantial information exists on the nutritional composition and quality of plants eaten by moose (Cowan et al. 1950; Kubota et al. 1970; Oldemeyer 1974; Oldemeyer et al. 1977; Hjeljord et al. 1982; Crête and Jordan 1982b; Eastman 1983; Schwartz et al. 1988; Spaeth et al. In press) as well as fecal indices of forage quality (Leslie et al. 1989). Quality of forage during the growing season is much higher than during winter. Moreover, plants growing in the shade tend to have larger leaves and be more nutritious than those growing in direct sunlight (Hjeljord et al. 1990; Bø and Hjeljord 1991; Hjeljord 1992; Molvar et al. 1993). Forage species selected by moose, however, have been difficult to predict based solely on their nutritional composition, especially during winter (Weixelman et al. 1998).

Quality of most browse declines from current annual growth to woody tissue laid down 2–3 years previously (Cowan et al. 1950; Spaeth et al. In press)—the older and larger the stem diameter, the lower is its forage quality. Accordingly, selection of particular stem diameters for a browse species by moose is thought to represent a tradeoff between

biomass and quality obtained in a particular bite (Vivas and Sæther 1987; Molvar et al. 1993), resulting in moose eating an optimal twig size (Vivas et al. 1991). Several factors, however, complicate interpreting bite-size selection in moose. Species of browse available and the size of their stems or twigs undoubtedly affect the size of a bite taken. Moreover, browsing in winter positively affects the size of stems regrown the following spring (Bowyer and Bowyer 1997), provided that browsing is not too severe wherein regrowth takes on a hedged appearance with smaller twigs (Molvar et al. 1993). Moose preferentially feed on stems regrown from those browsed in previous years (Bergstrom and Danell 1987; Bowyer and Bowyer 1997). Conversely, defoliation of shrubs (often by leaf stripping) by moose and subsequent regrowth of foliage in summer results in low-biomass foliage, which moose avoid (Miquelle 1983). These processes alter the size of twigs available for moose to forage on and, undoubtedly, their twig-size selection. Snow also can affect the availability of browse (Coady 1974; Weixelman et al. 1998), thereby affecting size of twigs moose are willing to forage on and whether they will eat leaders browsed previously that year. The sexes of moose also have incisor arcades of differing size (Spaeth et al. 2001); adult males take larger bites than do adult females (Miquelle et al. 1992; Bowyer et al. 2001b). Thus, knowledge of which sex predominates in a particular area may be necessary to interpret bite-size selection in moose.

Risk of predation also influences feeding behavior of moose (Edwards 1983; Berger 1999; Kie 1999; Berger et al. 2001a, 2001b; White et al. 2001). Molvar and Bowyer (1994) reported that stem diameter at the point of browsing increased with the distance moose moved from the edge of the forest (Fig. 45.10). Moose presumably took larger, less-nutritious bites as they ventured farther from concealment cover and, in consequence, foraged less selectively because of predation risk (Molvar and Bowyer 1994). Moreover, larger groups of moose formed at greater distances from cover, but foraged less efficiently than moose in smaller groups or those nearer cover (Molvar and Bowyer 1994). Females with young were especially sensitive to risk of predation and altered their feeding behavior more than other sex and age classes (Molvar and Bowyer 1994). Weixelman et al. (1998) also reported that moose altered patterns of diet selection and foraged on less-preferred species at greater distances from concealment cover in winter.

## ECOLOGY

**Home Range, Migration, and Dispersal.** Young moose accompany, and consequently have the same home range as, their mother during their

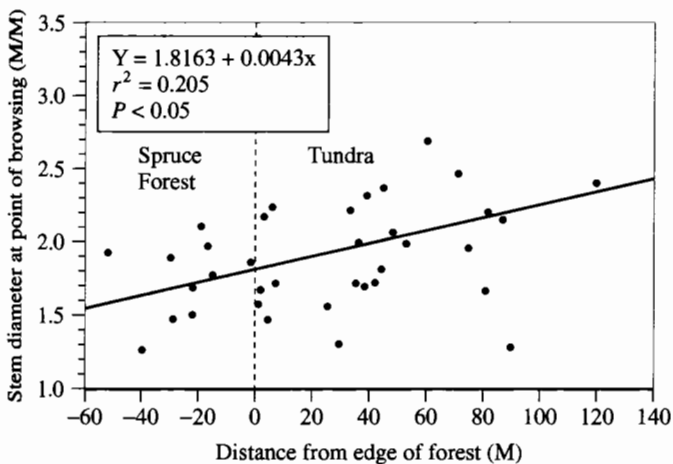


FIGURE 45.10. Diameter at point of browsing on twigs of fletleaf willow (*Salix pulchra*) eaten by moose (*Alces alces gigas*) in interior Alaska. Note that quality of forage eaten declines (larger diameters) as moose venture farther from concealment cover provided by the forest into open tundra; this outcome likely results from predation risk. SOURCE: Data from Molvar and Bowyer (1994).

first year of life (Altmann 1958). Females with young may have smaller home ranges, however, than those without them (Ballard et al. 1991). Separation of young from the mother typically occurs at 12–16 months of age (Ballard et al. 1991). Yearlings may wander and not occupy traditional home ranges, but moose usually have established relatively permanent home ranges by 2–3 years of age (Houston 1968; Addison et al. 1980). The ultimate sizes of home ranges occupied by young are related linearly to the home-range size of their mother (Ballard et al. 1991). Female moose tend to be philopatric and are more likely to establish home ranges overlapping with those of their mothers than are young males (Ballard et al. 1991).

Hundertmark (1998) reviewed home-range size in moose and reported variation (excluding migratory movements) from 3.6 to 92 km<sup>2</sup>. Moose may inhabit the same range throughout the year or migrate to separate summer and winter ranges; considerable variation occurs among populations as to which seasonal range is larger (Hundertmark 1998). Moose also may use traditional rutting and calving areas in autumn and spring, respectively (Houston 1968; Van Ballenberghe and Miquelle 1996; Bowyer et al. 1999b). The sexes of moose are spatially segregated during winter and spring (Miller and Litvaitis 1992a; Miquelle et al. 1992; Bowyer et al. 2001b).

A trend exists for increasing size of summer and winter home ranges with increasing northern latitude (Hundertmark 1998); home ranges at >60° N latitude are exceptionally large (Stenhouse et al. 1995). Population density also plays a role—home ranges tend to be smaller at higher densities than at lower ones (Sweanor and Sandegren 1989; Mytton and Keith 1981). Furthermore, deep snow can limit movements and thereby home-range size during winter (Sweanor and Sandegren 1989).

Size of home range also differs based on gender. Ballard et al. (1991) reported that males had larger home ranges than females, but Phillips et al. (1973), Hauge and Keith (1981), and Sweanor and Sandegren (1989) did not observe that difference. Cederlund and Sand (1994), however, noted that male, but not female moose increased the size of their home range with age. Consequently, comparison of home-range size between the sexes needs to account for age.

Individual moose may migrate seasonally. Such movements are common among cervids and often involve seasonal home ranges separated by long distances. Sinclair (1983) suggested that migratory movements place an animal in an area with abundant food resources before mating, thereby enhancing individual reproductive fitness. Unlike elk and caribou, which migrate in herds, moose typically move as individuals, although timing of migration may be synchronized by weather events, including snowfall. Migratory movements are directional and often follow traditional routes (Andersen 1991), but the pattern of migration may vary greatly from year to year depending on factors such as extent and duration of snowfall. Individuals may leave their summer ranges in response to accumulation of deep snow when it occurs, or remain on summer ranges if snow depths are shallow, or may even undergo partial migration under conditions of moderate snowfall (Van Ballenberghe 1977). Variability in snowfall has been implicated in maintaining migratory and nonmigratory elements in the same population of mule deer (*Odocoileus hemionus*; Nicholson et al. 1997). Moose populations also may contain segments that display long-distance migrations and other segments that do not migrate. Sinclair (1983) asserted that in stable populations, migratory and nonmigratory segments reach equilibrium whereby the benefits of leaving versus staying were equal. Migration in moose is apparently a learned behavior, because young moose follow the movement patterns of their mothers and acquire not only seasonal home ranges, but also migration routes. Migratory females in a moose population in Alberta, Canada, had higher fecundity than nonmigrant females (Mytton and Keith 1981), indicating that eventually migratory moose would outnumber those failing to move.

Distances between summer and winter home ranges in migratory populations vary greatly and may depend on terrain features and habitat dispersion (Sandegren and Sweanor 1988). Often, moose move along elevational gradients seeking lower elevations in winter where snow depth and hardness may be less, and returning to high-elevation summer

ranges where forage quality and quantity is greater. Phillips et al. (1973) observed migration distances of 14–34 km in northwestern Minnesota, longer than those (2–13 km) of moose in northwestern Ontario (Addison et al. 1980) or Quebec (7 km; Roussel et al. 1975). Mytton and Keith (1981) observed males in Alberta migrating a mean of 13.4 km, whereas females moved a mean of 6.8 km. Moose in Alaska generally migrated much longer distances. Van Ballenberghe (1977) documented movements of 8–94 km, whereas Ballard et al. (1991) reported movements of 16–93 km for populations of moose in a mountainous area of south-central Alaska. Mauer (1998) reported maximum distances between summer and winter range were 18–196 km in northern Alaska; movements to summer range were underway in late March, and migration to winter range was completed by early October. Atypical migratory patterns also may occur in which moose move to lowland habitats in late winter and remain there during summer, returning to higher elevations in time for the rut (Gasaway et al. 1983). Such patterns are poorly explained, but are apparently related to exploitation of spatial distribution of favorable habitats and seasonal changes in quality of forage.

Unlike migration, which involves a repeated pattern of movements between traditionally used areas, dispersal results in animals leaving previously used areas to settle in new areas where they may remain and reproduce (or attempt to do so) for the remainder of their lives. Migration and dispersal may affect the reproductive fitness of an individual moose, potentially through providing access to improved food quality and environmental conditions, as well as by increasing the probability of finding suitable mates compared with animals that do not undertake such movements. Dispersal of young males also reduces inbreeding (Hjeljord 2001). As with migration, individuals in the same moose population may display different tendencies to disperse. Young may undertake extensive dispersal movements or not disperse at all.

Gasaway et al. (1985a) and Cederland and Sand (1992) used a conceptual model of dispersal postulated for small mammals by Lidicker (1975), who contrasted dispersal from growing populations below  $K$  to that from populations at or near  $K$ . These two types of dispersal were termed presaturation and saturation dispersal, respectively. Stenseth (1983), however, recognized that some individuals dispersed regardless of population density ("ambient" dispersal) and suggested that pattern and presaturation dispersal were adaptive. Nonadaptive dispersal was defined as that occurring as individuals were forced from existing home ranges by competition and social pressure in high-density populations. The latter would include younger, immature animals and nonreproducing adults. Both classes would suffer poor survival when forced to disperse.

Studies of moose do not indicate clear patterns of dispersal or definitively explain factors that drive animals to disperse. Gasaway et al. (1985a) noted that only 1 of 36 collared moose established a home range that did not overlap that of its mother in a moderately dense population in interior Alaska. In south-central Alaska, Ballard et al. (1991) reported 5 of 15 young displayed a similar pattern in a high-density population. Dispersers moved to areas of lower population density. Dispersal rates between males and females did not differ in Sweden (Cederland et al. 1987). Lynch (1976) reported higher rates of dispersal by subadults versus adults in Alberta. Many (33% of 147) yearlings that dispersed from reserves to areas where hunting was permitted in Quebec were harvested the following year as adults (Labonté et al. 1998).

Dispersal distances vary greatly. A mean dispersal distance of 3 km was noted by Gasaway et al. (1985a) in Alaska, compared with a female that moved 177 km in another area of Alaska (Ballard et al. 1991). Four young moose in Alberta moved at least 50 km and one male dispersed 250 km (Mytton and Keith 1981). Kufeld and Bowden (1996) reported that female dispersal from natal areas ranged from 13 to 120 km in Colorado. Studies have not been conducted to examine survival and reproductive success of long-distance dispersers in moose. Global positioning systems should aid in future studies of moose movements (Rodgers et al. 1996).

Dispersal may play an important role in population dynamics as animals immigrate to and emigrate from different areas. Rolley and Keith (1980) studied a moose population in Alberta that increased about

40-fold in a 14-year period. During the first part of that period, the observed finite rate of increase exceeded that possible by survival and reproduction. The reverse occurred in the later years, leading to the conclusion that immigration (by dispersers) accounted for the high rate of increase initially, in contrast to dispersal out of the population (emigration) in the later years.

Dispersal also may result in population expansion of moose, either on a small scale, whereby moose occupy areas of newly created habitat, or on a large scale, where populations may expand greatly or pioneer into previously unused areas. An example of the former was documented in Minnesota by Peek (1974a), who observed greatly increased use of a burned area. Coady (1980) and Mercer and Kitchen (1968) provided examples of the latter, where distribution of moose populations expanded at rates up to 18 km/year.

**Effects on Ecosystem Structure and Function.** Moose can markedly modify structure and function of ecosystems they inhabit and thereby govern the well-being of other species. Those abilities to alter ecosystem processes make moose a keystone species (Simberloff 1998). The nature of such change, however, is associated with the population density of moose relative to  $K$  of the environment (Bowyer et al. 1997). Correspondingly, moose are a critical component of northern environments, and knowledge of their ecology is prerequisite to understanding and managing productivity and species composition of boreal regions (Bowyer et al. 1997). The trend is to ignore megafauna in managing species diversity (Crichton 1998a). Such a view is shortsighted where large herbivores drive ecosystem dynamics (McNaughton 1984; Ruess and McNaughton 1987; Frank and McNaughton 1993). Understanding the role of moose and other large herbivores in such systems offers unique opportunities to unite the best features of single-species and ecosystem management (Simberloff 1998; Snaith and Beazley 2002).

Foraging behavior of moose may alter environments they inhabit, especially by adjusting patterns of plant structure and succession (Risenhoover and Maass 1987; Pastor and Naiman 1992; Pastor et al. 1993). On Isle Royale, Michigan, browsing by moderate to high densities of moose accelerated rates of succession from hardwoods to conifers (Risenhoover and Maass 1987; Brandner et al. 1990; Pastor and Naiman 1992; McLaren and Peterson 1994), thereby lowering rates of nutrient cycling in conifer-dominated habitats (Pastor et al. 1993). High density of moose can lower species diversity and alter composition of plant communities (Connor et al. 2000). A low-density population of moose inhabiting floodplain habitat in interior Alaska also influenced patterns of early succession and lowered rates of nutrient cycling (Kielland et al. 1997; Kielland and Bryant 1998), including negative effects on root dynamics (Ruess et al. 1998). Cascading effects of moose browsing have been reported on invertebrates (Suominen et al. 1999a, 1999b) and birds (Berger et al. 2001a).

Conversely, moderate densities of moose in interior Alaska living in treeline habitat, which was not undergoing rapid succession, had a positive affect on rates of nitrogen mineralization, ostensibly because of deposition of urine and feces (Molvar et al. 1993). Likewise, regrowth of stems and leaves following browsing by moose may be larger, more nutritious, and decompose more rapidly in terrestrial (Bryant et al. 1983; Molvar et al. 1993) and aquatic (Irons et al. 1991) systems. Indeed, moose may positively affect their food supply in three ways. First, browsing in autumn and winter release stems from apical dominance, resulting in regrowth of larger stems with larger leaves the following spring (Bergstrom and Danell 1987; Molvar et al. 1993). Likewise, browsing may enhance adventitious growth. Willows responded by increasing biomass per growing point with overall levels of browsing on the entire plant (Molvar et al. 1993) or from browsing on individual leaders of current annual growth (Bowyer and Bowyer 1997). Saliva of moose also may promote branching of saplings (Bergman 2002). Moose selected current annual growth from stems that had been browsed in previous years over those that had not been foraged on (Bowyer and Bowyer 1997). Second, moderate levels of browsing affect the carbon–nitrogen balance of shrubs and trees. Regrowth is poorly defended by secondary compounds, and has a lower lignin-to-nitrogen ratio, allowing more

rapid decomposition of litter from browsed versus unbrowsed plants (Molvar et al. 1993; Bowyer et al. 1997). Third, moose fertilize the plants they feed on via deposition of urine and feces (Molvar et al. 1993). Nitrogen content of feces increases with increasing forage quality (Leslie and Starkey 1985). These processes combine to enhance rate of nitrogen cycling on areas frequented by moose and other large herbivores (Ruess and McNaughton 1987; Molvar et al. 1993).

Such alterations of ecosystems by moose are best viewed in terms of the "herbivore optimization" curve of Hik and Jefferies (1990), where herbivores have negative effects on productivity at low and high population densities, but promote positive ones at moderate densities. Moreover, presence or absence of large mammalian carnivores has a substantial effect on feeding behavior (Berger 1999; Berger et al. 2001b) and population dynamics (Gasaway et al. 1992) of moose, outcomes that have far-reaching implications for managing ecosystems. Comprehending the nature of these complex processes is critical for understanding the ecology of northern systems inhabited by moose, and is a necessity for the wise management these unique ungulates (Bowyer et al. 1997).

**Habitat Use and Selection.** Telfer (1984) and Peek (1998) provide overviews of habitats used by moose in North America. Telfer (1984) categorized the primary habitats of moose into five broad vegetation communities: (1) boreal forest in which fire plays a dominant role, (2) mixed forest representing the coniferous-deciduous ecotone, (3) large delta floodplains, (4) tundra and subalpine zones, and (5) stream-valley shrub including riparian zones. Delta floodplains provide a high biomass of forage for moose and can be exceptionally productive habitats (Telfer 1984; MacCracken et al. 1997; Peek 1998; Bowyer et al. 2002a In press). Floodplains offer relatively permanent habitat for moose compared with more successional types of vegetation (Peek 1998). Stream-valley shrub likewise provides riparian habitat for moose because rivers and streams drive patterns of primary succession via ice action and flooding, which favor plants eaten by moose. Aspen (*Populus*) parklands are used by moose (Peek 1998), as are mature coniferous forest in some areas (Stevens 1970; Pierce and Peek 1984; Van Dyke et al. 1995; Balsom et al. 1996). The value of boreal forest to moose is strongly influenced by fire and subsequent plant succession, which provides abundant forage following burns. Fire, however, is less important in treeline habitats in the boreal forest (Van Ballenberghe 1992) and in boreal regions with higher precipitation and, consequently, longer fire cycles (Jandt 1992). Summer habitat also may include aquatic foraging areas associated with riparian zones around streams, rivers, oxbows, and ponds (Peek 1998).

In many areas, fire plays an important role in the ecology of moose year-round. Quality and abundance of forage, and ultimately moose density, often increase following fire (Aldous and Krefting 1946; Cowan et al. 1950; Spencer and Chatelain 1953; Dewitt and Derby 1955; Spencer and Hakala 1964; Peek et al. 1976; Oldemeyer et al. 1977; Bangs and Bailey 1980; Bangs et al. 1985). In the Kenai Mountains of Alaska, some production of browse occurred by 7–10 years after fire, peaked following 20–30 years of succession, and then declined markedly by 70–80 years after burning (Weixelman et al. 1998) (Fig. 45.11). Fire cycles and the time necessary for production of abundant and succulent vegetation in warmer areas of Alaska (Wolff 1978; MacCracken and Viereck 1990), however, may be more rapid than on the Kenai Peninsula; specifically how moose respond to that more-rapid pattern of succession requires additional study. Peterson (1978) noted that moose on Isle Royale, Michigan, concentrated in areas with more forage as vegetation in burns grew out of their reach (Krefting 1974a). Indeed, Loranger et al. (1991) reported an inverse relation between moose density and years following fire in Alaska. Weixelman et al. (1998) and Peek (1998) cautioned that moose populations held at low density by predation would be less likely to respond to fire than those nearer *K*. Such low-density populations already are reproducing at near maxima and would be unlikely to benefit from enhanced forage abundance (Kie et al. 2003). Kie et al. (2002) noted the importance of habitat heterogeneity in affecting the distribution of mule deer; similar investigations of moose have yet to be undertaken.

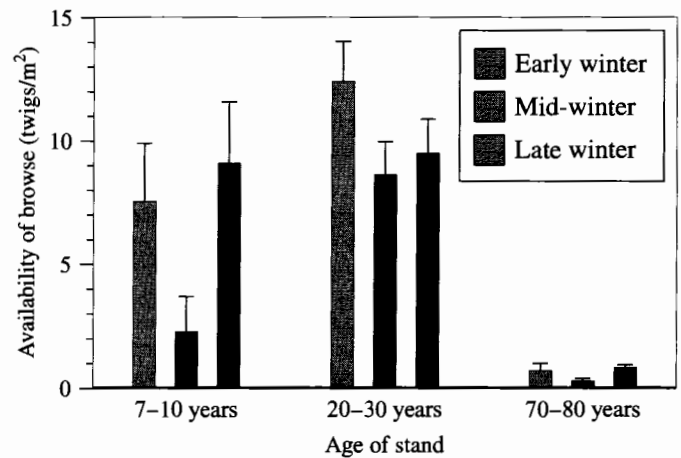


FIGURE 45.11. Relationship between age of burns and available forage for moose (*Alces alces gigas*) on the Kenai Peninsula, Alaska. Note that maximal availability of browse occurs in the 20- to 30-year-old burns, and that snow covers forage during midwinter 7–10 years after fire. SOURCE: Data from Weixelman et al. (1998).

Substantial overstory cover, which intercepts snow, characterizes winter habitat for moose throughout much of their distribution (Peek 1998); yarding is prevalent in the East (Telfer 1967a; Proulx 1983; Crête and Jordan 1982a, 1982b). Yards may occur in level, low-elevation sites (Proulx 1983) or on steep terrain at higher elevations (Kelsall and Prescott 1971). Moose also concentrate in areas without substantial overstories where abundant food is available during winter (Telfer 1978), including river deltas (MacCracken et al. 1997) and riverine areas or riparian zones with willows (Risenhoover 1989; Miquelle et al. 1992; Bowyer et al. 2001b). Nonetheless, snow characteristics play a critical role in winter selection of habitat by moose (Peek 1998), which may cover browse in early successional stages of burns (Weixelman et al. 1998). Depth of snow in late winter also influences selection of bedding sites (Minzey and Robinson 1991). Depths of snow  $\geq 70$  cm may cause moose to seek winter shelter or other microhabitats with lower snow depths (Kelsall and Prescott 1971; Coady 1974; Hundertmark et al. 1990). Crusted snow also can impede movements and injure legs. Moose will break through snow not capable of supporting  $1 \text{ kg/cm}^2$  (Kelsall and Prescott 1971).

Habitat used for parturition by moose is critical for the survival of neonates (Bowyer et al. 1999b). Risk of predation is thought to play a major role in selection of habitats for giving birth (Bailey and Bangs 1980; Stephens and Peterson 1984; Leptich and Gilbert 1986; Addison et al. 1990; Wilton and Garner 1991; Langely and Pletscher 1994; Chekchak et al. 1998; Welch et al. 2000; Testa et al. 2000a). In areas with islands, females may seek those secluded sites for parturition as an antipredator strategy (Addison et al. 1990). Moose also may select high-elevation areas to give birth (Wilton and Garner 1991), and such sites likely provide a better view of approaching predators (Bowyer et al. 1999b). Bowyer et al. (1999b), however, rejected the hypothesis that moose moved to high elevations to "space away" from predators. Langely and Pletscher (1994) and Bowyer et al. (1999b) also noted that moose did not give birth near human developments to avoid predation. Birth sites were farther from human developments than random sites, and proximity of such developments did little to dissuade predators from killing neonates (Bowyer et al. 1998, 1999b). If undisturbed, females remain at birth sites with young for several weeks, likely to help thwart predators (Addison et al. 1990; Bowyer et al. 1999b). Females remaining near the birth site require substantial food to support the high costs of lactation; forage, especially willows, was far more abundant at birth than random sites (Bowyer et al. 1999b).

Bowyer et al. (1999b) hypothesized that maternal females behaved unpredictably to thwart the hunting tactics of predators. Female moose made erratic movements before giving birth and did not select any of

the broadly distributed vegetation communities for parturition; birth sites were neither clumped nor overly dispersed spatially (Bowyer et al. 1999b). Instead, females selected microsites with more food, a view of approaching predators, and a southeasterly exposure to give birth, a strategy that balanced the need for forage against the risk of predation (Bowyer et al. 1999b), a pattern common to northern ungulates (Barten et al. 2001).

**Sexual Segregation.** Sexual segregation is the differential use of space by the sexes outside the mating season (Barboza and Bowyer 2000), and often includes differential use of habitats or forages. Spatial segregation of the sexes is prevalent among sexually dimorphic and polygynous ruminants (Bleich et al. 1997; Mysterud 2000), including all North American cervids (McCullough 1979; Bowyer 1984; Bowyer et al. 1996; Kie and Bowyer 1999; Barboza and Bowyer 2001). This phenomenon is especially pronounced in moose and plays a crucial role in their ecology (Miller and Litvaitis 1992a; Miquelle et al. 1992; Bowyer et al. 2001b). Sexual dimorphism, which is positively related to the degree of polygyny (Weckerly 1998; Loison et al. 1999a), affects digestive morphology and physiology (Barboza and Bowyer 2000, 2001) as well as susceptibility to predation (Bleich et al. 1997) differentially for the genders. Many other hypotheses forwarded to explain sexual segregation in ungulates have been rejected (Miquelle et al. 1992; Bleich et al. 1997; Barboza and Bowyer 2001). Risk of predation and differences in digestive capability between the sexes may be the only hypotheses necessary to explain spatial segregation of the sexes.

In moose, spatial separation of the sexes occurs because adult males select habitats with greater forage abundance and females select areas with more concealment cover during winter (Miquelle et al. 1992; Bowyer et al. 2001b). Such differences in the use of space have implications for sampling of moose populations (Peek 1998; Bowyer et al. 2002). Moreover, Kie and Bowyer (1999) suggested that the habitat requirements of the sexes of white-tailed deer were sufficiently different that they should be managed as if they were different species. Indeed, Bowyer et al. (2001b) reported that mechanical crushing of willows markedly enhanced forage abundance. Males, however, moved into the opening to forage, whereas females and young remained in areas with less forage but more cover. Thus, that habitat modification for moose likely benefited one sex at the expense of the other because the manipulation resulted in a net loss of winter habitat for females (Bowyer et al. 2001b). Similarly, spatial segregation of the sexes has implications for population dynamics of ruminants because females compete more intensely with each other and young than do males, which are spatially separated from females for most of the year. Consequently, density of females relative to  $K$  has a greater effect on recruitment of young than does density of males (McCullough 1979; Bowyer et al. 1999a).

**Density Dependence and Population Regulation.** Most life-history characteristics of large mammals are influenced by density-dependent mechanisms (McCullough 1979, 1999; Fowler 1987; Kie et al. 2003). Convincing empirical evidence of density dependence and its role in population regulation exists for cervids (Klein 1968, 1981; McCullough 1979; Clutton-Brock et al. 1982; Skogland 1985; Boyce 1989), including moose (Edwards and Ritchey 1958; Pimlott 1959, 1961; Coady 1982; Bowyer et al. 1999a; Ferguson et al. 2000). These studies provide strong support for conceptual models forwarded by Bowyer et al. (1997), Van Ballenberghe and Ballard (1998), and Kie et al. (2003) that density dependence as modified by predation, hunting, other mortality factors, and severe weather offer the best explanation for population dynamics among large herbivores. Evidence that intrinsic mechanisms regulate populations of large mammals is nil; likewise, documentation that altruistic behavior mediated via group selection plays a role in population processes of ungulates or their predators is lacking (McCullough 1979; Van Ballenberghe and Ballard 1998; Pierce et al. 2000). Some populations of northern cervids were thought to lack strong density dependence (Bergerud 1983a, 1983b; Gasaway et al. 1983; Boertje et al. 1996). That view resulted, in part, from difficulties in understanding complex interactions with weather, not examining populations over sufficient time or densities relative to  $K$ , and mistaking an overharvest

for a lack of density dependence (McCullough 1990; Bowyer et al. 1999a).

Effects of population density on dynamics of moose populations are mediated principally through the influence of nutrition on reproduction and successful recruitment of young into the population (Simkin 1974; Sæther and Haagenrud 1983; Schwartz and Hundertmark 1993; Keech et al. 2000). Quantity and quality of forage typically regulate moose populations at high density (Messier 1991). Nutritional effects on reproduction are the result of lax intraspecific competition at low population densities and intense competition at high densities relative to  $K$  (McCullough 1979; Kie et al. 2003). The outcome of that relationship is a parabolic function between recruitment of young and population size (Bowyer et al. 1999a) (Fig. 45.12). Maximum sustained yield (MSY), at the tip of the recruitment parabola (Fig. 45.12), is the maximal harvest from any source (or combination of causes) that a population can sustain on an annual basis without being driven to low density or extirpation. Kie et al. (2003) offered criteria for determining where the population is with respect to  $K$ .

Density-dependent mechanisms also may affect survivorship of adults, but reported survival rates generally are high (92%, Bangs et al. 1989; 91%, Larsen et al. 1989; 94.8%, Ballard et al. 1991; 88%, Bertram and Vivion 2002). Van Ballenberghe and Ballard (1998) noted that survival rates for adults generally ranged between 75% and 94%, depending on degree of human harvest. Moose populations exhibit a classic U-shaped curve with respect to mortality rate and age (Peterson 1978). For example, Gasaway et al. (1983) noted that survivorship decreased from 93% among 6- to 10-year olds to 79% among moose >10 years old.

How rapidly a moose population can increase and its potential yield are a result of the maximal intrinsic rate of increase ( $r_{max}$ ). Van Ballenberghe (1983b) believed that  $r_{max} = 0.35$  might be the limit moose could achieve under natural conditions. Cederlund and Sand (1991) observed  $r = 0.40$  for a moose population not experiencing heavy predation and suggested that  $r_{max} = 0.47$  might be possible. Bowyer et al. (1999b) reported values of  $r_{max}$  between 0.35 and 0.44 for moose on an island without predators or a severe winter climate. Such high values of  $r_{max}$  and the associated high potential yields indicate losses of moose to predation and severe weather might be higher than previously suspected (Bowyer et al. 1999b). Van Ballenberghe and Ballard (1998) provide additional population metrics for moose and equations for calculating those parameters.

Ballard et al. (1991) reported that crude densities of moose in Alaska ranged from 0.05 to 1.2 animals/km<sup>2</sup>. Gasaway et al. (1992) noted that moose densities were much lower (0.05–0.4 moose/km<sup>2</sup>)

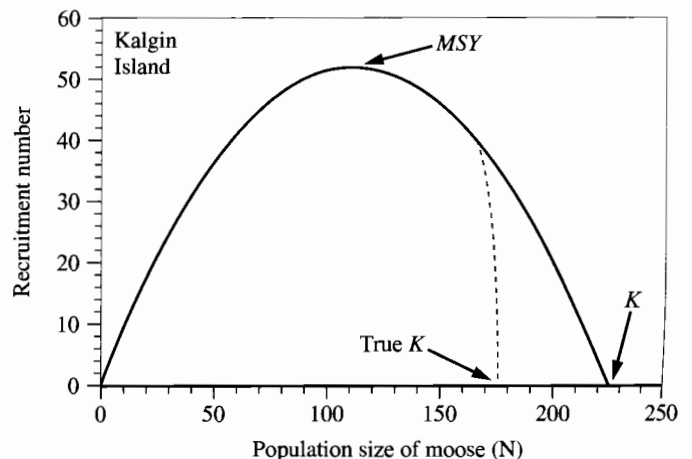


FIGURE 45.12. A recruitment parabola, illustrating yearlings successfully added to the population at differing population sizes for adult moose (*Alces alces gigas*), Kalgin Island, Alaska. Positions of maximum sustained yield (MSY) and ecological carrying capacity ( $K$ ) are depicted; true  $K$  is a correction for an overestimate of  $K$ . SOURCE: Data from Bowyer et al. (1999b).

across broad regions of Alaska where populations were subjected to heavy predation, but substantially higher densities (0.2–1.4 moose/km<sup>2</sup>) occurred where predators had been controlled. Peek et al. (1976) reported densities of 0.6–0.8 moose/km<sup>2</sup> in Minnesota, and Crête (1987) noted densities of 0.3–2.0 moose/km<sup>2</sup> in eastern Canada. Bowyer et al. (1999a) noted a peak of 3.5 moose/km<sup>2</sup> on Kalgin Island in Cook Inlet, Alaska. Comparisons of crude densities across broad areas, however, should be interpreted with caution because localized densities, such as moose congregating on rutting grounds, can be much higher (Molvar et al. 1993). Moreover, moose concentrating in riparian habitats, including surrounding areas that received less use, can confound assessments of crude density. Comparisons of crude density across populations also can be misleading because *K* may vary among populations, and some populations may be well below *K* (Weixelman et al. 1998; Bowyer et al. 1999b; Kie et al. 2003). Van Ballenberghe and Ballard (1998) emphasized that some populations might temporarily reach 5 moose/km<sup>2</sup>, but such high densities probably could not be sustained (Gasaway et al. 1992; Peterson 1999). Overshoots of *K* can be caused by populations irrupting after release from an important source of mortality and rapidly approaching *K*, an outcome that has implications for stability at *K*. McCullough (1979) noted that an overshoot of *K* resulted in a disproportionate decline in the ability of the habitat to support large herbivores.

Severe weather, especially deep snow, holds the potential to affect moose populations adversely (Peterson and Allen 1974; Peterson 1978; Mech et al. 1987). Young, old, and male moose may be most susceptible to mortality, including predation, during winters with deep snow (Coady 1982). Effects of severe weather, however, are seldom independent of population density (Bowyer et al. 1999b; Kie et al. 2003). Moose populations at low density relative to *K* may exhibit high twinning rates even following winters with unusually deep snow (Bowyer et al. 1998). Conversely, malnourished populations near *K* may suffer substantial mortality during winter, especially among young moose (Bishop and Rausch 1974). Understanding complex interactions between stochastic environmental conditions and population dynamics of large herbivores is a topic requiring more study (Sæther 1997).

**Interspecific Competition.** The geographic distribution of moose overlaps that of eight native ungulates as well as range cattle and, less commonly, domestic sheep. Competitive interactions with hares (*Lepus* spp.) and beaver (*Castor canadensis*) also are possible because of their similar range distributions and use of habitats (Boer 1998). Little interspecific competition is likely for moose and bighorn sheep (*Ovis canadensis*), Dall's sheep (*O. dalli*), or mountain goat (*Oreamnos americanus*) because those mountain ungulates occupy rugged, precipitous habitats at higher elevations than those generally used by moose (Bowyer et al. 2000; Krausman and Shackleton 2000; Peek 2000). Similarly, limited competition is expected between moose and muskoxen (*Ovibos moschatus*) because muskoxen inhabit tundra regions at the northern extent of the distribution of moose, and those bovids feed principally on graminoids (Klein 2000). Bison (*Bison bison*) similarly are primarily grazers and exhibit disparate food habits from moose where the two species are sympatric (Cairns and Telfer 1980). Nonetheless, willows compose a substantial proportion of the diet of bison translocated to interior Alaska (Campbell and Hinkes 1983), which might lead to dietary competition with moose.

Competition between caribou (*Rangifer tarandus*) and moose is thought to be slight (Davis and Franzmann 1979; Boonstra and Sinclair 1984), in part because of the more specialized diet of caribou and their more extensive use of lichens (Peterson 1955; Boer 1998). Indeed, analysis of stable isotope ratios ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) from moose and caribou indicate dietary differences between those large herbivores (Ben-David et al. 2001). Moreover, introduction of moose into Newfoundland did not reduce caribou numbers (Peterson 1955). Seip (1992) postulated that in multiple-prey ecosystems, high densities of moose could maintain wolf populations at levels that would intensify predation on caribou. Dale et al. (1994), however, noted that wolves preferred caribou to moose, and Coady (1980) ascribed an increase in moose numbers in

northern Alaska to wolves preferring caribou. Multiple-prey systems are complex (Gasaway et al. 1992; Dale et al. 1994) and variation in abundance of one ungulate is likely to have effects on that of another.

The distributional overlap between moose and mule deer is not extensive, although these cervids are sympatric in portions of the northern Rocky Mountains and along the southern border of the boreal forest (Boer 1998). Mule deer consume more forbs than do moose during summer (Kie and Czech 2000). Although both species eat browse in winter and some competition may occur (Prescott 1974), mule deer often overwinter at lower elevations than moose, thereby limiting competitive interactions (Telfer 1978; Boer 1998). Elk are primarily grazers, but have broad, flexible feeding habit, which include browse, especially in winter (Houston 1982; Boyce 1989; Boer 1998; Stewart et al. 2002). Cowan (1950) and Flook (1964) believed that elk possessed the capability to outcompete moose for food. More research is needed to elucidate interspecific relationships between these two cervid species.

White-tailed deer and moose are sympatric near the northern distribution of white-tailed deer and the southerly extent of moose (Boer 1998). The northern (and altitudinal) distribution of white-tailed deer is limited by winter conditions, especially snow depth, whereas moose are more affected by availability of browse than winter severity (Telfer 1970, 1978; Prescott 1974; Cairns and Telfer 1980; Telfer and Cairns 1986). In the Northeast, white-tailed deer yard in areas with coniferous overstories, which intercept snow and provide for easier travel (Telfer and Kelsall 1979); moose habitat is more dependent on stands of balsam fir. Competition for food between these cervids is only likely when moose move to areas with substantial overstory cover (Telfer 1970; Peek et al. 1976). Even where the spatial distribution of moose and white-tailed deer coincide and both consume largely conifers, only a 41.2% overlap occurred in their winter diets (Ludewig and Bowyer 1985). Habitat and dietary differences indicate strong niche partitioning between these cervids. Nonetheless, white-tailed deer in the Northeast may affect moose adversely via parasite-mediated competition by harboring meningeal worms (*Parelaphostrongylus tenuis*), which are benign in white-tailed deer, but can cause a neurological disorder and death in moose (Lankester and Peterson 1996).

Hares also may compete with moose for browse (Dodds 1960; Wood 1974). A high degree of overlap in winter diets has been reported (Telfer 1972; Oldemeyer 1975, 1983). Some partitioning of niche by hares and moose may occur based on foraging height (Telfer 1972; Oldemeyer 1974), but Belovsky (1984) noted that accumulating snow may allow hares access to higher branches because they can walk on top of snow. Competition between snowshoe hares (*Lepus americanus*) and moose likely occurs at peak hare densities (Wolff 1980). Beavers also may affect moose by creating aquatic habitat favored by moose, but browsing by moose may suppress growth of large trees preferred by beavers (Wolfe 1974). Because beavers are alternative prey for wolves, high densities of beavers may lessen predation on young moose in summer, but intensify predation on moose in winter when beavers are less susceptible to wolves (Shelton and Peterson 1983).

## MORTALITY

**Predation.** Considerable controversy exists over whether predation can regulate populations of moose, as well as the intensity of predation and species of predators that might be necessary to bring about regulation (Van Ballenberghe and Ballard 1998). Van Ballenberghe (1987), Skogland (1991), Boutin (1992), Messier (1994), Van Ballenberghe and Ballard (1994), and Ballard and Van Ballenberghe (1998) discussed hypotheses, study designs, and types of data critical to answering this ecologically important question. Whatever the exact mechanism and most appropriate model (McLaren and Peterson 1994; Peterson et al. 1998; Eberhardt and Peterson 1999; Eberhardt 2000; Messier and Joly 2000; Post et al. 2002; Vucetich et al. 2002), there is little doubt that large mammalian carnivores have the capability of holding moose populations at densities well beneath *K* (Crête and Jordan 1982a, 1982b; Bergerud et al. 1983a; Gasaway et al. 1983; Messier 1991; Gasaway et al. 1992; Bergerud and Elliott 1998). Predator control has brought

about increases in moose populations in some instances (Gasaway et al. 1992; Boertje et al. 1996), but has been less effective in others (Van Ballenberghe and Ballard 1998). Demonstrating population regulation (which requires density dependence) is difficult, however, and Crête and Courtois (1997) cautioned that limiting factors could obscure evidence of regulation in relatively unproductive habitats. Moreover, most studies considering moose-wolf relationships follow the method of Fuller (1989) by combining ungulate species into a single value for biomass available to wolves. That procedure does not consider differences in  $r_{max}$  among ungulate species. Thus, effects of population dynamics of prey on their abundance and, hence, availability to predators are not incorporated in such approaches (Person et al. 2001).

Debate also exists over the type of functional response (Holling 1959) that wolves exhibit with regard to changing densities of prey, including moose. Empirical evidence indicates a type II functional response, which has implication for potential equilibria between wolves and their ungulate prey (Dale et al. 1994; Messier 1994; Hayes and Harestad, 2000). Marshal and Boutin (1998) noted, however, that gathering data necessary to determine the shape of the functional response at low densities of prey (where type II and III curves differ most) was problematic. Person et al. (2001) reported that the shape of the functional-response curve affected equilibria only at extremely low densities of ungulate prey; relation of the ungulate population to  $K$  was more influential at higher densities.

Predation is the primary source of mortality for young moose in many populations, with most neonates killed by predators perishing within 6 weeks of birth (Franzmann et al. 1980; Ballard et al. 1981, 1990, 1991; Franzmann and Schwartz 1986; Larsen et al. 1989; Osborne et al. 1991; Testa et al. 200b). In those studies, brown and grizzly bears (*Ursus arctos*) or black bears (*U. americanus*), rather than gray wolves (*Canis lupus*), were largely responsible for killing neonatal moose. A review by Ballard and Van Ballenberghe (1998) reported that grizzly bears killed 3–52% and black bears 2–50% of young moose. Bertram and Vivion (2002) reported that black bears (45%) and grizzly bears (39%) killed most young moose in interior Alaska. Bowyer et al. (1998) noted that survivorship of young moose in a low-density population in Denali National Park and Preserve, Alaska, was reduced to about 0.2 after only 30 days of life, largely the result of predation by grizzly bears. Keech et al. (2000), however, observed nearly equal mortality of young caused by grizzly bears, black bears, and wolves in a growing population of moose in interior Alaska, where survivorship was about 0.5 after 1 year of life. Kill rates for grizzly bears on moose were 0.14–0.85 young/bear/day, whereas black bears killed moose at a rate of 0.02–0.09 young/bear/day in spring and summer (Ballard 1992).

Wolf predation on young moose is most pronounced in winter when bears are denning (Ballard et al. 1987; Gasaway et al. 1992). Wolves kill young moose disproportional to their occurrence in the population during that season (Ballard et al. 1987; Hayes et al. 2000). Mortality from wolves may reach 18% of young killed in some populations (Gasaway et al. 1983); Hayes et al. (2000) reported 12–55% of young moose killed by wolves, with a kill rate of 0.024 young/wolf/day during winter (Hayes and Harestad 2000). Mountain lions (*Puma concolor*) also may kill young and sometimes adult moose (Kunkel et al. 1999); principally male mountain lions kill moose (Ross and Jalkotzy 1996).

Losses of young moose to predators may be either additive or compensatory, depending on the population density of moose in relation to  $K$  (Ballard 1992; Ballard and Van Ballenberghe 1998; Person et al. 2001; Kie et al. 2003). Mortality in low-density populations tends to be additive, whereas populations near  $K$  exhibit higher levels of compensatory mortality, wherein one source of mortality is substituted for another (McCullough 1979; Ballard and Van Ballenberghe 1998; Person et al. 2001; Kie et al. 2003). Grizzly bears also may prey on adult moose at rates of about 0.02 moose/bear/day (Ballard 1992); black bears occasionally kill adult moose, but are not considered important predators on adults (Ballard and Van Ballenberghe 1998). Wolves kill older adults at rates of one adult /5–16 days (Peterson et al. 1984). Hayes et al. (2000) reported an overall kill rate of 0.045 moose/wolf/day during winter.

Physical condition of moose killed by wolves may be either poor or good (Peterson et al. 1984; Ballard et al. 1987), likely depending on the relationship of the population to  $K$  and winter conditions. Peterson et al. (1984) reported higher kill rates of moose by wolves in winter than during summer, but Ballard et al. (1987) observed no seasonal differences.

Ratios of predators to prey have been used widely to interpret effects of wolf predation on their ungulate prey (Person et al. 2001). If densities of wolves were greater than predicted, or if ungulate-wolf ratios were less than predicted, then wolves were presumed to be causing a decline in the ungulate population. Person et al. (2001) cautioned that these models assumed that wolf and ungulate populations were at or near equilibrium, and that the density of prey with respect to  $K$  had no effect on the number of wolves that could be supported. Moreover, Ballard et al. (1995) noted that predator-prey ratios were too variable to be predictive. Theberge (1990) argued that variation in the functional response of wolves to changing density of prey, prey-switching behavior by wolves, and the relation of the prey population to  $K$  would complicate interpretation of such ratios. Person et al. (2001) reported that equilibrium ratios between prey and wolves increased rapidly as the ungulate population grew beyond MSY toward  $K$ , and that wide confidence intervals occurred around wolf-ungulate ratios, necessitating caution in even a general interpretation of such values.

**Incidental Mortality.** Child (1998) provided an overview of incidental causes of mortality in moose. Collisions with automobiles (Grenier 1973; Child et al. 1991; Oosenbrug et al. 1991; DelFrate and Spraker 1991; McDonald 1991; Belant 1995) and trains (Child 1983; Child et al. 1991; Modiferi 1991; Belant 1995; Gundersen and Andreassen 1998) by far cause the most losses in this category of mortality. For instance, in the 1990s, automobiles killed 713, 600, 460, and 265 moose/year in British Columbia, Minnesota, Newfoundland, and Quebec, respectively. Similarly, annual mortality from collisions with trains killed >700 moose in one deep-snow winter in Alaska (Child 1998). Characteristics of highways and railways, including creating successional habitat and foods favored by moose and providing travel routes through deep snow, often lure moose to these dangerous thoroughfares. Moose naturally fluoresce under ultraviolet light, and car manufactures in Fennoscandia and Europe have equipped automobiles with ultraviolet headlights to make moose more visible at night (Child 1998).

Moose occasionally drown, especially in association with hydroelectric projects and reservoirs (Child 1998). Like most mammals, moose also suffer from accidental falls (Child 1998). Near Fairbanks, Alaska, a moose perished when it fell through the top of a septic tank and became tightly wedged in the tank and subsequently frozen into contents therein. Moose also are killed by avalanches and by becoming entangled in wire, cables, fencing, and even a garden hose (Child 1998). Attempts to mitigate some of this mortality have included creating pathways leading away from dangerous roads and railways, creating barriers to prevent moose from reaching such areas, and using light reflectors (Schwartz and Bartley 1991; Child 1998). Reducing speed of trains or having a pilot car precede the train has reduced accidental mortality in moose (Child 1998). Partial drainage of roadside salt pools, however, did not reduce moose-vehicle collisions in Quebec (Jolicoeur and Crête 1994).

**Diseases, Parasites, and Pests.** Anderson and Lankester (1974), Samuel et al. (1976), Lankester (1987), and Lankester and Samuel (1998) provided extensive reviews of those organisms capable of infecting or infesting moose. Population density of moose and their resultant physical condition, severe weather and its effects on moose as well as on intermediate hosts of parasites or directly on parasites and pests themselves, and the abundance of additional definitive hosts that serve as vectors all may exacerbate or limit diseases in moose populations. Indeed, moose are beset with a plethora of pests and parasites, some of which can cause serious diseases (Table 45.3). Only some of those disease-causing agents, however, are suspected of having the potential to adversely affect populations of moose. Although chronic wasting

TABLE 45.3. Selected parasites, pests, and diseases of moose (*Alces alces*)

Disease-Causing Organisms	Comment	Reference
<b>Viruses</b>		
<b>Arboviruses</b>		
Epizootic hemorrhagic disease (EHDV)	Transmitted by sand flies	Trainer and Jochim 1969
Bluetongue (BTV)	—	Hoff and Trainer 1978; Kocan et al. 1986b
<b>Bovine respiratory viruses</b>		
Bovine rhinotracheitis (IBRV)	Moose are seropositive, but no disease obvious	Kocan et al. 1986a
Parainfluenza type 3 (PI-3)	—	Lankester 1987
Bovine viral diarrhea (BVDV)	—	Kocan et al. 1986b
<b>Other viruses</b>		
Malignant catarrhal fever (MCF)	Domestic sheep likely vector; also present in free-ranging ungulates in Alaska	Thorne and Honess 1982; Williams et al. 1984; Zarnke et al. 2002
Contagious ecthyma	Experimental infection only	Zarnke et al. 1983
Rabies	Rare	Lankester and Samuel 1998
Adenovirus	In captive moose only	Shilton et al. 2002
<b>Spirochaetes</b>		
Leptospirosis ( <i>Leptospira interrogans</i> )	May cause abortion in severe cases	Thorne and Honess 1982; Kocan et al. 1986b
<b>Fibromas and other tumors</b>		
Infectious cutaneous fibromas	Infection by direct contact or maybe biting flies; self-limiting	Lankester and Samuel 1998
Lymphosarcoma	In abdominal cavity	Garner and Schwartz 1969
Myxoma	Cauliflower-like growth	Lankester and Bellhouse 1982
<b>Bacteria</b>		
Brucellosis ( <i>Brucella abortus</i> , <i>B. suis</i> , <i>B. ovis</i> )	Can cause abortion, stillbirths, and sterility; often infects joints	McCorquodale and DiGiacomo 1985; Dieterich et al. 1991; Honour and Hickling 1993; Forbes et al. 1996; O'Hara et al. 1998
Listeriosis ( <i>Listeria monocytogenes</i> )	Spread by direct contact or biting arthropods; rare in moose	Archibald 1960
Johne disease ( <i>Mycobacterium paratuberculosis</i> )	Lower digestive track; rare in moose	Soltys et al. 1967
Anthrax ( <i>Bacillus anthracis</i> )	Rare in moose	Choquette 1970
Tularemia ( <i>Francisella tularensis</i> )	More common in lagomorphs and rodents; rare in moose	Bourque and Higgins 1984
Erysipelas ( <i>Erysipelothrix rhusiopathiae</i> )	Cutaneous infection associated with hair loss caused by ticks	Campbell et al. 1994
Pinkeye ( <i>Moraxella</i> sp.)	From Wyoming	Thorne and Honess 1982
Actinomycosis ( <i>Actinomyces</i> sp.)	Abscesses and bone erosion of lower jaw (lumpy jaw)	Ritcey and Edwards 1958
Foot rot ( <i>Fusobacterium necrophorum</i> )	Necrotizing lesions in hooves; abscess formation in oral cavity and internal organs	Lankester 1987
Puss pockets or abscesses ( <i>Staphylococcus aureus</i> , <i>Acinetobacter</i> sp., <i>Actinomyces</i> sp.)	Often located on flank	Thorne and Honess 1982
<b>Protozoans</b>		
Toxoplasmosis ( <i>Toxoplasma gondii</i> )	Often spread by felids, can infect humans	Dubey 1981; Kocan et al. 1986a; Siepierski et al. 1990; Zarnke et al. 2000
<b>Other coccidia</b>		
<i>Sarcocystis</i> sp.	Spread by canids; causes unsightly cysts in muscles of moose	Dubey 1980; Dubey and Williams 1980; Lankester 1987
<i>S. alceslatrans</i>		
<b>Other protozoans</b>		
<i>Trypanosoma cervi</i>	Transmitted by horse flies; blood flagellate	Kingston 1981b
Amoeba resembling <i>Entamoeba bovis</i>	In cecum	Kingston 1981a
<b>Trematodes</b>		
Fascioloidiasis ( <i>Fascioloides magna</i> )	Does not reach maturity in liver of moose; can cause substantial pathology; aquatic snail intermediate host	Lankester 1974, 1987
Paramphistomiasis ( <i>Paramphistomum cervi</i> , <i>P. liorochis</i> )	No clinical disease, but large numbers of rumen flukes reported; snail is intermediate host	Snider and Lankester 1986
<b>Other flukes</b>		
<i>Zygocotyle lunata</i>	Occurs in intestine of waterfowl and occasionally moose; snail is intermediate host	Samuel et al. 1976; Stock and Barrett 1983; Hoeve et al. 1988
<b>Cestodes</b>		
Hydatid cysts ( <i>Echinococcus granulosus</i> )	Adult tapeworm in wolves; cysts occur mostly in lungs and may debilitate moose; eggs in wolf feces infective to humans, but cysts in moose are not	Anderson and Lankester 1974; Lankester 1987; McNeill and Rau 1987; Messier et al. 1989
Cysticerci ( <i>Taenia hydatigena</i> , <i>T. ovis krabbei</i> )	Wild canids definitive host; cysts occur in liver and muscles of moose, including heart; not substantial pathogens to moose; cysts in moose not infective to humans	Samuel 1972; Addison et al. 1979; Pybus 1990

(Continues)

TABLE 45.3—Continued

Disease-Causing Organisms	Comment	Reference
Fringed tapeworm ( <i>Thysanosoma actinoides</i> )	Bark lice intermediate host; occurs in small intestine and bile ducts; no obvious pathology	Stock and Barrett 1983
<i>Moniezia benedeni</i> , <i>M. expansa</i>	Free-living lice intermediate host; tapeworms can be long, but no obvious pathology to intestine	Thorne and Honess 1982
<b>Nematodes</b>		
Parelaphostrongylosis ( <i>Parelaphostrongylus tenuis</i> )	A parasite of white-tailed deer; gastropods are intermediate hosts; can cause severe neurological disorder in moose	Anderson 1972; Lankester and Anderson 1968; Anderson and Lankester 1974; Anderson and Prestwood 1981; Lankester 1987; Lankester and Samuel 1998
Elaphostrongylosis Tissue worm ( <i>Elaphostrongylus rangiferi</i> )	Restricted to Newfoundland; experimental infection produced neurological disease, but not yet observed in free-ranging moose	Lankester 1977; Lankester and Fong 1989; Olsson et al. 1995; Steen et al. 1997
<b>Lung nematodes</b>		
<i>Dictyocaulus viviparus</i>	Direct life cycle; adults occur in smaller bronchi; no obvious disease; most common in young	Gupta and Gibbs 1971
<i>Orthostrongylus macrotis</i>	Intermediate host slug or snail; parasite of mule deer reported in moose only from Alberta	Samuel et al. 1976; Stock and Barrett 1983
<b>Gastrointestinal nematodes</b>		
<i>Nematodirella alcidis</i>	Direct life cycle; occur in abomasum and duodenum; can cause enteritis and scouring	Stock and Barrett 1983; Fruetel and Lankester 1988; Hoeve et al. 1988
<i>Trichostrongylus</i> spp.	In abomasum; no obvious disease observed in moose	Stock and Barrett 1983
<i>Ostertagia</i> spp. Whipworm ( <i>Trichuris discolor</i> )	In cecum and colon; parasite of cattle; rarely associated with death in moose	Lankester and Samuel 1998
<b>Filarioid nematodes</b>		
Arterial worm ( <i>Elaeophora schneideri</i> )	Transmitted by horseflies; first-stage microfilariae in skin or blood; parasite of mule deer infects elk and occasionally moose; causes blindness	Worley et al. 1972; Madden et al. 1991
Legworm ( <i>Onchocerca cervipedis</i> )	Likely transmitted by black flies; adults occur in subcutaneous tissue around legs and feet; only reported from western Canada and Alaska, but may be more widespread	Samuel et al. 1976; Pledger et al. 1980
Abdominal worm ( <i>Setaria yehi</i> )	Perhaps transmitted by mosquito or stable fly; adults free in body cavity; may cause peritonitis	Anderson and Lankester 1974; Samuel et al. 1976
Rumen filarioids ( <i>Rumenfilaria andersoni</i> )	Vector unknown; in folds of rumen; only from northwestern Ontario; no obvious pathology	Lankester and Snider 1982
<b>Ticks</b>		
Winter tick ( <i>Dermacentor albipictus</i> )	All three parasitic stages occur on moose; spread by seed ticks on vegetation; grooming associated with ticks causes hair loss, which can kill moose; absent from Alaska and Newfoundland	Welch et al. 1991; Samuel and Welch 1991; Lankester and Samuel 1998
<b>Flies</b>		
Throat and nasal bot flies ( <i>Cephenemyia jellisoni</i> , <i>C. phobifera</i> )	Larvae deposited on muzzle, migrate to pharyngeal pouches at back of throat; not significant pathogen	Bennett and Sabrosky 1962
Moose fly ( <i>Haematobosca alcis</i> )	Closely associated with moose; both males and females feed on moose, often on rump or hindquarters; females deposit eggs in moose feces; may cause skin lesions on back legs of moose	Anderson and Lankester 1974; Burger and Anderson 1974; Pledger et al. 1980; Lankester and Sein 1986
Other biting flies	Most information from captive moose	Smith et al. 1970; Pledger et al. 1980
Stable fly ( <i>Stomoxys calcitrans</i> )		
Deer fly ( <i>Chrysops</i> spp.)		
Horse fly ( <i>Hybomitra</i> spp., <i>Tabanus</i> spp.)		
Black fly ( <i>Simulium</i> spp., <i>Prosimulium</i> spp.)		
Mosquitoes (Culicidae)		

SOURCE: Adapted from Lankester and Samuel (1998).

disease occurs in other free-ranging cervids in North America, moose have not been reported to harbor that disease (Williams et al. 2002). Lankester and Samuel (1998) proposed that pathogens capable of affecting populations of moose included the meningeal worm in eastern North America, the winter tick (*Dermacentor albipictus*), and perhaps the arterial worm (*Elaeophora schneideri*) in localized areas of western North America. In addition, the tapeworm that causes hydatid disease (*Echinococcus granulosus*) may debilitate moose, thereby making them more susceptible to wolf predation (Messier et al. 1989). We restrict our discussion to those important diseases of moose, although a broader

treatment based primarily on Lankester and Samuel (1998) is provided in Table 45.3.

The nematode *Parelaphostrongylus tenuis* (meningeal worm), which can cause a severe neurological disorder in moose, normally infects and is spread by white-tailed deer (Anderson 1972; Anderson and Lankester 1974; Anderson and Prestwood 1981; Lankester 1987, 2001; Dumont and Crête 1996; Nankervis et al. 2000). Lankester and Samuel (1998) provided an excellent overview of the life cycle of *P. tenuis*. First-stage larvae are passed in the feces of infected white-tailed deer. Those larvae are present only in the mucous layer on the

surface of fecal pellets (Lankester and Anderson 1968). First-stage larvae are extremely resistant to freezing and can withstand some drying (Shostak and Samuel 1984). Melting snow or rain release larvae into the soil, where some penetrate the foot of woodland snails or slugs; *P. tenuis* larvae then molt to the infective third stage. Those third-stage larvae are long lived and can overwinter in gastropods (Lankester and Anderson 1968). Numerous species of snails or slugs can serve as intermediate hosts. The small snails *Discus cronkhitei*, *Zonitoides* spp., *Succinea* spp., and *Cochlicopa* spp. and the slugs *Deroceras leae* and *D. reticulatum*, which are inadvertently eaten by ungulates, serve as primary sources for infection.

Once consumed by the herbivore, *P. tenuis* larvae penetrate the wall of the abomasum, move into the abdominal cavity, and migrate along nerves in the body wall to the vertebral canal. Larvae enter the tissue of the spinal cord and dorsal horns of the gray matter, where they molt to fourth and fifth stages. Adults ultimately migrate into the cranium and position themselves along large veins and sinuses in the dura. Following mating, female worms lay eggs, which are carried by the blood via the jugular to the right side of the heart, through the pulmonary artery, and into the lungs. First-stage larvae develop in the lungs and are moved by cilia on bronchi into the oral cavity, where they are swallowed and ultimately occur in deer feces. The life cycle requires 90–137 days from the time of infection (Lankester and Samuel 1998).

In white-tailed deer, *P. tenuis* causes no obvious disease, and deer may develop immunity to this parasite on initial infection (Slomke et al. 1995). In moose, however, considerable tissue damage to the spinal cord as well as a strong cellular reaction occur (Lankester and Samuel 1998); adult worms also may enter the brain tissue causing further neurological damage (Anderson and Prestwood 1981). The result for infected moose can include an abnormal tilting of the head, weakness in the hindquarters, aimless circling, and often death.

Although *P. tenuis* may complete its life cycle in moose with first-stage larvae released in feces, maintenance of this disease complex is thought to require white-tailed deer. For instance, several authors related frequency of disease in moose to the density of white-tailed deer (Karns 1967; Telfer 1967b; Gilbert 1974; Whitlaw and Lankester 1994a, 1994b). Strong circumstantial evidence exists that *P. tenuis* can limit moose numbers—infection with meningeal worms was long thought to be fatal for moose. Indeed, experimental infections with large numbers of larvae had catastrophic effects on moose, especially young animals (Lankester and Samuel 1998).

Expanding populations of moose in eastern North America in areas with substantial numbers of white-tailed deer (Lautenschlager and Bowyer 1985; Upshall et al. 1987; Thomas and Dodds 1988), however, caused a rethinking of traditional ideas concerning *P. tenuis* (Clark and Bowyer 1986; Nudds 1990; Lankester and Samuel 1998). Indeed, moose have increased elsewhere in the presence of high population densities of white-tailed deer (Aho and Hendrickson 1989). One explanation for that increase is that low-dose infections with *P. tenuis* provide a degree of immunity to moose (Lankester and Samuel 1998; Lankester 2001). That explanation alone, however, will not account for recent expansions of moose when they failed to do so in the past, even though adequate habitat was available. Consequently, some alteration in pathogenicity of *P. tenuis*, or an improved ability of moose to accommodate infection with this nematode more synergistically than in the past, is necessary to explain population expansion by moose; both are viable hypotheses (Clark and Bowyer 1986).

Winter ticks infest moose throughout much of their distribution, especially south of 60° N latitude. These parasites are absent from Newfoundland and Alaska (Lankester and Samuel 1998), although experimental evidence indicates winter ticks could survive in Alaska if introduced (Zarnke et al. 1990). Winter ticks have been recovered from moose in northern British Columbia (Samuel and Welch 1991). Winter ticks spend their three parasitic stages (larva, nymph, and adult) on a single host, which most often includes moose (Welch et al. 1991). Adult females drop off their host in late March or early April and lay eggs (Addison et al. 1998a), which do not hatch until summer. Infestation of moose occurs in late summer and autumn when moose brush against clumps of small (1 mm) seed ticks (larvae with three rather than

four pairs of legs) that have aggregated in large clumps at the tips of vegetation (Lankester and Samuel 1998).

Once larval winter ticks are on a moose, those parasites begin feeding on blood, which fuels the molt to the nymphal stage in November; nymphs (1.7 mm in length) likewise feed on blood from their host (Lankester and Samuel 1998). By mid-February, nymphs reach peak numbers and molt into adults. Adult males are 6.5 mm in length and are dark brown with a white cross-hatching on their backs, whereas females (7 mm) are dark reddish brown. Large ( $\leq 9.8$  mm) grayish ticks observed in late winter and spring are females engorged with blood. Adults reach peak numbers in late March–April; all ticks have dropped off moose by mid-May, and moose are free of ticks during summer (Lankester and Samuel 1998).

Samuel and Welch (1991) estimated the mean number of individual winter ticks on a moose from various areas in western North America was 32,500, with 18% of 212 moose with >50,000 ticks. This massive infestation with ticks results in excessive grooming by moose with concomitant loss of hair. Grooming begins in late February and results in a distinctive pattern of hair loss: damage to the coat starts at the neck and shoulders and progresses toward the withers and tail region (Samuel et al. 1986; Samuel 1991). Samuel and Welch (1991) reported that 89% of 724 moose from across North America exhibited evidence of hair loss from infestations with winter ticks. In addition to suffering hair loss, moose infested with winter ticks exhibit restlessness and chronic anemia, and have reduced fat reserves (Glines and Samuel 1989; Samuel 1991; Addison and McLaughlin 1993; DelGiudice et al. 1997; Addison et al. 1998b). Also, growth is reduced in young moose infested with ticks (Addison et al. 1994). Moose may help reduce infestation with ticks by evading seed ticks on vegetation, tolerating tick-foraging birds, and via grooming, which can reduce tick numbers (Samuel et al. 2000). Direct evidence that winter ticks affect population dynamics of moose is difficult to obtain. Nonetheless, losses of moose have coincided with major epizootics of winter tick (Lankester and Samuel 1998). Moreover, tick-induced loss of hair and other associated maladies likely interact with other factors, such as nutrition and climate, to affect mortality in moose (Lankester and Samuel 1998).

Mule deer are thought to be the usual host for the arterial worm, which is transmitted to moose by horse flies (*Hybomitra* and *Tabanus*), in localized areas of northwestern North America (Worley et al. 1972; Worley 1975; Madden et al. 1991). This nematode, which also infects domestic sheep, can complete its life cycle in moose. Adult arterial worms reside in small branches of the common carotid and internal maxillary arteries, where they can persist for up to 4 years (Hibler and Adcock 1971). First-stage larvae (microfilariae) are released and carried to capillaries of the skin on the face and forehead, where they are transmitted to horse flies seeking a blood meal. Few instances of this disease have been reported in moose, but arterial worms can be serious parasites of elk, where they cause blindness, necrosis of ears and muzzle, antler deformities, and damage to the central nervous system (Hibler and Adcock 1971). Infection of moose by arterial worms is restricted to where their distribution overlaps mule deer and black-tailed deer; whether this parasite can affect moose populations is uncertain (Lankester and Samuel 1998).

*Echinococcus granulosus* are diminutive, three-segmented tapeworms that reside in the small intestine of wolves, where these cestodes cause little harm. Proglottids of adult worms are passed in wolf feces, and eggs (oncospheres) are released into the environment, where they are consumed inadvertently by foraging moose (Lankester and Samuel 1998). Ultimately, eggs develop into hydatid cysts, which are bladder-like structures filled with fluid and numerous larvae (protoscoleces) resembling grains of sand. The most common location for hydatid cysts is the lungs, but cysts also occur in the liver of moose (Lankester 1987). The life cycle is completed when a wolf eats an infected moose; this parasite is uncommon outside the distribution of wolves (Anderson and Lankester 1974; Lankester 1987). Hydatid disease occurs in numerous ungulates and can infect domestic dogs. Human also can acquire this parasite, but only from eggs released in feces of canids, not from hydatid cysts in moose (Lankester and Samuel 1998).

The number and size of hydatid cysts, which range from pea sized to several centimeters in diameter, increase with the age of moose (McNeill and Rau 1987; Messier et al. 1989). Severity of infection with hydatid cysts also intensifies with increasing population density of moose (Messier et al. 1989). Cysts in the lungs make moose more prone to predation by reducing their stamina during pursuits by wolves (McNeill and Rau 1987), and wolves may recognize the vulnerability of infected individuals (Messier et al. 1989). Because predation has the potential to hold moose populations at low density (Gasaway et al. 1992), this parasite may affect dynamics of moose.

## MANAGEMENT

**Habitat.** Modification of habitat to benefit moose has included logging, mechanical crushing and disturbance, prescribed fire, and application of fertilizer and herbicides (for reviews Eastman and Ritcey 1987; Joyal 1987; Peek et al. 1987; Thompson and Euler 1987; Thompson and Stewart 1998). Outcomes from many management techniques, however, were not evaluated and their value to moose was uncertain (Oldemeyer and Regelin 1980). More recent studies have rectified that shortcoming (Lautenschlager et al. 1997; Rempel et al. 1997; Collins and Schwartz 1998; Stephenson et al. 1998b; Weixelman et al. 1998; Bowyer et al. 2001b), but much remains to be learned about manipulating moose habitat, especially from opportunities offered through adaptive management of boreal forests (Thompson and Stewart 1998).

Throughout much of the distribution of moose in North America, logging and subsequent production of forest products are the dominant land use; moose management often is a byproduct of industrial processes (Thompson and Stewart 1998). Use of herbicides following logging also can affect composition and abundance of browse in regenerating stands (Lautenschlager et al. 1989; Eschholz et al. 1996; Raymond et al. 1996). Clearly, logging can create successional habitats of value to moose. Peek et al. (1976) suggested that logging was more important than fire in producing high-quality habitat for moose in Minnesota. Indeed, clearcutting of forests has resulted in an increase in use of those areas by moose (Parker and Morton 1978; Monthey 1984).

Moose respond to regenerating browse in understories resulting from clearcutting; clearcuts with insufficient browse receive little use by moose (Matchett 1985; Kufeld and Bowden 1996). Moreover, even clearcuts with adequate browse may receive limited use by moose if those logged areas are too large and consequently have regrowing shrubs and trees far from concealment cover. Numerous authors have noted negative effects of distance from cover on habitat use and foraging behavior by moose (Hamilton et al. 1980; Mastenbrook and Cumming 1989; Molvar and Bowyer 1994; Tyers and Irby 1995; Weixelman et al. 1998). Kufeld and Bowden (1996) recommended that no point in a clearcut be >100 m from concealment cover. Bowyer et al. (2001b) further reported that male moose used an open area (200–800 m wide) of crushed willows with substantial forage, but females and young did so less often, ostensibly because of predation risk. Moose were more likely to be killed by wolves away from edges of small forest patches, indicating that sites farther from cover were more dangerous (Kunkel and Pletscher 2000). Alternatively, logged areas situated too near forest cover may lessen their value for moose. Todesco et al. (1985) reported that strip cuts 40–50 m wide accumulated more snow than nearby clearcuts, thereby making forage less available to moose in winter on those narrow cuts. Bowyer et al. (2001c) observed that foraging efficiency of mule deer declined both near and far from concealment cover, presumably because they were more vulnerable to ambush predators near cover and coursing predators farther away from cover. Moose also, may be susceptible to ambush predators such as mountain lions on small clearcuts and alter their behavior accordingly, but that outcome remains to be demonstrated.

Not all types of habitat manipulations will produce equivalent amounts of browse for moose. For instance, Lautenschlager et al. (1997) noted that forage production and digestibility of browse following cutting and controlled burning were similar. Those treatments were greater than on control plots or those defoliated by spruce budworm

(*Choristoneura fumiferana*) in Maine. Stephenson et al. (1998) reported that mechanical manipulation of plant communities without willow understories in Alaska were prone to colonization with unpalatable blue-joint reedgrass (*Calamagrostis canadensis*) unless mineral soil was exposed to allow seeds of willows to germinate. Collins and Schwartz (1998) reached similar conclusions for logged areas in that state. Temporal variation in the availability of browse also occurs on different types of habitat manipulations. Clearcutting and fire may take 15–20 years for maximal browse production for moose (Timmermann and Buss 1998; Weixelman et al. 1998), whereas Bowyer et al. (2001b) reported a threefold increase in dry weight of current annual growth for willows 3 years following mechanical crushing compared with an uncrushed site.

Habitat suitability models also have been developed and evaluated for moose (Allen et al. 1991). Timmermann and Buss (1998) emphasized that forest practices, especially clearcutting, needed to consider proximal relationships among cover, water, mineral licks, aquatic vegetation, and human disturbances if they are to be of value to moose. Indeed, Colecott and Gillingham (1998) reported that moose within 300 m of snowmobile activity altered their behavior and were displaced to less favorable habitats. Creating access for hunters also can affect moose populations. Several studies have reported disproportionately high moose harvests associated with increased road access (Lynch 1973; Eason et al. 1981; Bangs et al. 1984). Schneider and Wasel (2000) also noted effects of human settlement on density of moose. Moreover, manipulation of habitat to produce browse will have little benefit for populations held well below *K* by predation or overharvest (Bowyer et al. 2001b; Kie et al. 2003). Consequently, long-term planning for manipulations and subsequent production of suitable habitat is essential for productive populations of moose (Timmermann and Buss 1998).

**Harvest.** In the 1990s, moose were managed in 2 territories and 9 provinces in Canada and in 11 states of the United States; moose had stable or expanding populations in 3 additional states; in 2001, moose were harvested in Vermont (Timmermann and Buss 1995, 1998; Timmermann 2003). Goals for moose management include subsistence and sport harvests as well as nonconsumptive uses such as viewing (Timmermann and Buss 1998). Satisfying multiple objectives of landowners, hunters, and wildlife agencies is not simple (Messmer et al. 1998). Co-management of moose involving indigenous people is common in Canada (Marshal 1999). Wildlife species, including moose, have become an increasingly important component of the tourism industry (Snepenger and Bowyer 1990).

Population assessment underpins moose management throughout North America, and includes total counts, estimates, and indices of abundances as well as information on sex and age composition and harvests (Crichton 1987; Timmermann and Buss 1998). Groups of moose fecal pellets have been used widely as an index to population density (Bergerud and Manuel 1968; Krefting 1974b; Franzmann et al. 1976a). Defecation rates for moose in winter range from 13 to 21 groups/moose/day (Timmermann and Buss 1998); females defecate less often (14.6 groups/day) than males (19.6 groups/day) (Franzmann et al. 1976b, 1976c). Tracks in snow also have been used as an index to moose abundance (Weixelman et al. 1998; Bowyer et al. 2001); Lautenschlager and Jordan (1993) combined track and pellet group counts to improve the methodology. Controversy exists over use of those indirect methods to estimate moose numbers, especially counts of pellet groups (Timmermann and Buss 1998). Both techniques are best used as indices to population size rather than estimates. The volume of fecal pellets in winter also has been used to determine sex and age classes of moose (MacCracken and Van Ballenberghe 1987).

Ground-based surveys of moose (Peterson 1955; Pimlott 1959) as well as sightings by hunters or others have been used to index moose abundance, although dense vegetation may reduce detection of moose in some habitats (Timmermann and Buss 1998). Crichton (1993) noted the need for consistency in recording such data for valid comparisons among years. Road kills also have been employed as an index to population size (Alexander 1993; Hicks 1993). Hunter effort and success

(catch per unit effort) have been used to detect changes in population size of moose (Mercer and Manuel 1974; Crête et al. 1981; Crête and Dussault 1987; Hatter 1998, 2001). Bowyer et al. (1999b) cautioned, however, that catch per unit effort should not be used without an independent measure of population size because potential variation in skill of hunters over time led to anomalies in this measure. Where data on age structure are available, population reconstructions, including cohort analysis, also have been employed to estimate population size of moose from harvest (Fryxell et al. 1988; Ferguson 1993; Bowyer et al. 1999b). Such reconstructions assume equal catchability, as well as fixed fecundity and survivorship, which result in a stable age distribution; those assumptions are difficult to meet (Bowyer et al. 1999b).

Aerial surveys, including sampling transects and quadrats, are the most widespread method of estimating the size of moose populations. Timmermann and Buss (1998) provided a historical account detailing the development of methods that culminated in modern survey techniques for moose. Those techniques involve helicopters and fixed-wing aircraft (Crête et al. 1986; Smits et al. 1994). LeResche and Rausch (1974) and Bisset and Rempel (1991) noted that numerous variables could affect accuracy and precision of aerial surveys of moose, and that survey conditions needed to be similar among years to yield comparable results. Snow conditions and openness of habitat, in particular, affect census results (Gasaway et al. 1986). Modern techniques that stratify moose density before intensive sampling, thereby reducing variability in counts and increasing precision (Ward et al. 2000), stem from methods developed by Gasaway et al. (1986). These surveys recently have been improved by geostatistical analyses of spatial data, including use of the cokriging method to make predictions (Ver Hoef and Barry 1998; Ver Hoef 2000). Some aerial surveys have been augmented with infrared thermal imagery (Bontaites et al. 2000). Aerial surveys often incorporate a sightability correction factor (Gasaway et al. 1985b; Timmermann 1993; Anderson and Lindzey 1996; Lenarz 1998) to account for moose missed in the initial survey. This correction factor usually is obtained by intensively sampling some portion of a quadrat with an airplane or more efficient helicopter (Gasaway et al. 1986) or using radio-collared or obviously marked moose to account for missed individuals (Oosenbrug and Ferguson 1992; Peterson and Page 1993). Data on sex and age classes of moose often are obtained during aerial surveys; Timmermann (1993) and Timmermann and Buss (1998) provided criteria for determining sex and age classes of moose. Such data may supply information valuable for evaluating harvest (Timmermann and Rempel 1998), although composition estimates may be biased by the sexes spatially segregating during winter and some sex or age classes of moose being more difficult to observe than others (Peek et al. 1974; Miquelle et al. 1992). Data on age ratios, however, should not be used to estimate population size without some independent measure of rate of increase (Caughley 1974).

Timmermann and Buss (1998) discussed seasons, bag limits, firearm and other restrictions, including hunter eligibility and education, for legally taking moose in North America. Traditionally, harvests of moose have emphasized adult males. Alaska has restrictive regulations designed to prevent low male-to-female ratios (Schwartz et al. 1992). Those regulations allow the harvest of small males with a spike or fork on either antler (usually yearlings) or of large males with  $\geq 50$ -in. spreads (127 cm) or with at least three tines on the brow palm. The largest antlered males mate most often in moose (Van Ballenberghe and Miquelle 1993, 1996); hence, some hunting regulations based on antler size have the potential to eliminate high-quality males from the population. Simulations involving the genetics of antler growth coupled with density-dependent population responses indicated that particular hunting regulations could adversely affect the size of moose antlers, but that such changes would be small, slow, and easily altered by changes in management (Hundertmark et al. 1998).

Male-only harvests work well for populations held well below  $K$  by predation (Gasaway et al. 1992); the goal is to obtain the maximum number of recruits from females, and that outcome cannot be achieved if females are harvested from populations at low density (Fig. 45.12). Populations near  $K$ , however, benefit little from a harvest of all males if the

management objective is to maximize harvest. Males in populations of ungulates have a limited effect on recruitment rates of young, and high densities of females depress recruitment (McCullough 1979; Bowyer et al. 1999b; Kie et al. 2003). Consideration should be given to total sources of mortality in managing populations because harvest, crippling of animals in the hunting season that ultimately perish (Gasaway et al. 1983), predation (Gasaway et al. 1992), and other sources of mortality are likely to be additive at lower population densities with respect to  $K$  (Bowyer et al. 1999b; Kie et al. 2003). Obtaining data necessary to assess density-dependent recruitment (Fig. 45.12) or evaluate sources of mortality, however, can be a daunting task (Kie et al. 2003).

**Value and Hunting.** Moose have long played a role in myth, human subsistence, and recreation as well as served important roles in ecosystem structure and function. Wherever they have occurred in North America, moose have been intertwined inextricably with human culture since the late Pleistocene (Guthrie 1995; Reeves and McCabe 1998). These large mammals have provided spiritual, cultural, and subsistence values to indigenous people for centuries, and those values continue among many North American tribes throughout the range of moose (Feit 1987; Wolfe 1987).

Crichton (1998b) provided an excellent review of the means and methods of hunting moose as well as field dressing and the proper care and processing of hide and meat. In 1991, hunters across the northern United States and Canada killed an estimated 88,630 moose (Table 45.4). This harvest represents an approximate increase of 22% over the period from 1972 to 1982, when the annual harvest remained relatively stable. Timmermann (In press) estimated 82,619 moose harvested in North America during 2001, a decline of about 7% since 1991. Today, moose provide recreational hunting opportunities and are important components in local economies (Condon and Adamowicz 1995). Moose hunting in Alaska generates about \$31 million/year for the economy (Regelin and Franzmann 1998). In Ontario, hunters contribute  $>$ \$50 million annually (Ontario Ministry of Natural Resources 1980). Continent-wide, moose hunters spend about CDN\$464 million annually in pursuit of their sport (Bisset 1987). On a per-hunter basis, those expenditures amount to about \$600 per resident hunter, and

TABLE 45.4. Moose harvest in North America, 1972–2001

Jurisdiction	1972	1982	1991	2001
Alaska	5,700	5,900	6,100	5,509
Washington	—	—	8	64
Idaho	90	150	490	774
Utah	70	90	290	175
Wyoming	1,300	1,300	1,400	1,365
Montana	400	360	114	596
North Dakota	—	20	109	117
Colorado	—	—	7	64
Minnesota	370	760	410	125
Maine	—	880	960	2,550
Vermont	—	—	—	137
New Hampshire	—	—	89	378
Yukon <sup>a</sup>	—	1,000	640	743
Northwest Territories	—	130	140	1,400
British Columbia	14,300	12,800	13,500	9,200
Alberta	9,400	12,400	12,200	7,971
Saskatchewan	4,100	2,600	4,100	3,412
Manitoba	2,100	1,700	1,100	1,000
Ontario	13,800	10,700	11,000	11,000
Quebec	6,800	11,800	11,900	14,000
New Brunswick	1,000	1,300	1,700	2,537
Nova Scotia	400	160 <sup>b</sup>	113	180
Newfoundland	11,000	7,000	21,000	19,322
Total	70,830	71,070	88,370	82,619

SOURCE: Data from Timmermann and Buss (1995, 1998) and Timmermann (In press).

<sup>a</sup>Not counting harvest by Natives.

<sup>b</sup>Data from 1981.

more than \$1000 per nonresident hunter (Timmermann and Buss 1998). Moose hunting, however, occasionally has engendered controversy (Lautenschlager and Bowyer 1985; Crichton 1998b). Moose also have aesthetic values as well. Being able to see moose when afield or simply knowing they are present in boreal ecosystems is an important, if intangible, value attributable to moose (Franzmann 2000).

Moose can have negative economic effects as well. Each year, moose are involved in collisions with automobiles, trains, and even airplanes. Conservative estimates indicate 3500 moose/year are killed in vehicle collisions across North America (Child 1998). Negative aspects of such collisions, economic and otherwise, can include reductions in moose numbers, loss of recreational opportunities, increased risk to human life and property, rising insurance costs, and increased public dissatisfaction in seeing moose on roadways (Child 1998).

Perhaps most important, moose play significant roles in healthy ecosystems throughout their range. These herbivores can influence species composition dramatically among plants, alter forest structure, influence rates of nutrient cycling, and modify biological diversity (Molvar et al. 1993; Kie et al. 2003). Moose justifiably can be considered keystone species and as such, used as indicators of forest-management practices (Wallis de Vries 1995; Hobbs 1996).

### MANAGEMENT, CONSERVATION, AND RESEARCH NEEDS

Determining where a moose population is with respect to  $K$  (Kie et al. 2003) remains a major challenge. That knowledge is essential for the wise management of populations and for determining when predator control may be effective. Indeed, understanding that relationship is essential to managing predator-prey systems. Losses of young to predators in moose populations near  $K$  have little effect on population dynamics because of their compensatory nature (i.e., young likely would have perished from other causes anyway), but fatalities of young in low-density populations are added to other sources of mortality and can limit or regulate populations (Ballard and Van Ballenberghe 1998; Person et al. 2001; Kie et al. 2003). Interactions with harvest and severe weather may further complicate matters. Sorting among those factors and how they relate to the size of moose populations in relation to  $K$  is a fundamental management need. Moreover, there is a need to develop spatially explicit models for moose populations (McKenney et al. 1998).

Populations of moose should no longer be managed as if the sexes have similar requirements; they do not. The failure to consider sexual segregation in the management of moose has implications for estimates and indices of population size, understanding habitat requirements, habitat manipulation, and allowable harvest. Kie and Bowyer (1999) suggested the sexes of polygynous ungulates should be managed as if they were separate species. We concur.

Understanding how moose interact with their environment and their role in trophic cascades is an essential research need. Evidence exists that moose browsing and their deposition of urine and feces may have either positive or negative effects on nutrient cycling and other ecosystem processes. Knowledge of how moose population density influences that process is essential. We cannot manage all components of diverse ecosystems, and defining the role of keystone species, such as moose, is critical to the future management of boreal regions.

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