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Ovis canadensis.

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Ovis canadensis Shaw, 1804

Bighorn Sheep

Ovis canadensis Shaw, 1804:pl. 610. Type locality Exshaw, Alberta, Canada.

Ovis cervina Desmarest, 1804:5 (=Shaw's *O. canadensis*).

Ovis montana Schreber, 1804:pl. 294 (=Shaw's *O. canadensis*).

Ovis pygargus Griffith, 1827:318 (=Shaw's *O. canadensis*).

Ovis californianus Douglas, 1829:332. Type locality near Mt. Adams, Yakima County, Washington.

Ovis nelsoni Merriam, 1897:218. Type locality Grapevine Mountains, boundary of Inyo County California and Esmeralda County, Nevada, south of lat. 37°.

Ovis mexicanus Merriam, 1901:30. Type locality Lake Santa Maria, Chihuahua, Mexico.

Ovis sheldoni Merriam, 1916:130. Type locality El Rasario, Sonora, Mexico.

CONTEXT AND CONTENT. Order Artiodactyla, Suborder Ruminantia, Infraorder Pecora, Family Bovidae, Subfamily Caprinae, Tribe Caprini. The genus *Ovis* has six extant species in two subgenera. There are seven recognized subspecies of *Ovis canadensis* of which one is extinct:

O. c. canadensis (Shaw, 1804:pl. 610), see above (*typica* Lydekker, *cervina* Desmarest, *montana* Cuvier, *ammon* Mitchell, and *pygargus* Hamilton-Smith are synonyms).

O. c. californiana (Douglas, 1829:332), see above (*similkameenensis* Millais, *sierrae* Lydekker, and *ellioti* Kowarzig are synonyms).

O. c. nelsoni (Merriam, 1897:218), see above.

O. c. mexicana (Merriam, 1901:30), see above (*gaillardi* Mearns, *texianus* Bailey, and *sheldoni* Merriam are synonyms).

O. c. auduboni Merriam, 1901:31. Type locality upper Missouri, probably badlands between Cheyenne and White rivers, South Dakota. Recently extinct (Cowan, 1940).

O. c. cremnobates Elliot, 1903:239. Type locality Mattomi, Sierra San Pedro Martir, Baja California.

O. c. weemsi Goldman, 1937:30. Type locality Conjon de Tecomaja, Sierra de la Giganta, about 30 mi S Cerro de la Giganta, southern Baja California.

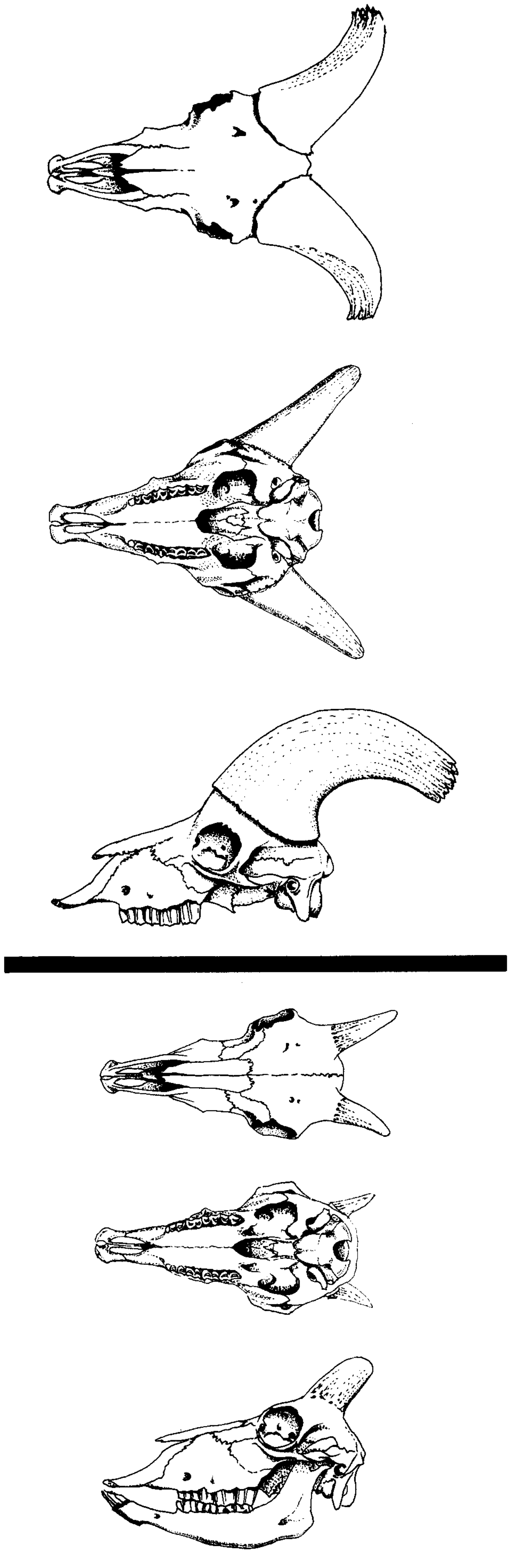
DIAGNOSIS. *Ovis canadensis* is the largest of the two species of North American mountain sheep, although size-ranges overlap. Color is always brown but varies between reddish brown and dark chocolate. Muzzle, rump patch, posterior of legs, and usually belly are white (Fig. 1). Upper side of short tail (70 to 130 mm) is always dark brown-black. There is no neck ruff. Horns are massive and curled forward alongside face (Fig. 1), and together with skull, may represent over 10% of total body mass in adult males (Blood et al., 1970; Geist, 1971). Underlying horn cores have blunt tips (Fig. 2). The lacrimal pit is shallow and weakly defined.

Ovis canadensis can be readily distinguished externally from *O. dalli dalli* because latter is all white, except in some individuals with a dark tail. The subspecies *O. d. stonei* varies in color from grizzled white to brownish black but is generally greyer than *O. canadensis* (Cowan, 1940).

GENERAL CHARACTERISTICS. *Ovis c. canadensis* and *O. c. californiana* generally appear darker brown than other subspecies (Cowan, 1940; Hansen, 1980*a*). The anterior portion of the rostrum, underbelly and posterior margins of the legs are light colored, verging on white. The light fur on the hindlegs is continuous with a distinctive white rump patch (Fig. 1). A blackish-brown stripe, originating at the tip of the tail, extends anteriorly across the rump patch, continuously in some populations.

External sexual dimorphism is obvious (Fig. 1); horn and body size are the key secondary sex characteristics (Cowan, 1940; Geist, 1971). The greatest mass for an adult male is 137 kg, recorded for an *O. c. canadensis* ram in Jasper National Park, Alberta (Stelfox and McGillis, 1970). Mean weights (in kg) for males 4 years and older are: *O. c. canadensis* and *O. c. californiana*, 95 (Blood et al., 1970; Shackleton and Shank, in press); *O. c. nelsoni*, 73 to 91 (Hansen, 1980*a*); *O. c. mexicana*, 76 (Remington, 1982). For females the maximum recorded weight is 91 kg for *O. c. canadensis* from Waterton Lakes National Park Alberta (Blood et al., 1970), with mean adult female weights (in kg) being: *O. c. canadensis* 71 (Blood et al., 1970); *O. c. californiana*, 61 (W. L. Harper, pers. comm.); and *O. c. nelsoni*, 48 (Hansen, 1980*a*); and *O. c. mexicana*, 59 (Remington, 1982). Body dimensions (in mm) of adults vary between subspecies and populations, ranging as follows: total length, 1,530 to 1,953 (males), and 1,245 to 1,530 (females); tail length, 100 to 127 and 70 to 130; hindfoot length, 394 to 440 and 315 to 420; ear length, 100 to 130 and 90 to 127 (Cowan, 1940; Geist, 1971; Hansen and Deming, 1980). Significant variation in cranial dimensions is apparent within and between subspecies (Bradley and Baker, 1967; Shackleton, 1973). Ranges of some mean cranial dimensions (in mm) are: basilar length, 258 to 287 (males) and 228 to 252 (females); nasal length, 112 to 124 and 91 to 102; zygomatic width, 125 to 135 and 109 to 120 mm; orbital width, 119 to 128 and 99 to 108; upper alveolar length, 84 to 88 and 80 to 86 (Baker and Bradley, 1965; Cowan, 1940).

FIG. 1. Adult male and female bighorn sheep (*Ovis canadensis*) in winter pelage. Photograph by author.



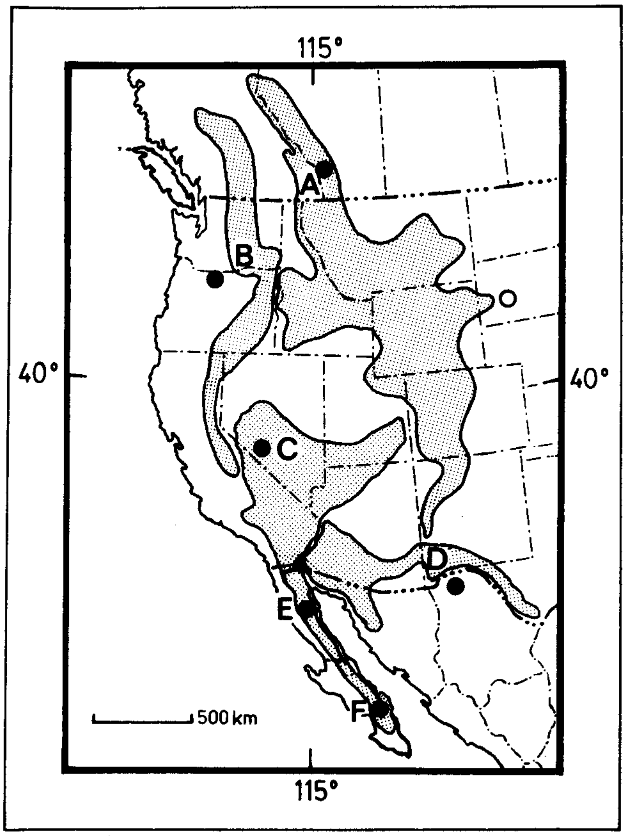


FIG. 3. Present distribution of subspecies of *Ovis canadensis*: A, *O. c. canadensis*; B, *O. c. californiana*; C, *O. c. nelsoni*; D, *O. c. mexicana*; E, *O. c. cremnobates*; F, *O. c. weemsi*; (after Spillett and Bunch, 1979; Trefethen, 1975). Solid circles indicate locations of type specimens; open circle designates location of type for *O. c. auduboni*. Within range outlines, actual population distributions frequently are scattered and discrete.

DISTRIBUTION. Cowan (1940) characterized bighorn sheep distribution in North America as being correlated with low precipitation levels in winter and spring. They range from the high elevation alpine meadows of the Rocky Mountains and Sierra Nevadas, down to the low elevation desert mountain ranges in the southwest United States and northern Mexico (Fig. 3). Historically distributions extended farther from the mountains, particularly eastward in association with major rivers and badland formations (Buechner, 1960; Cowan 1940; Manville, 1980). Although their present distribution (Trefethan, 1975) is much reduced (Buechner, 1960; Manville, 1980), many extinct or relict populations have been reestablished and sometimes transplants have been made outside the historic distribution of a subspecies (Monson, 1980; Trefethen, 1975).

FOSSIL RECORD. The earliest known remains of *Ovis* in North America are from 100,000 years B.P. Sangamonian interglacial deposits at Medicine Hat, Alberta (Stalker and Churcher, 1982), indicating that the genus probably arrived from Eurasia sometime during the preceding glacial (Illinoian). Fossil *Ovis* from Alaska and the Yukon Territory have been assigned to *O. dalli* (Kurtén and Anderson, 1980). Korobitsyna et al. (1974) supported the idea that North American sheep belong to the separate subgenus *Pachyceros* that developed its distinctive characteristics when first isolated in the Beringian refugium. After spreading southward fol-

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FIG. 2. Dorsal, ventral, and lateral views of male (upper) and female (lower) skulls of *Ovis canadensis*. Male specimen (basilar length, 269 mm) from Cascade Valley, Banff National Park, Alberta; female specimen (basilar length, 247 mm) from Vaseux Lake, British Columbia. Drawings by author.

lowing the retreat of ice they finally became recognizable as *O. canadensis* by the latter part of the last glacial (Harris and Mundel, 1974).

Ovis canadensis has been reported from over 30 late Pleistocene sites (125,000–10,000 years B.P.) in western North America, including Alberta, Arizona, British Columbia, California, Idaho, Nevada, New Mexico, Oregon, Texas, Utah, and Wyoming (Kurtén and Anderson, 1980; Logan, in press; Mead et al., 1982). Many of the specimens dated before 10,000 years B.P. are larger in skull and postcranial dimensions than modern *O. canadensis* (Harris and Mundel, 1974), which led to their original separation as *O. catclawensis* (Hibbard and Wright, 1956). Although some authors now regard *catclawensis* as a temporal subspecies of *O. canadensis* (Harris and Mundel, 1974; Kurtén and Anderson, 1980), others believe it is distinct (Martin and Gilbert, 1978). Geist (1971, 1983) hypothesized that larger size may have resulted from the early *Ovis* migrants entering into extremely favorable conditions as they spread into North America.

The recently extinct subspecies, *O. c. auduboni*, was distributed in the badlands region of North and South Dakota, western Nebraska and possibly eastern Wyoming (Fig. 3).

FORM AND FUNCTION. The skin is generally thicker in males than in females, and also varies on different regions of the body, being thickest on the face (Geist, 1971). Skin color ranges from black through dark to light brown, depending on age and area of the body (Hansen, 1980*a*). The tongue usually is black, but in some individuals it is pink or has pink spots (Hansen, 1980*a*). Small areas lacking pigmentation also occur on the nasal septum or inside the nares, and the normally pink palate may have black spots. The annual molt begins in early spring (Geist, 1971) when the animals actively rub off the old winter hair. The dorsal guard hairs are unbanded and reach a length of 48 mm and 322 μm in diameter (Moore et al., 1974). The underfur is of similar length but it is effectively reduced by crimping; it forms a layer approximately 15 mm thick (Hansen, 1980*a*).

Females have two teats; during lactation enlarged mammaries are visible. Gross composition of the milk determined from four female *O. c. canadensis* at various stages of lactation showed mean values of: total solids, 26.5%; water (by difference), 73.5%; ash, 1.2%; fat, 12.0%; non-fat solids (by difference), 14.4%; lactose, 4.3%; and total protein, 8.8% (Chen et al., 1965). The pH of milk samples ranged between 6.33 and 6.60, with the specific gravity (23°C) between 1.012 and 1.045 (Chen et al., 1965; Forrester and Senger, 1965).

Each year a new horn sheath grows around the bony horn core and inside the sheath of the previous year. Mean dimensions (in mm) for horns of mature males and females, respectively are: total length, 900 and 262; circumference, 373 and 128 (Baker and Bradley, 1965; Shackleton, 1973). Distinct demarcations or annuli form by cessation of growth of the horn sheath each winter (Taylor, 1962) and can be used to estimate age of individuals (Geist, 1966*a*). However, during fights the horn tips frequently are damaged ("brooming") and up to 30 cm of the distal horn tip can be lost (Shackleton and Hutton, 1972). Patterns of annual horn growth vary between populations and may be relative indicators of nutrition and general production (Geist, 1971; Shackleton, 1973; Smith and Wishart, 1978).

The most striking features of the skeleton are structures of the skull (Fig. 2) related to horns and intraspecific interactions. The large horn cores and expansions of the cornual and frontal sinuses of males, together with their internal bony septa, form a system believed to protect the brain by absorbing the impact of clashes during fighting (Geist, 1966*b*, 1966*c*, 1971; Schaffer and Reed, 1972). Lydekker (1913) gave typical vertebral numbers for *Ovis* as cervical 7, thoracic 13, lumbar 6, sacral 4 and caudal 7. Except for two additional caudal vertebrae, I found these numbers in a male *O. c. californiana*. The complete dental formula is i 0/3, c 0/1, p 3/3, m 3/3, total 32, and is attained by 4 years of age (Cowan, 1940). Incisors are appressed and canines incisiform. Upper canine teeth occur rarely in *O. c. nelsoni* (Hansen, 1980*a*) and in *O. c. californiana*. Premolars and molars are subhypsodont (Geist, 1971) with a selenodont crown pattern. The second premolar, particularly in the lower jaw (Hansen, 1980*a*), is often absent.

In addition to sweat glands, bighorns have lacrimal or preorbital glands located on the anterior corner of each eye, inguinal glands in the groin, and interdigital or pedal glands on each foot. Secretions of the lacrimal gland may function in dominance interactions (Geist, 1971), and the pedal glands have a possible scent-marking function along trails and at bedding sites (Lydekker, 1912).

Rectal temperature varies with ambient temperature, excitability, and season; the normal value is between 38.3 and 38.9°C (Franzman and Hebert, 1971). Resting metabolic rates (RMR) at +10°C of captive *O. c. canadensis* between September and May showed no seasonal pattern, except for a decrease in February, and male rates were found to be greater than those of females (Chappel and Hudson, 1978). At −10°C, RMR showed a seasonal trend decreasing from September to February, increasing to May. The lower critical temperature of fed sheep in winter pelage was −20°C; lowering the temperature to −30°C increased RMR 1.37 to 1.39 times, but winds of 4 to 8 m/s increased RMR only below −20°C (Chappel and Hudson, 1978). Bunch et al. (1980) found significant differences in the mean (±*SE*) pulse and respiration rates between *O. c. nelsoni* captured by drop-net (pulse 148.0 ± 8.1; respiration 82.7 ± 5.4) and those immobilized with etorphine (117.3 ± 3.4; 30.8 ± 0.8). Heart rates (beats/min) of three free-ranging, adult female *O. c. canadensis* obtained by remote telemetry had the following mean values: bedded, 43.3 to 62.5; feeding, 60.3 to 87.4; walking, 74.4 to 92.1; trot/run, 109.3 (MacArthur et al., 1979, 1982). Even agonistic social interactions rarely increased heart rate, but significant elevation occurred in response to the sudden appearance of running conspecifics. Free-ranging dogs evoked the maximum increases (MacArthur et al., 1979).

Baseline blood chemistry and hematological values for *O. c. canadensis*, *O. c. californiana*, *O. c. nelsoni*, and *O. c. mexicana* have been established (Davies, 1976; Franzman and Thorne, 1970; Franzman, 1972; Hebert, 1978; Peterson and Bottrell, 1978). Variations were related to body condition, season, excitability, age, health, and wild or captive condition. Packed cell volume and hemoglobin may reflect body condition, whereas excitability resulting from handling can elevate blood glucose, leukocyte, and serum glutamic-oxaloacetic transaminase levels and lower lactate dehydrogenase values (Bunch et al., 1980; Davies, 1976; Franzman and Thorne, 1970; Franzman, 1972). Blood urea nitrogen (BUN) levels may be related directly to protein intake (Franzman, 1972), but, because they also can be elevated by protein catabolism, separate anabolic and catabolic BUN curves need to be established before protein intake can be estimated (Hebert, 1978). Allele frequencies of blood transferrins differ among *O. canadensis*, *O. dalli*, and *O. musimon* (Nadler et al., 1971), and between *O. c. nelsoni* in Nevada and Utah (Bunch et al., 1981). However, Bunch et al. (1976) could not separate *O. c. nelsoni* hemoglobins from those of *O. aries* sufficiently for forensic law enforcement purposes.

ONTOGENY AND REPRODUCTION. The mean (±*SD*) gestation period of captive bighorns is 174.2 ± 1.7 days (Shackleton et al., 1984). During gestation plasma progesterone levels fluctuate, increase during the first 50 days, drop for the next 30 days, then increase rapidly until just before parturition when they fall again (Whitehead and McEwan, 1980). Serum progesterone levels (Ramsay and Sadleir, 1979) and Doppler ultrasound (Harper and Cohen, in press) were used to detect pregnancy in wild and captive bighorns.

The few published records of parturition and associated behavior are available only for captive bighorn sheep (Deming, 1955; Shackleton and Haywood, in press). One to 2 days before parturition swelling of the vulva usually is noticeable (Welles and Welles, 1961), and females invariably leave their group. Several days before birth they may move to steep cliff areas that may afford protection from predators, allow undisturbed development of maternal bonds, and provide some reduction in thermal stress for the neonate (Geist, 1971; Shackleton and Shank, in press). Rupture of the amnion can precede birth by several hours, and the placenta may be retained up to 5 h postpartum (Turner and Hansen, 1980). Following birth, the female and lamb may remain isolated as long as 1 week (Geist, 1971). Usually only single young are born, but twins were recorded in one wild and several captive populations (Eccles and Shackleton, 1979; Spalding, 1966). Natality rates, estimated from lamb and female counts, vary considerably between populations and range from 8 lambs : 100 adult ewes (3 years and older) in a declining population (Morgan, 1970) to 100 lambs : 100 adult ewes in an introduced, expanding population (Woodgerd, 1964).

Females are seasonally polyestrous (Whitehead and McEwan,

1980) and male testosterone levels fluctuate seasonally, with high levels associated with the mating period (McEwan, 1975; Turner, 1976). Mature testes are approximately 120 mm long and 60 mm wide but vary in size seasonally; testicular volume increases two- to three-fold before the mating season (Turner, 1976). I found motile sperm in both testes of a captive mature *O. c. californiana* in March. Lenarz (1979) found free-ranging males of *O. c. mexicana* to actively court females year-round, although, in *O. c. nelsoni*, Turner (1976) found a strong seasonal cycle in spermatogenesis with a distinct quiescent period (late December to June). The onset, degree of synchrony, and duration of the mating period are adapted to local environmental conditions favorable to the requirements of the neonate and lactating female. Thus, mating usually occurs in fall, with the onset and duration of the subsequent lambing period correlated broadly with latitude, such that it begins earlier and ends later in southern populations (Bunnell, 1982; Geist, 1971; Turner and Hansen, 1980). Variation in timing of lambing, and hence mating, seems to be a response primarily to differences in the predictability of plant growth in relation to energy requirements of the sheep (Bunnell, 1982), and to climatic factors (Geist, 1971; Lenarz, 1979).

Fetal weights (in kg) and measurements (in mm) for a female *O. c. mexicana*, gestated 4.5 months, a male gestated about 4.0 months, and a near-term male *O. c. canadensis*, respectively, were (Forrester and Senger, 1965): body mass, 0.3, 0.8, 5.5; total length, 345, 391, 695; girth, 194, 391, 695; hindfoot length, 94, 109, 248; ear length, 29, 31, 72; tail length, 21, 21, 70. Weights of captive lambs at birth range between 2.8 and 5.5 kg (Blunt et al., 1977; Geist, 1971; Hansen and Deming, 1980). Mean body measurements (in mm) of two captive *O. c. nelsoni* neonates (Hansen and Deming, 1980) were: shoulder height, 420; ear length, 77; hindfoot length, 175; tail length, 58. The dried umbilical cord may still be present 1 week postpartum (Hansen and Deming, 1980). The neonate is precocial and classed as a typical "follower" (Lent, 1974). The mousy grey or pale fawn coat color is retained until the appearance of the first winter coat, which resembles the adult pelage. The tail of the neonate is black-brown, often with an indication of a dorsal stripe. The hooves initially are soft with white at tips that wear off quickly; the hooves harden and darken to a uniform black (Hansen and Deming, 1980). The face profile is concave, with the distance between the black nose and the eye less than the distance between the eye and the back of the head (Hansen and Deming, 1980). Bighorn lambs suckle in short bouts (mean 14 to 28 s) but frequently (up to 3 suckles/h); their dependency on milk decreases and use of forage increases with age (Geist, 1971; Horejsi, 1976; Shackleton, 1973). Although some lambs begin grazing when about 14 days old, most begin later (Shackleton, 1973), and weaning usually is complete by 4 to 6 months (Geist, 1971); these values differ among populations (Berger, 1979).

Growth is rapid during the first 6 months of life (Hansen and Deming, 1980; Shackleton and Shank, in press), after which it slows or ceases over winter and begins again the next spring. Males are heavier than females when 6 months of age, and female growth is limited after 3 to 4 years of age, but males continue to grow until at least 8 years of age. Horn growth also differs between sexes (Figs. 1 and 2) and forms the basis of Geist's (1968*a*, 1968*b*) age-sex classification system for bighorns.

Sexual maturity, based solely on physiological criteria, is attained as early as 18 months (Blunt et al., 1977; Geist, 1971; Turner, 1976; Woodgerd, 1964). Geist (1968*b*) proposed female bighorns are paedogenic, and males neotenic in their postpuberal development patterns. Females typically mate for the first time at 30 months of age (Geist, 1971), but in some expanding or captive populations in deserts they may mate a year earlier (Turner and Hansen, 1980; Van Dyke, 1978; Woodgerd, 1964). Males actively and successfully participate in mating much later, typically at 7 to 8 years (Geist, 1971), but this varies among populations (Shackleton, 1973).

Mortality is highest in the first year of life, and probably occurs primarily during the neonatal stage, in summer in desert and during winter in northern populations. In subsequent age classes, mortality may vary between populations, but gradually increases with advancing age (Hanson, 1980*b*; Shackleton and Shank, in press; Stewart, 1980). Suggestions that females have a higher mortality rate than males (Hansen, 1980*b*; Woodgerd, 1964) may be the result of difficulty in determining ages of females older than 5 years. Thus, longevity in females is not documented, but male *O. c. canadensis* frequently live 15 or 16 years, with one living 20 years in the wild (Geist, 1971), and male *O. c. nelsoni* live 10 to 12 years (Hansen, 1980*b*).

ECOLOGY. The habitat of bighorns is typified by mesic to xeric grasslands (Cowan, 1940) associated with mountains, foothills, or major river canyons, ranging from high alpine areas to deserts. In addition to grasslands, precipitous areas such as cliffs or rock bluffs usually are required by bighorns for use as escape terrain. Except for bighorns on low desert ranges, sheep migrate between seasonal home ranges (Geist, 1971). The upward altitudinal movements in spring and summer, probably are related to plant phenology (Hebert, 1973), and the downward migrations in late fall or early winter probably are dictated by snow accumulation at high elevations (Becker et al., 1978; Blood, 1963). Distribution of waterholes significantly influences patterns of home-range use by *O. c. nelsoni* (Leslie and Douglas, 1979). Other factors identified with seasonal distributions include slope, salt availability, aspect, forest cover, shrub productivity, snow, and forage quality and quantity (Shannon et al., 1975). As many as five home ranges may be used each year by a bighorn group (Geist, 1971), but others occupy only one summer and one winter range. Maximum distances moved between seasonal ranges approach 48 km (Shackleton and Shank, in press). Mean (±*SD*) annual home-range size for five radio-collared, adult *O. c. nelsoni* ewes, was 16.9 ± 3.38 km^2, but home-range size for males increased with age, ranging from 11.7 km^2 for a 1-year-old to 37.3 km^2 for a 6-year-old (Leslie and Douglas, 1979). Slightly larger home ranges were reported for an adult and a yearling female in western Arizona (Seegmiller and Ohmart, 1981).

Within limitations of traditional diet analysis (Cooperrider et al., 1980; Wilson, 1976), bighorn sheep clearly eat a wide variety of species and classes of plants, and although primarily graminivorous, they consume significant quantities of shrubs and forbs (Brown et al., 1977; Browning and Monson, 1980; Stelfox, 1976). Seasonal changes in diet occur within bighorn populations, but there is no consistent species-specific pattern (Shackleton and Shank, in press). Published studies of diet selection with both use and availability measures are limited in number (Blood, 1967; Johnson and Smith, 1980; Shank, 1982; Stelfox, 1976; Wikeem and Pitt, 1979) and tend to be population specific. Minerals are obtained from natural salt-licks, or in some areas, from artificial blocks provided by game managers. Often water requirements can be satisfied by preformed water in ingested forages, and from snow, but desert races in particular require access to surface water (Geist, 1971; Turner and Weaver, 1980).

Historically, wolves (*Canis lupus*) likely were a major predator on bighorn sheep, but today they occur sympatrically only in some parts of the Rocky Mountains. Coyote (*C. latrans*) predation is widespread, but it affects mainly young sheep, and its impact upon bighorn populations is unknown (Buechner, 1960; Kelly, 1980). Isolated observations of other predation on sheep by eagles (*Aquila chrysaetos*), bobcats (*Felis canadensis*), cougars (*F. concolor*), and wolverines (*Gulo gulo*) are recorded (Buechner, 1960; Geist, 1971; Hornocker, 1969; Kelly, 1980; McCann, 1956). Use of precipitous escape terrain and group-living by bighorns appear to be successful antipredator strategies, but instances of defense against predators are known (Geist, 1971; Hornocker, 1969; Shank, 1977).

Competition between bighorn sheep and other ungulates, wild or domestic, has not been shown, but studies have revealed varying levels of diet and habitat overlap among them. Of wild sympatrics, wapiti (*Cervus elaphus nelsoni*) have the most overlap in diet with bighorns (Constan, 1972), and deer (*Odocoileus hemionus*) often use the same habitats (Jones, 1980; Stelfox, 1976). Burros (*Equus asinus*) have diet and habitat overlap with *O. c. nelsoni* (Jones, 1980; Seegmiller and Ohmart, 1981; Ginnett and Douglas 1982). Bighorns also overlap in diet with cattle (*Bos taurus*) but show separate habitat use in steep terrain (McCollough et al., 1980; Morgan, 1970). The main potential competitor probably is the domestic sheep (Buechner, 1960; Jones, 1980; Morgan, 1970), and for bighorns in arid regions the introduced *Ammotragus lervia* poses a major competitive threat (Simpson et al., 1978).

Bighorns suffer from blue tongue (Robinson et al, 1967), contagious ecthyma (Blood, 1971; Samuel et al., 1975), parainfluenza: 3 virus (Parks et al., 1972), encephalitis, *Actinomyces bovis*, *Actinobacillus lignieresi*, *Corynebacterium*, *Clostridium*, and *Pas-*

turella hemolytica (Allen, 1980; Lawson and Johnson, 1982). Chronic sinusitis, possibly the result of invasions by *Oestrus ovis* larvae and secondary infection by corynebacterium, can be a major mortality agent in *O. c. californiana*, *O. c. nelsoni* and *O. c. mexicana* (Bunch, 1980). At least 29 parasite species were identified in bighorns (Allen, 1980; Becklund and Senger, 1967; Cowan, 1951; Uhazy and Holmes, 1971; Uhazy et al., 1971, 1973). The lungworms *Portostrongylus rushi* and *P. stilesi* play a major role in hemorragic septicemia (pneumonia-lungworm complex) to which bighorns are highly susceptible (Forrester and Senger, 1964*a*; Post, 1971; Thorne, 1971; Woodard et al., 1974). Their larvae can be transmitted transplacentally (Forrester and Senger, 1964*b*; Gates and Samuel, 1977) but, though probably not eradicable, control may be possible (Hibler et al., 1977). Introduced mites of domestic sheep, *Psoroptes equivar* and *P. ovis*, both cause scabies in bighorns, which can result in considerable mortality (Buechner, 1960; Sandoval, 1980). Capture and handling bighorns without adequate precautions can lead to myopathy and death (Dalton et al., 1978).

Male bighorn sheep are a major big-game trophy species, highly prized by hunters for their horns. Consequently, they are subject to significant management efforts by state and provincial wildlife agencies. Usually only males are hunted, though in some areas females are harvested (Smith and Wishart, 1978). Management varies but includes regulation of harvests, winter feeding, parasite control, habitat management, and population transplants. Bighorns can be successfully raised in captivity (Sausman, 1982; Wilson and Douglas, in press). Various capture techniques for bighorns have proven useful, and perhaps the most common involves trapping in permanent or semipermanent corrals into which the animals are baited with food, apple mash, or salt blocks (Hansen et al., 1980; Wilson and Douglas, 1982; Wishart et al., 1980). Individual immobilization by use of projectile syringes and capchur-type guns also is practical (Hebert and McFetridge, 1977; Wilson and Douglas, 1982), as are drop-nets and net-gunning (Andryk et al., 1983). After capture, bighorns are marked most readily for field identification with collars or ear tags. Radio-collars are invaluable for studying movements (Becker et al., 1978; Leslie and Douglas, 1979; Morgan, 1970; Seegmiller and Ohmart, 1981) and heart rate (MacArthur et al., 1979, 1982). Marking without capture also is possible with dye-spraying units (Hansen et al. 1980). Aerial-census techniques from fixed-wing aircraft or helicopters are successful. Under special circumstances or where topography and accessibility permit, other techniques including ground, boat, and waterhole surveys may be used (Simmons and Hansen, 1980).

BEHAVIOR. Bighorns live in groups, but for most of the year, males over 3 years of age usually live separate from the females and young (Geist, 1971). These male and maternal (females and young) groups often occupy separate, undefended home ranges. Group-living in bighorns probably is an antipredator strategy (Berger, 1978), and segregation of the sexes may minimize competition and disturbance of females and young by adult males (Geist and Petocz, 1977; Shank, 1982). Group size varies with season and among populations (Blood, 1963; Chilelli and Krausman, 1981; Geist, 1971; Shackleton and Shank, in press); the overall mode ranges from two to nine animals (Shackleton and Shank, in press). Males are not excluded, but leave maternal groups to join male groups when they become physically and socially dominant to adult females (Geist, 1971), whereas young females usually stay with their maternal group (Geist, 1971; Leslie and Douglas, 1979). In male groups, dominance relationships are strong with social status being founded mainly on horn size and fighting ability (Geist, 1971). Apparently, no such obvious determinants of social status occur among adult females in maternal groups where dominance relationships are weak (Eccles, 1981).

Maintenance and comfort behavior includes stretching, shaking, rubbing (against trees, boulders, erosion banks), scratching (with horns and hindfeet), urinating, and defecating. Females squat to urinate, but males of all ages stand, as do both sexes during defecation. Locomotion varies from a slow walk to a fast run, estimated at between 10 and 50 km/h (Welles and Welles, 1961). Stiff-legged bounding locomotion or "stotting" is observed, particularly when alert to danger, and usually is preceded by the alarm posture when the bighorn holds head and neck erect (Geist, 1971; Hansen, 1980*a*). Vocal communications appear limited. All age-sex classes bleat, a sound similar to that of domestic sheep, and adult males utter a growl or gutteral, ululating sound when performing the twist pattern (Geist, 1971; Welles and Welles, 1961). Intraspecific communication by olfaction and glandular secretions are speculative (Geist, 1971; Lydekker, 1912).

Bighorns, particularly males, exhibit a wide spectrum of social-behavior patterns and are amongst the most socially active of North American ungulates. Contrary to common belief, most agonistic social interactions do not occur during the rut, but usually just before the rut, and sometimes in spring. The longest dominance interactions involve animals of similar size and development; until dominance status is settled between individuals, agonistic interaction may consist of repeated clashes and displays (Geist, 1971). The clash invariably is preceded by one or both sheep turning and walking away from each other a few steps, turning to face each other, then advancing in a threat jump before lunging into the clash. Immediately following the clash, opponents may freeze with heads raised in a "present" posture, thought to be a horn display (Geist, 1971). If one interactor cedes dominance to the other, he may either come and rub his horns over the face and chest of the dominant, or turn away and begin to feed. The dominant male frequently treats the subordinate like an estrous female, performing mostly courtship patterns: low stretch, twist, kick or laufschlag, nosing, and even mounting (Geist, 1971). The subordinate male usually stands or feeds, only occasionally rearing in a threat jump and clashing with the dominant (Geist, 1971). Females and young also interact aggressively, but their patterns usually are restricted to the overt contact patterns (clashes, butts, threat jumps) and only rarely involve displays (Geist, 1971).

The first evidence of the mating season, or rut, is the males joining and moving through maternal groups approaching and sniffing adult females in low stretches. The female typically responds by squatting and urinating, then the male sniffs the vulva and urine, and lip curls (flehmen). The lip-curl possibly brings into play the vomeronasal organs and may aid males in detecting estrus (Ladewig and Hart, 1980). When an estrous female is identified, the male begins courtship, a series of increasing contact patterns (twist, nose, kick, chest push) eventually leading to mounting and successful copulation (Geist, 1971; Shackleton, 1973). No competition occurs among males testing female urine, but during courtship the tending male vigorously guards the estrous female from other males. Social status determined before the mating season helps dominant males gain priority and access to estrous females, but subordinate males may interfere and attempt to mount estrous females. Females do not accept these attempts and chases may ensue with the female pursued by numerous rams all attempting to mount her (Buechner, 1960; Geist, 1971). Fighting among males during these chases is different from that in dominance interactions; fights are almost entirely physical and lack displays (Geist, 1971). In one population, *O. c. canadensis* males were observed to herd anestrous females (Shackleton, 1973); herding also may occur in some *O. c. nelsoni* populations (Wilson, 1968). Female sheep are not passive during courtship, though the frequency and intensity of their behavior varies among populations (Geist, 1971; Shackleton, 1973). Courtship by females consists primarily of rubbing their bodies and horns on the male, and rarely they may mount him. The most significant aspect probably is acceptance or rejection of mates by the females, determined mainly by courtship behavior (Shackleton, 1973) and social status of the male.

Bighorns are diurnal, but also may be active on moonlit nights. Daily activity patterns consist of alternate feeding and rest-rumination bouts (Blood, 1963; Chilelli and Krausman, 1981; Eccles, 1981; Geist, 1971; Olech, 1979; Welles and Welles, 1961; Van Dyke, 1978). Feeding bouts usually occur near dawn and dusk; strong seasonal effects are observed in the number of feeding and rest-rumination bouts (Chilelli and Krausman, 1981; Eccles, 1981; Van Dyke, 1978; Welles and Welles, 1961). Eccles (1981) found the mean number of daily, daylight feeding bouts to be 1.3 to 2.3 between September and March, and 4.3 to 5.3 between April and August. He related these changes to forage conditions, energy requirements, physiological condition, and social organization. Despite changes in the number of bouts, total feeding time during daylight remained relatively constant throughout the year, decreasing only in winter when daylength was short. To maintain total daily feeding times during periods of short daylength, rest-rumination bouts were sacrificed (Eccles, 1981; Van Dyke, 1978), except during cold periods when rest-rumination was found to increase over the monthly average (Eccles, 1981). Although some rest-rumination bouts may occur while sheep stand, particularly in hot weather (Eccles, 1981), bighorns usually lie down. Usually a shallow depression is scraped with the front feet before the sheep lie down. Some areas are used repeatedly as bedding sites by groups and typically are on exposed ridges, rocky areas, or erosion sites (Geist, 1971), or near waterholes in the desert (Olech, 1979).

Probably most social-behavior patterns used by the sheep are under strong genetic control, and they show a chronological development in both appearance and development during ontogeny of the individual (Geist, 1971). Attainment of behavioral maturity of individuals, at least for males, varies among populations (Shackleton, 1973), but usually is reached by 2 to 3 years in females and by 6 or 7 years in males (Geist, 1971). During the first year of life, young use mainly overt agonistic and sexual patterns, with few or no displays; thus, threat jumps, clashes, and mounting are the most frequent social patterns used by lambs in what usually is classed as play (Geist, 1971). The capacity for learning is shown in their aquisition of home-range behavior and seasonal movements, together with their habituation to humans both in the wild (Geist, 1971) and in captivity (Hansen, 1980*c*). Learning also is important in dominance relationships among rams for individual recognition, and for recognizing social status from the size of an opponent's horn (Geist, 1971). Mutual recognition between mother and young also are learned; whereas the female appears to rely primarily on olfaction with sight and sound secondary, the lamb seems to use sound and sight most often to find the dam (Geist, 1971; Shackleton and Shank, in press).

GENETICS. Karyotype studies of *O. c. canadensis* and *O. c. californiana* have established that the diploid chromosome number is $2n = 54$ (Bottrell et al. 1978; Nadler et al., 1973). Cytogenetic comparisons among *Ovis* were shown to be useful in investigating evolutionary relationships within the genus (Korobitsyna et al., 1974; Nadler et al., 1973; Spillet and Bunch, 1979). There are no reports of either albinos or melanistic individuals. Hybridization of bighorns with *O. aries* and *O. musimon* result in fertile offspring (Gray, 1972).

REMARKS. As Schaller (1977) and others have commented, confusion regarding taxonomy of the genus *Ovis* is rampant. The number of recognized species ranges between 2 and 20, with the number of subspecies exceeding 40. Until an exhaustive systematic study is undertaken there is little hope of reducing the current state of perplexity. Taxonomic revision is equally necessary for the subspecies of *O. canadensis.* Bradley and Baker (1967) and Shackleton (1973) clearly showed that variation in cranial dimensions (Cowan, 1940) among populations of the same subspecies is as great as among subspecies.

It is a moot point whether Shaw or Desmarest was the first to describe *Ovis canadensis.* Both authors published material about 1804, but Shaw's account was part of 24 volumes published between 1789 and 1813, with the section describing *O. canadensis* variously credited to publication in 1803 and 1804. The question of priority was debated extensively (Allen, 1912; Biddulph, 1885; Merriam, 1901) with Shaw currently accepted as oldest. Neither Desmarest nor Shaw may have seen more than an illustration of the original specimen, although Shaw definitely saw a specimen in the British Museum. The specimen each author refers to as the holotype was collected by D. McGillivray in 1800 in the upper Bow River valley, near present day Exshaw, Alberta. McGillivray gave the latitude and longitude as 50° north and 115°30′ west, but Allen (1912) corrected the latitude for the locality to 57°20′.

Hall (1981:1115) cites Cragin's (1900) *Nemorhoedus palmeri* as synonymous with *O. c. canadensis.* I did not because Cragin (1900) states that he compared the two post-cranial elements comprising the specimen with *O. canadensis* material and concluded that "they widely differed" from them. In addition, the specimens are now lost and all that remains are the rough sketches given in Cragin's (1900) paper.

According to Lydekker (1912), both the Latin *ovis* and Greek *ois*, together with other terms for domestic sheep, are derived from the sanskrit *avi*, from the root *av*, meaning to keep or to guard.

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