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Alces alces.

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***Alces* Gray, 1821**

Alces Gray, 1821:307. Type species *Cervus alces* Linnaeus 1758:66.
Alce Hamilton-Smith 1827:72. Renaming of Gray's *Alces*.
Alcelaphus Gloger 1841:143. Renaming of Gray's *Alces*, not of Blainville, 1816.
Paralces Allen 1902:160. Renaming of Gray's *Alces*.
Alce Simpson 1945:155. Proposed acceptance of *Alce* Frisch, 1775. Hershkovitz (1948:273) showed *Alce* Frisch, 1775, to be non-Linnaean and unavailable.

CONTEXT AND CONTENT. Order Artiodactyla, Suborder Ruminantia, Infraorder Cervoidea, Family Cervidae. The genus *Alces* has one extant species.

***Alces alces* (Linnaeus, 1758)**

Moose (North America), Elk (Eurasia)

Cervus alces Linnaeus, 1758:66 Type locality Sweden.
Cervus americanus Clinton, 1822:193. Type locality "country north of Whitestown" (probably in the western Adirondack region), New York.
Cervus coronatus Lesson, 1827:356. Type locality "Sa patrie est inconnue."
Alces europaeus Burnett, 1830:2. A *nomen nudum*.
Alces machlis Ogilby, 1837:135. Renaming of *alces*.
Alcelaphus alce Gloger, 1841:143 (not seen).
Alces antiquorum Rüppell, 1842:183. Renaming of *alces*.
Alces palmatus Gray, 1843:182. Renaming of *alces*.
Alces jubata Fitzinger, 1860:86. Renaming of *alces*.
Cervus cameloides Milne-Edwards 1867:377. Type locality Manchuria?
Alces gigas Miller, 1899:57. Type locality north side Tustumena Lake, Kenai Peninsula, Alaska.
Alces bedfordiae Lydekker, 1902:109. Indefinite locality.
Alces pfizenmayeri Zukowsky, 1910:807. Type locality Aldan River, Yakutia, Russia.
Alces columbae Lydekker, 1907:182. Type locality from Ontario. Regarded as indeterminable by Peterson (1950).

CONTEXT AND CONTENT (from Peterson, 1955). Context noted in generic account above. Formerly, distinct species were recognized from North America and Eurasia but now a single living species represented by seven geographic subspecies is recognized (Hall and Kelson, 1959; Peterson, 1952, 1955; Walker et al., 1968).

A. a. alces (Linnaeus, 1758), see above (*antiquorum* Rüppell, *palmatus* Gray, *jubata* Fitzinger, *typicus* Ward, *uralensis* Matschie, *machlis* Ogilby, *meridionalis* Matschie, *tymensis* Zukowsky, and *angusticephalus* Zukowsky are synonyms).
A. a. americana (Clinton, 1822), see above.
A. a. cameloides (Milne-Edwards, 1867), see above (*bedfordiae* Lydekker a synonym).
A. a. gigas (Miller, 1899), see above.
A. a. pfizenmayeri (Zukowsky, 1910), see above (*yakutskensis* Millais a synonym).
A. a. shirasi Nelson, 1914:72. Type locality Snake River, Lincoln County, Wyoming.
A. a. andersoni Peterson, 1952:24. Type locality "section 27, township 10, range 16, Sprucewood forest reserve (15 mi. E. Brandon), Manitoba."

DIAGNOSIS. Largest living member of the family Cervidae (Fig. 1). Means of measurements (mm) for adult females of *A. a. gigas* (n = 23) were: total length 3015, chest girth 2013, length of hind foot 815, and height at shoulder 1855. Measurements for adult males from the same population (n = 5) were: total length 3055, chest girth 2041 (Franzmann et al., 1978). Heaviest recorded live weights from *A. a. gigas* were 490 kg for an adult female and 595.5 kg for an adult male. Greater weights have been estimated and undoubtedly exist, but they lack confirmation (Franzmann, 1978). Peterson (1955) listed skeletal characteristics as: "skull greatly lengthened in premaxillary region; nasal region shortened with sizable nasal aperture; distance from front of nasal to front of premaxilla about equal to that from back of nasal to back of occiput; vomer lower posteriorly, not dividing aperture of posterior nares; lacrimal vacuity widely open, the pit well developed; maxillary canines usually absent in both sexes; lower canines incisiform, incisors but little differentiated; molars and premolars rather broad and low crowned. Median metacarpals united at cannon bone; lateral metacarpals strongly attenuated, rudimentary, with only distal ends developed as styloid vestiges (teleometacarpalian)." Adult males develop the largest antlers of living members of Family Cervidae, characterized by broad palmate structure with projecting tines. Maximum recorded antler measurements (mm) are: spread 2048; length of palm 1422; width of palm 705; circumference of beam 321 (Nesbitt and Parker, 1977). Ranges of cranial dimensions for adults of six subspecies (Peterson, 1952) (mm) were: length of skull, 538 to 686; mastoid breadth, 139 to 183; median palatal length, 297 to 390; and length of upper toothrow crowns, 136 to 162 (Fig. 2).

The "bell" (a pendulous dewlap of skin and hair at the throat) and the large, flexible, overhanging upper lip are distinguishing characteristics. Metatarsal and interdigital external glands are absent. Lacrimal and small tarsal glands are present. The coat consists of gray wool interspersed with light brown to black guard hairs. Guard hairs attain a length of 254 mm on the shoulder hump (Franzmann, 1978). The guard hairs of moose have a scale pattern distinguishable from that of other cervids (Williamson, 1951).

GENERAL CHARACTERISTICS. This largest of cervids has a heavy and deep body, long legs, short tail (80 to 120 mm), long ears (250 mm), and a long head with an overhanging muzzle marked by a triangular bare spot (Fig. 1). The scalelike guard hairs of adults vary from a light brown to black with shades of red and gray. Black shading occurs primarily on upper parts of the body and in low extremities. Some in prime coat, particularly males, appear nearly black. The underparts are generally shaded lighter, either gray or brown. White hair around the vulva on females generally is characteristic, but may be absent. Albinism may occur (Franzmann, 1978), and white or partially white moose have been reported (Troyer, 1980). Males develop large

FIGURE 1. An Alaskan cow moose with newborn calf (photograph by author).

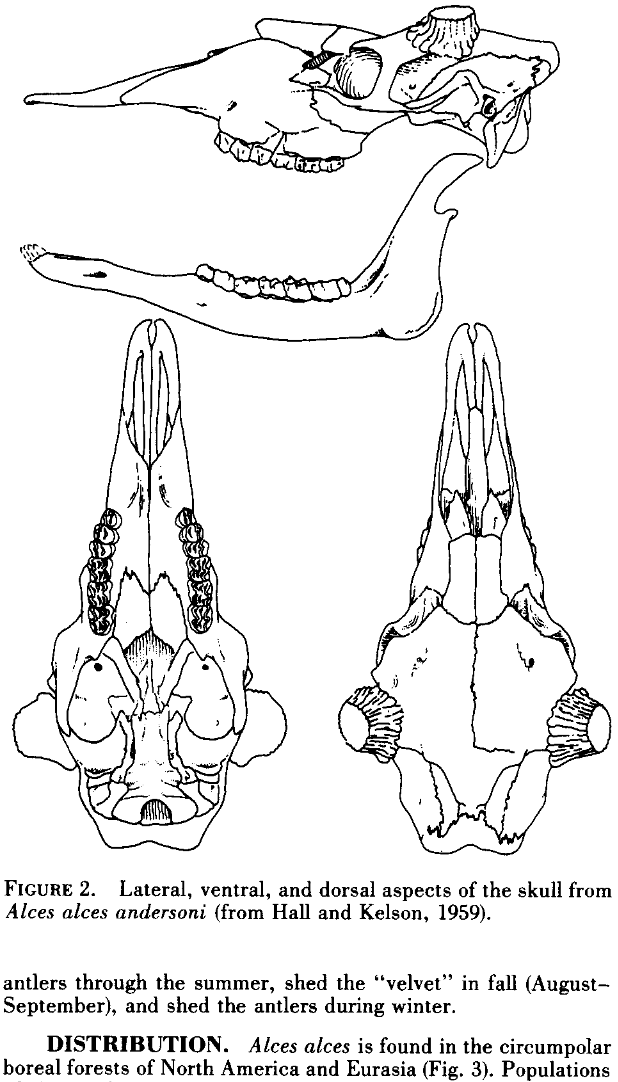

FIGURE 2. Lateral, ventral, and dorsal aspects of the skull from *Alces alces andersoni* (from Hall and Kelson, 1959).

antlers through the summer, shed the "velvet" in fall (August–September), and shed the antlers during winter.

DISTRIBUTION. *Alces alces* is found in the circumpolar boreal forests of North America and Eurasia (Fig. 3). Populations of *A. a. alces* occur in northern Europe and western Siberia, eastward probably as far as Yenisey River and Altai Mountains (Flerov, 1931). *A. a. americana* occurs from Maine and Nova Scotia westward through Quebec to central Ontario where it apparently intergrades with *A. a. andersoni* (Peterson, 1955). *A. a. americana* was introduced and established in Newfoundland. *A. a. cameloides* occurs in the Amur River region of extreme southeastern Siberia, northern Manchuria, and eastern Mongolia. Limits of its range are unknown. *A. a. gigas* occurs in Alaska, western Yukon Territories, and northwestern British Columbia. Peterson (1955) indicated that *A. a. pfizenmayeri* is similar to *A. a. gigas*, but that the nasal processes of the premaxillary bone extended further up the rim of the nasal aperture in the former. Yegorov (1972) referred to populations from the Kolyma and Indigirka basins in northeastern Siberia as *A. a. gigas*. Kistchinski (1974) indicated that *A. a. gigas* probably inhabited areas eastward of the Kolyma Basin. *A. a. pfizenmayeri* occurs in northern Siberia, eastward from the Yenisey River (Flerov, 1931), probably south to Sayan, Yablonovyy and Dzhugdzhur mountain ranges. *A. a. shirasi* occurs in western Wyoming, eastern and northern Idaho, northeastern Utah (Durrant, 1952), western Montana, northward into southwestern Alberta and southeastern British Columbia. A successful transplant of *A. a. shirasi* was made from Utah to western Colorado (Nowlin et al., 1979). *A. a. andersoni* occurs in northern Michigan and Minnesota, western Ontario, westward to British Columbia, north to eastern Yukon Territory and MacKenzie Delta, Northwest Territories (Peterson, 1955).

FOSSIL RECORD. The earliest known *Alces* was the savannah-dwelling *Alces gallicus* Azzarolli, which appeared in later Villafranchian (late Pliocene) to middle Pleistocene deposits in Europe. *A. gallicus* was similar in size to extant *A. alces* but antlers were characterized by a long beam and small palmation cupped upward and rimmed with small tines (Kurtén, 1968). Antler span was about 3 m. The largest known cervid was *Alces latifrons* Johnson from middle to late Pleistocene in northern Eurasia, Alaska, and Yukon Territory. *A. latifrons* measured 1900 to 2000 mm at withers and was characterized by reduction in length of beam, increase in size of palmation, heavy skull, and long and slender limbs (Kurtén, 1968).

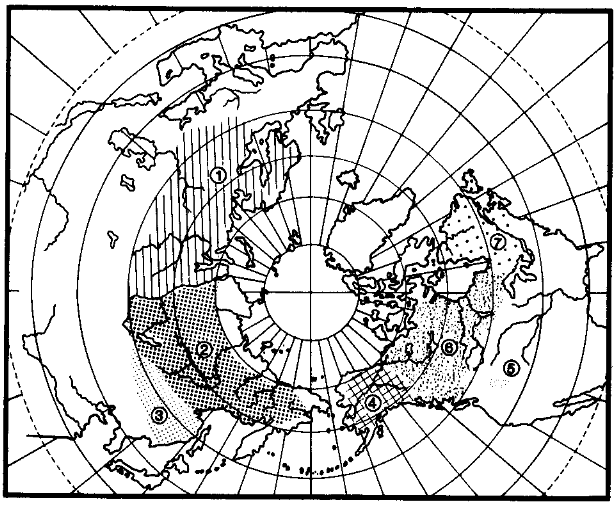

FIGURE 3. Circumpolar distribution of moose (from Peterson, 1974). 1, *A. a. alces*; 2, *A. a. pfizenmayeri*; 3, *A. a. cameloides*; 4, *A. a. gigas*; 5, *A. a. shirasi*; 6, *A. a. andersoni*; 7, *A. a. americana*.

Alces alces Linnaeus was first recorded from Riss Glaciation deposits (200,000 to 100,000 years B.P.) in Europe and from late Pleistocene in Siberia (Kurtén, 1968). *A. alces* reached North America during the late Wisconsinan in Alaska (Eschscholt Bay, Fairbanks, Gold Run) and the Yukon Territory (Old Crow River) and spread southward in the very late Wisconsinan/early Holocene (thus *Alces* was a late immigrant to North America) (Kurtén and Anderson, 1980). *A. alces* has been reported from 15 sites in British Columbia, Illinois, Kentucky, Michigan, Minnesota, Ohio, South Carolina, Washington, and perhaps Missouri, Oklahoma, and Pennsylvania. Some of these records may pertain to *Cervalces scotti* (Lydekker), a mooselike animal with long nasal bones and with a shorter antler beam than *A. latifrons*, but with complicated palmation. *Cervalces scotti* probably represents a transitional stage between *Libralces* (late Villafranchian, Europe) and *A. latifrons*. *A. alces* probably evolved in Eurasia from an *A. latifrons*-like ancestor. A trend in the evolution of *Alces* is the gradual shortening of the antler beam. European Pleistocene moose were larger than extant ones (Kurtén and Anderson, 1980).

FORM AND FUNCTION. The guard hairs, which may attain a length of 254 mm on the shoulder hump, and the undercoat of fine wool provide the insulating qualities which allow moose to inhabit the coldest regions of the world (Kelsall and Telfer, 1974).

Hair from 1,250 *A. a. gigas* collected from 12 regions in Alaska and analyzed for four macro-elements (Ca, K, Mg, and Na), four essential micro-elements (Cu, Fe, Mn, and Zn) and two non-essential micro-elements (Cd and Pb) indicated seasonal variation (Franzmann et al., 1975c) and variation among monthly regional samples (Franzmann et al., 1977). Use of the analysis of minerals in hair was proposed as a means of monitoring mineral intake and identifying the origin of hair samples (Franzmann et al., 1977).

Four mammae, located in the perineal region, produce milk with the following gross composition: total solids 24.54 ± 6.11% (n = 20); lipids 5.83 ± 2.78% (n = 8); ash 2.01 ± 0.26% (n = 5); crude protein 10.32 ± 2.24% (n = 17); lactose 6.81 ± 2.54% (n = 5); Kcal/g gross energy 1.42 ± 0.48 (n = 20); specific gravity 1.038 ± 0.014 (n = 3); and pH 6.76 ± 0.40 (n = 20) (Franzmann et al., 1975b). The ash component of milk from 21 *A. a. gigas* was analyzed for 18 elements and the means (ppm) and standard deviations reported were: Ca 1562.0 (232.4); K 1006.0 (85.4); Mg 192.8 (22.7); Na 394.3 (34.8); Al 1.24 (0.5); As < 0.05; Cd 0.06; Co < 0.01; Cr < 0.01; Cu 2.9 (0.128); Fe 3.12 (1.25); Hg < 0.05; Mn < 0.01; Mo < 0.01; Ni < 0.05; Pb 0.39; Se 0.11; and Zn 6.23 (2.34) (Franzmann et al., 1976a). Knorre (1961) concluded that wild moose produce about 150 liters of milk, but when domesticated produce 430 liters (Yazan and Knorre, 1964).

Antler growth was described by Peterson (1955) and follows a cycle similar to that of other cervids. Antlers in moose function primarily as organs of display and secondarily as weapons (Altman, 1959).

Comprehensive anatomical descriptions of moose are lacking. Peterson (1955) described some skeletal characteristics (see Diagnosis above) and pointed out differences in average size and shape of nasal apertures of subspecies. The dental formula for moose is i 0/3, c 0/1, p 3/3, m 3/3, total 32. At birth, deciduous incisors are generally functional and deciduous premolars are functional at 4 to 6 weeks of age. The first permanent incisors may erupt as early as month 6 after birth. The first molars are functional at month 4 to 6, second molars at month 10 to 13, and third molars at month 16 to 19 when full permanent dentition has been attained (Peterson, 1955). Tooth eruption (Peterson, 1955), tooth wear (Passmore et al., 1955), and incisor cross sectioning (Sergeant and Pimlott, 1959) have been used for ageing moose.

Baseline blood chemistry and hematological values from *A. a. gigas* were reported (Franzmann et al., 1976*b*; Franzmann and LeResche, 1978). Variations in blood values were detected for season, excitability, location, condition, sex, and lactation. Condition assessment of moose populations was described using selected blood parameters (packed cell volume, hemoglobin, calcium, phosphorus, glucose, total protein, albumin, and beta globulin) (Franzmann and LeResche, 1978). Blood urea nitrogen values reflected protein intake up to the point where protein catabolism provides substantial physiologic requirements (Franzmann et al., 1976*b*). Serum corticoid levels from 75 adults of *A. a. gigas* ranged from 17.6 to 148 mg/dl with levels increasing relative to increased handling stress (Franzmann et al., 1975*d*). Selected mineral elements levels in the blood (Ca, Mg, Cu, Zn) and hoof tissue (Cd, Cu, Fe, Mo, S, Zn) were reported for copper deficiency studies of moose (Flynn et al., 1977).

Moose consume large quantities of browse, but intake varies considerably with season. Weight of rumen and reticulum contents of an adult *A. a. gigas* in October was 59 kg, and in May averaged 29 kg ($n = 4$) (Coady and Gasaway, 1972). Visceral weight of six adults of *A. a. andersoni* whose body weight was over 385 kg ranged between 90.7 and 113.4 kg (20.5 to 28.7% of body weight) (Peterson, 1974). The digestive system of moose is adapted to handle primarily woody browse as indicated by food habit studies (Peek, 1974; Schwartz et al., in press). Browse is high in fiber lignin while grass is low in lignin (Oldemeyer et al., 1977).

ONTOGENY AND REPRODUCTION. Moose are seasonally polyestrus. The breeding season or rut is from early September to late October, peaking in late September and early October. The period of receptiveness for the cow lasts 7 to 12 days, but true estrus lasts less than 24 hours (Markgren, 1969). The interval between heats is approximately 20 to 22 days (Edwards and Ritcey, 1958). The peak breeding season falls within one estrous period, with one period earlier and perhaps one or two later periods accounting for only a small part of total pregnancies (Peterson, 1974); 89% of moose in British Columbia conceived within a 2-week period (Edwards and Ritcey, 1958). Females may potentially breed as yearlings (16 to 18 months) and reproduce yearly until year 18, but their maximum reproductive potential is from years 4 to 12. Spermatogenesis occurs in yearling males; thus they are physiologically capable of breeding (Houston, 1968). Breeding of yearling moose occurred in fall of 1979 at the Moose Research Center, Soldotna, Alaska, and a healthy male calf was born in May 1980 (author observation). Single calves are generally produced, but twins are not uncommon. Triplets were seen by the author in 1978 on the Kenai Peninsula, Alaska, and were reported previously by Peterson (1955), Hosley and Glaser (1952), and Skunke (1949), but are rare. Pregnancy and twinning rates of moose are functions of nutrition. The percentages of yearlings reported as pregnant from various regions reflect varying levels of nutrition: Ontario 17% (Simkin, 1965); Newfoundland 46% (Pimlott, 1959); British Columbia 0% (Edwards and Ritcey, 1958); Wyoming 5 to 6% (Houston, 1968); Montana 0% (Peek, 1962); and Sweden 75% (Markgren, 1969). The percentages of adults that are pregnant are more consistent and relatively high: Newfoundland 81% (Pimlott, 1959); Ontario 87% (Simkin, 1965); British Columbia 75% (Edwards and Ritcey, 1958); Alaska 93% (Rausch and Bratlie, 1965); Wyoming 90% (Houston, 1968); and Nova Scotia 70% (Pimlott, 1959). A low adult pregnancy rate (59.5%) was reported for an Alaskan population which was known to be undernourished (Franzmann et al., 1976*b*). A population may vary in twinning rate over time. A twinning rate of 22.2% was reported in 1978 for a population on the Kenai Peninsula, Alaska (Franzmann and Schwartz, 1979) and a rate of 12% was reported in the early 1950's (Spencer and Chatelain, 1953). Populations from other areas of Alaska had rates of 12% (Susitna Valley) and 33% (Alaska Peninsula) (Spencer and Chatelain, 1953). Other populations also have different rates such as: central Newfoundland 11% (Pimlott, 1959); southern Newfoundland 24% (Pimlott, 1959); Isle Royale, Michigan 5% (Murie, 1934); British Columbia 12% (Hatter, 1950); Ontario 23% (Peterson, 1955); Quebec 28% (Moisan, 1952); New Brunswick 17% (Wright, 1956); and Wyoming 15% (Denniston, 1956). The same area of Wyoming but 12 years later had a rate of 4.5% (Houston, 1968). Skunke (1949) indicated twins were the rule in the wild in Sweden, and reported two captive cows that had 36 calves from 19 pregnancies. Markgren (1969) also reported high, but variable, twinning rates from Sweden.

Markgren (1969) reported gestation ranged from 226 to 244 days ($\bar{x} = 234$) in Sweden which is shorter than the 240 to 246 days reported for North America (Peterson, 1955). Most calving occurs in late May and early June. As parturition approaches, the pregnant female seeks seclusion, and begins to drive her young of the previous year away. Yearlings do not stray far and may reassociate with their mothers within a few weeks after parturition (Altmann, 1958, 1959; Peterson, 1955). The cow generally gives birth lying down but may rise and lie intermittently through labor, which may take 15 minutes. After delivery the cow will rest and expell the afterbirth. The calf may initially nurse while the cow is lying down (Knorre, 1959). Markgren (1969) reported many observations of the cow consuming the afterbirth. The calf, weighing 11 to 16 kg, is generally up and standing the first day (Franzmann, 1978). The calf is licked copiously soon after birth and this activity continues regularly, establishing and maintaining the cow-calf bond (Stringham, 1974).

The pelage of newborn moose is light red to reddish-brown, with shades of gray to black on the lower abdomen, chest, and legs. The muzzle, hooves, eye rings, and ears are also shaded black. White hair is found in the inguinal area and inside the ears (Franzmann, 1978). After 2 or 3 months, the juvenile coat is replaced by a coat with similar but darker patterns of shading. In spring, moose shed their winter coat, which is rather dull in appearance. The new coat of short, fine hair is nearly black. As summer progresses, the guard hairs, which are scalelike structures, grow rapidly and generally produce a lustrous red-brown general appearance, with blackish shading, particularly on the lower extremities. Calves grow rapidly during their first 5 months averaging over 1 kg weight gain per day (Franzmann et al., 1978).

ECOLOGY. Moose require large quantities of food (19.5 kg/day; Morow, 1976) as well as high quality forage (Oldemeyer et al., 1977). Foods vary considerably, but in general are from early successional woody vegetation resulting from disturbances by fire, logging, clearing, flooding, and glacial action. Peek (1974) reviewed foods of moose in North America and concluded that willows (*Salix* spp.) were important to *A. a. shirasi* and *A. a. gigas*, and balsam fir (*Abies balsamea*), quaking aspen (*Populus tremuloides*), and paper birch (*Betula papyrifera*) were important to *A. a. americana* and *A. a. andersoni*. Local variations in forage preferences and availability are important as well (Krefting, 1974; Peterson, 1955). Morow (1976) reported that trees and shrubs constituted 87% of the diet of *A. a. alces* in Poland and that the most important species in quantity was pine (*Pinus silvestris*), composing 51.6% of diet. Ahlen (1975) reported that food of *A. a. alces* varied with locality in Norway and Sweden. Morow (1976) reviewed the literature on food habits from the USSR and determined that moose consume plants of 355 species, cultivated plants excluded; however, only 40 species were considered basic in their diet. Moose as a pioneering animal adapt to a variety of available forage, but certain species are preferred. When preferred plants are abundant, moose populations respond with improved reproductive success. This accounts, in part, for the historic population fluctuations of moose throughout their range. The variety of edible forage available throughout the year is important in balancing nutritive intake (Oldemeyer et al., 1977). During summer, moose utilize forbs and aquatic plants in many areas. Ground vegetation such as low bush cranberry (*Vaccinium vitis-idaea*) is much used in winter on the Kenai Peninsula, Alaska (LeResche and Davis, 1973). Markgren (1969) characterized moose as "nitrogen collecting species," due to their preference for juvenile plants, young shoots, and insolated plants.

Coady (1974) summarized knowledge of snow and moose relationships, pioneered by DesMeules (1964), Formosov (1946), Nasimovitch (1955), and Telfer (1970). Seasonal snow cover is characteristic of moose habitat throughout their circumboreal distribution. Long legs and tolerance to deep snow, as well as movement to favorable habitat when travel is laborious and food difficult to obtain, are important factors facilitating winter survival. Snow depth is the most important property of snow affecting moose. Nasimovitch (1955) indicated that moose were unaffected by snow depths of 40 to 50 cm, while movement was impeded by depths of 60 to 70 cm. He concluded that depths of 90 to 100 cm were critically limiting. These findings were corroborated in other regions (Kelsall, 1969; Kelsall and Prescott, 1971; Telfer, 1970). Snow hardness is perhaps the next most important property of snow; it determines both the force which must be exerted to move through snow, and the ability of snow to support the animal (Coady, 1974). Density and temperature of snow interact to determine the degree of hardness, therefore both properties are important. Peterson and Allen (1974) reported that wolves (*Canis lupus*), a major predator of moose, are hampered by deep snow of low density, but benefit from increased density and crusting conditions associated with mature snow. Although snow may not cause moose migrations, it does influence the timing and distance of movements. A complex of factors primarily related to snow depth, density, hardness, and persistence was responsible for the death of nearly all calves produced in 1971 on the Kenai Peninsula, Alaska, during the following winter (Franzmann, 1978).

Moose winter successfully in some of the coldest regions of the world. Areas with climates that exceed 27°C for long periods and that lack shade or access to lakes or rivers do not support moose (Kelsall and Telfer, 1974).

The impact of wolves on moose populations is influenced by many factors which were outlined in a review of ungulate predation by Connolly (1978). Wolf to moose ratios of 1:20 or less result in high annual losses to predation which can cause declines in moose populations (Alaska Dept. Fish and Game, 1979). When the ratio of wolves to moose was relatively low, the moose population was stable (Mech, 1966, 1970), but when the ratio of wolves to moose increased, predation on moose increased and became the principal mortality factor (Peterson, 1977). When severe winter and snow conditions persisted, selective predation on weak, young, and old moose by wolves was not evident in Alaska (Franzmann and Arneson, 1976). Wolves kill vulnerable animals, and various conditions affect vulnerability.

On the Kenai Peninsula, Alaska, the black bear (*Ursus americanus*) was the most important predator of newborn calves during early summer, with 34% of the radio-collared calves killed by black bears, 6.4% by brown bears (*Ursus arctos*), and 6.4% by wolves (Franzmann and Schwartz, 1979). Brown bears are in low density on the Kenai Peninsula and are not major predators of moose. In other regions, brown bears are major predators; their impact depends upon the ratio of predator to prey numbers. In the Nelchina Basin, Alaska, brown bears were the primary predators of newborn moose calves (Ballard et al., 1979). Lykke and Cowan (1968) indicated that brown bears can kill all sex and age classes of moose; however, with a low ratio of brown bear to moose in Scandinavia, their impact was relatively insignificant (Haglund, 1974). Brown bears are present in Russia and their predation on moose has been reported (Knorre, 1959).

In eastern and central North America, where moose and white-tailed deer (*Odocoileus virginianus*) are in close association, a neurological disease occurs in moose (Anderson, 1964). White-tailed deer are the normal primary host for this parasite, *Parelaphostrongylus tenuis*, and suffer no apparent harm from its presence. However, when the parasite is ingested by moose, it invades the brain and causes incoordination, lameness, stiffness, weakness, circling associated with blindness, and eventually paralysis and death (Anderson, 1964). This disease has caused declines in moose populations in Nova Scotia and New Brunswick, and may have been responsible for similar declines in Maine and Minnesota (Anderson, 1972). The parasite is common in southwestern Ontario (Anderson, 1964) and has been found in Manitoba (Bindernagel and Anderson, 1972). Liver flukes (*Fascioloides magna*) greatly damage liver tissue of moose (Lankester, 1974) and may negatively affect their development (Karns, 1976). Liver lesions called "liver rot" have been observed (Anderson and Lankester, 1974). The moose tick (*Dermacentor albipictus*) infests moose in North America, except for Alaska and the Yukon Territory. Heavy infestations have a detrimental effect and may even cause death (Anderson and Lankester, 1974). Although many parasites and infectious diseases have been reported in moose (Anderson and Lankester, 1974; Peterson, 1955), most are not associated with significant mortality. Reports of noninfectious diseases of *Alces* are few, considering the potential syndromes of metabolic, deficiency, stress, degenerative, congenital, physical and chemical diseases which may occur. Noninfectious diseases reported are limited to capture myopathy (Haigh et al., 1977), malnutrition (Franzmann and Arneson, 1976; Franzmann and LeResche, 1978), copper deficiency (Flynn and Franzmann, 1974; Flynn et al., 1977), and various diseases of physical and chemical origin (Franzmann, in press; Peterson, 1955).

Accidents, such as falling through ice (Allen, 1979; Hosley, 1949; Peterson, 1955), miring in deep marshes and bogs (Chamberlin, 1975; Munro, 1947; Murie, 1934), falling into mine pits (Allen, 1979), locking antlers (Franzmann, 1978; Peterson, 1955), and forest fires (Peterson, 1955) have been reported to cause death. Motor vehicles and railroad trains are responsible for a significant number of deaths of moose (Franzmann, 1978; Atwood, 1952; Peterson, 1955; Rausch, 1957), primarily when deep snow conditions cause animals to travel on roads and railroads.

Direct competition for forage between moose and other animals is minimal except under conditions of extensive forage depletion and severe weather conditions (Wolfe, 1974).

Moose are classified and managed as game animals throughout most of their range. Sweden has the most productive populations, 70,000 being harvested in 1977 (Hansson and Malmfors, 1978) and 94,000 in 1978 (Wilhelmson and Sylven, 1979). The 1978 harvest produced 12 million kg of meat, which represented 2 to 3% of the total meat production of Sweden.

BEHAVIOR. Moose are essentially solitary and have one or several seasonally distinct home ranges to which they are strongly attached (Berg, 1971; Geist, 1963; Houston, 1968; Krafft, 1964; LeResche, 1974; Markgren, 1972; Pulliainen, 1974; VanBallenberghe and Peek, 1971). Movements between seasonal home ranges may be extensive, but home ranges are generally small, varying from 2.2 km^2 (Knowlton, 1960) to 16.9 km^2 (Berg, 1971). Individuals generally retain the same home ranges from year to year (DeVos, 1958; Geist, 1963; Houston, 1968; Knowlton, 1960; LeResche, 1972; Markgren, 1972; Pulliainen, 1974), and travel the same routes between ranges (Berg, 1971; Houston, 1968; LeResche, 1972). In addition to regular movements, moose may exhibit nomadic movements, which cause dispersal (Pulliainen, 1974). Vast areas of Europe have been successfully reinvaded by moose, especially since World War II (Pulliainen, 1974).

Although cows with calves may be the exception (Altmann, 1958; LeResche, 1966), moose are not considered territorial (Geist, 1963). The strength of the cow-calf bond may influence territorial behavior, as this bond is extremely strong during the first weeks of the calf's life. The strength of the bond diminishes with time and the calf becomes increasingly independent. Survival chances for the calf are somewhat dependent upon the cow-calf bond, but survival of motherless calves has been reported (Burris and McKnight, 1973; Markgren, 1975). Altmann (1958) listed four phenomena of calf maturation: (1) the solitary upbringing of the calf by its dam, applying a ring of "sliding territoriality" around it for 90 days; (2) the imprintability or heeling response of the calf and its possible later return to this condition if in need of attachment through the loss of its dam; (3) the social integration of the calf during the dam's rutting season; and (4) the continuation of bonds between the cow and calf beyond the nursing and weaning period.

Altmann (1959) outlined a sequence of behaviors of rutting bulls. The build-up, challenger gait is characterized as a swaying gait with the heavy antlers dipping from side to side, and is usually executed in stiff, long strides in circles around the rival bull. The mock-battle is marked by hitting and shredding trees and shrubs before the beginning of the fight. During these two stages it is possible for one of the rivals to withdraw. Displacement feeding is signaled by either browsing or grazing with hasty, jerky movements and exaggerated intensity, with the eyes fixed on the opponent. Reinforcement of drive is achieved by: occasional return to the cow, sniffing her, and curling the upper lip with head raised high; activation of a wallow or making a new wallow and rolling in it; or hitting and rubbing shrubs and young trees with the antlers. Next, the rivals fight, or yield. Battles are carried out as a constantly fluctuating affair. The antler-pushing action of one bull is received by yielding movements of the opponent. After six or more steps backwards, the yielding bull braces himself and pushes forward. If one of the opponents slips or stumbles, he may be hit in the ribs or flank. The battle may end with the rapid withdrawal of the beaten opponent (most cases), or there may be a gradual stalemate. In the latter case, the two rivals engage in displacement activities by browsing, grazing, or tussling in the shrubbery, keeping each other under tension for hours until one leaves the area. The cow stands quietly or browses nearby during the whole conflict. Lastly, the driving and mating stage ensues when the bull drives the cow, mounts her, and, if she stands, breeds her repeatedly over a 1- to 2-day period.

Variations of this behavior pattern occur. An encounter between two males may simply be a "sizing-up" of one another's antler development, size, and condition, followed by one or both moving off (Lent, 1974). The other extreme is aggressive fighting, which may on occasion result in death (Peterson, 1955; Markgren, 1969). During rut, cows are very aggressive and assume an active and independent role. Lent (1974) listed three aspects of this behavior: (1) the lack of male control over female activities; (2) the unusual use of vocal signals by females; and (3) under certain conditions, the great mobility of females.

Lent (1974) described male vocalization during the rut as a "croak," and distinguished it from the "grunt" of cows communicating with calves. During the breeding season cows emit a long quavering moan, audible at a distance of 3.2 km (Lent 1974). A whine of appeasement by both sexes and a "bark" by males in large breeding pods were described by Lent (1974). In extreme stress, a "roar bellow" is made by adults (Franzmann, 1978; Geist, 1963; Lent, 1974).

Geist (1963) described basic behavior patterns of *A. a. andersoni*. Comfort movements included stretching, yawning, shaking, rubbing, scratching, urinating, defecating, and lying down and getting up. He found that 67% of all comfort movements fell into the first and last 5 minutes of activity. Defecation rates were reported for *A. a. gigas* as 19.6 pellet groups/day for adult males, and 14.6 pellet groups/day for adult females during winter (Franzmann et al., 1975*a*). The mean number of beds per day during winter was 5.5. When excited, both males and females may urinate on their hind legs (Geist, 1963). Winter feeding on browse may be accomplished by reaching for a twig, seizing it between incisors and palate, and cutting it off with an upward jerk of the head. Thicker stems may be broken off in order to feed on the more palatable twigs (Geist, 1963).

Females generally fight by striking with front feet; males sometimes fight this way. Males generally fight with their antlers in fall and early winter, and threat and defense behaviors vary accordingly (Geist, 1963). In general, threat behavior in males is assumed by head-high, head-low, or antler threats. With a head-high threat, the ears are pointed back, but hairs are generally not raised. This threat appears to be a dominance threat. With the head-low threat, the ears are down and the hairs on the neck, withers, and rump are raised. The antler threat is generally from the head-high position with the bull facing its opponent (Geist, 1959). Bubenik (1973) considered antlers as releasers of behavior and of extreme significance in the social life of *Alces*. He described antler gestures as being either frontal or lateral, with the head held horizontally or directed down so that it nearly touches the ground. In each of these positions, the color patterns and the apparent size and shape of the antlers change abruptly (Bubenik, 1977). The opposing animal likely perceives these changes and responds appropriately (Bubenik, 1973).

Geist (1963) recognized several forms of play activity in *Alces*: running and turning in short radii; running through water; splashing in water; fake charges; fake fighting; and alternately chasing one another. More than 50% of the play activity involved running.

Studies of activity patterns have been made on a limited number of moose (Denniston, 1956; DeVos, 1958; Geist, 1959, 1963). There is general agreement that peaks of feeding activity occur at dawn and dusk. A nighttime peak in movements was reported by Phillips et al. (1973). VanBallenberghe and Peek (1971) noted equal amounts of movement by day and night for a cow and calf. Joyal and Scherrer (1978) reported that 60% of movements were nocturnal.

GENETICS. Karyotypes prepared from tissues of five *A. a. alces* in Sweden had chromosome counts of 2n = 68 (Gustavsson and Sundt, 1968). This is in agreement with findings of Aula and Kääriäinen (1964), who considered the Y to be a submetacentric chromosome. There are 66 autosomes; all are telocentric except two pairs, which are metacentric or submetacentric. Hsu and Benirschke (1969) found chromosome counts from skin biopsies of *A. a. shirasi* and *A. a. americana* of 2n = 70, with two submetacentric and 66 acrocentric chromosomes. Nadler et al. (1967) reported that serum proteins of *A. a. gigas* were similar to those of *A. a. alces* (Braend, 1962). There was no intraspecific polymorphism of the proteins, including transferrins.

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