

*Ovis dalli*. By R. Terry Bowyer and David M. Leslie, Jr.

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***Ovis dalli* Nelson 1884**

**Dall's Sheep**

- Ovis montana dalli* Nelson 1884:13. Type locality "mountains south of Fort Yukon on the west bank of the river," Alaska.
- O. dalli*: Allen 1897:112. First use of present name combination.
- O. stonei* Allen 1897:111. Type locality "Che-on-nee Mountains, headwaters Stikine River, British Columbia," Canada.
- O. fannini* Hornaday 1901; Appendix 1:2. Type locality "Dawson City, Yukon, Canada."
- O. cowani* Rothschild 1907:238. Type locality "near Mt. Logan, British Columbia, Canada."

**CONTEXT AND CONTENT.** Grandorder Ungulata, Order Artiodactyla, Suborder Ruminantia, Infraorder Pecora, Superfamily Bovidea, Family Bovidae, Subfamily Caprinae, Tribe Caprini. The genus *Ovis* is thought to contain seven species (Nadler et al., 1973). *Ovis dalli* includes three extant subspecies (Hall, 1981):

- O. dalli dalli* Allen 1897:12, see above.
- O. d. kenaiensis* Allen 1902:145. Type locality "head of Sheep Creek, Kenai Peninsula, Alaska."
- O. d. stonei* Allen 1897:117, see above (includes *fannini* and *cowani*).

**DIAGNOSIS.** *Ovis dalli* is generally smaller in body mass than its only North American congener, *O. canadensis* (Shackleton, 1985), and similar in size to *O. nivicola* of Siberia (Cherniavski, 1962; Geist, 1971). Horns of *O. dalli* are intermediate in size (Fig.

1) between massive horns of *O. canadensis* and smaller horns of *O. nivicola* (Clark, 1964; Geist, 1971). Maximum lengths and basal circumferences of horns for adult males (in cm) are 111 and 36, respectively, for *O. nivicola*; 124-130 and 38 for *O. dalli*; and 124 and 47 for *O. canadensis* (Clark, 1964; Geist, 1971; Hall, 1981). *O. dalli* has shorter and smaller horn cores and less pneumatation of the skull than *O. canadensis* (Geist, 1971). Horns of *O. dalli* diverge or flare more widely (88 cm tip to tip) than those of *O. canadensis* (66 cm; Hall, 1981). Although horns of *O. nivicola* are smaller than those of *O. dalli*, they flare similarly; *O. dalli* and *O. nivicola* are referred to as thinhorn sheep. Length of the upper molar series is shorter in *O. dalli* (males, 68-88 mm; females, 68-74 mm) than in *O. canadensis* (males, 80-95 mm; females, 77-96 mm; Hall, 1981); data are not available for *O. nivicola*. Nasal length usually separates *O. dalli* (males <105 mm; females <85 mm) from *O. canadensis*, which has longer nasals (Hall, 1981).

*Ovis dalli* has two distinct color morphs, *O. d. dalli* and *O. d. kenaiensis* typically possesses off-white pelage (Fig. 1), although some individuals have black tails (Guthrie, 1972). Horns may be amber or even semi-transparent (Cowan, 1940); this character separates *O. dalli* from *O. canadensis* and *O. nivicola*, which possess darker horn sheaths. Adult *O. d. stonei* are silver to greyish-black (Allen, 1897; Sheldon, 1932) with white muzzles, pronounced white leg-trimmings and white rump patches "bisected middorsally by a wide strip of dark hair connecting the dark tail with the dark body hair" (Geist, 1971:325; Fig. 1). The rump patch of *O. nivicola* is smaller and does not extend beyond the base of the tail; that of *O. canadensis* is comparable in size to *O. d. stonei*, but the connecting strip of dark hair is narrower or absent. Color intergradations, or "Fannin's" morph, of *O. d. dalli* and *O. d. stonei* occasionally are reported (Guthrie, 1972; Scotter, 1980). These animals are characterized by predominantly white pelage with a gray saddle across the back, and are most prevalent where the ranges of the subspecies are close (Cowan, 1936; Clark, 1964; Guthrie, 1972; Fig 2).

**GENERAL CHARACTERS.** *Ovis dalli* are sexually dimorphic; body and horn masses are the most disparate characteristics (Fig. 3). Adult body mass (in kg) of six males and eight females from the Yukon ranged from 72.5 to 82.3 and 46.4 to 50.4, respectively (Bunnell and Olsen, 1976). Maximum reported mass of males in autumn ranged from 80 to 110 kg (Nichols, 1978a; Ulmer, 1941). Both sexes lose mass during winter. For instance, mass of



FIG. 1. Male *Ovis dalli dalli* (above) and *O. d. stonei* (below). Note the darker pelage of *O. d. stonei*. Photograph of *O. d. dalli* by K. R. Whitten and *O. d. stonei* by D. R. Seip.

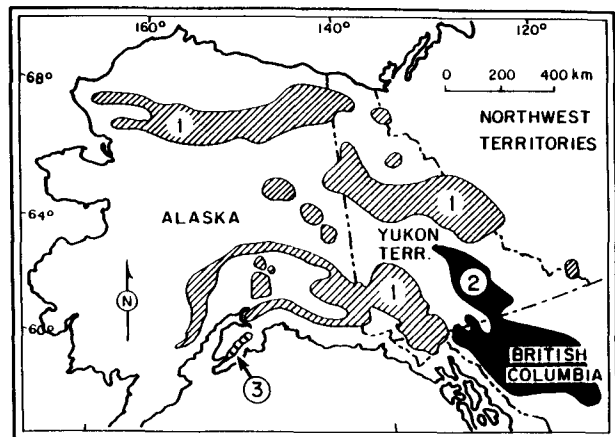


FIG. 2. Distribution of (1) *Ovis dalli dalli*, (2) *O. d. stonei*, and (3) *O. d. Kenaiensis* (adapted from Hoefs, 1985; Nichols, 1978a). Map drawn by D. Borchert.

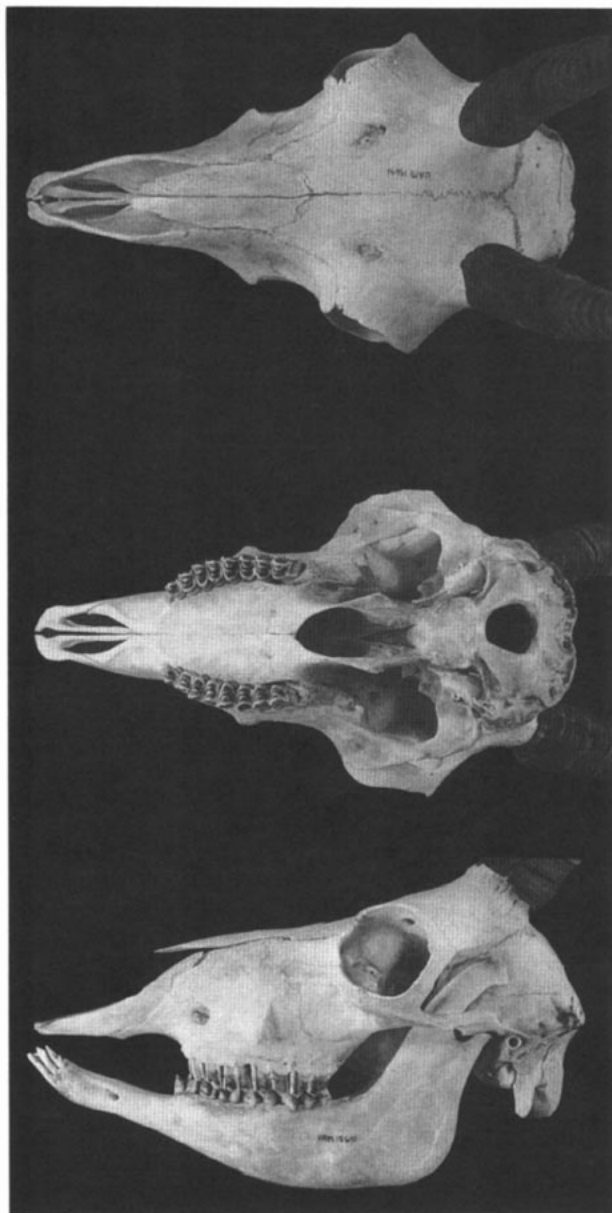


FIG. 3. Dorsal, ventral, and lateral views of skull and lateral view of mandible of adult female skull of *Ovis dalli*. Female skull is specimen No. 15641, University Museum, University of Alaska Fairbanks.

adult females averaged 48 kg in spring, a loss of 18% from autumn (Nichols, 1978a). Nichols (1978a) reported that height at shoulder averaged 93 cm for males and 84 cm for females. Differences in these characteristics between the subspecies of *O. dalli* are small (Clark, 1964).

Other reported body measurements (in mm) include: total length, 1,300–1,780 (males) and 1,324–1,620 (females); tail length, 70–115 and 70–99; length of hind foot, 370–450 and 350–390; length of ear, 74–92 and 80–90; height of shoulder, 916–1,090 (no data for females; Bunnell and Olsen, 1976; Cowan, 1940; Hall, 1981). Mean cranial dimensions (in mm) range as follows: basilar length, 235–274 (males) and 215–238 (females); zygomatic breadth, 114–134 and 107–117; mastoid breadth, 82–97 and 70–79; nasal length, 82–110 and 72–84; orbital width, 108–127 and 93–103 (Cowan, 1940; Hall, 1981).

Dentition for adult sheep is i 0/3, c 0/1, p 3/3, m 3/3, total 30. All permanent teeth are fully erupted by 48 months (Hemming, 1969). Premolars and molars are subhypodont (Geist, 1971). Supernumerary teeth are noted infrequently (Bunch et al., 1984a; Hoefs, 1974a). Tooth wear varies considerably between populations

(Hemming, 1969) and may be accelerated by wind-deposited silt on forages (Hoefs, 1975; Hoefs and Bayer, 1983).

**DISTRIBUTION.** The range of *Ovis* in North America has been influenced by human perturbations (Buechner, 1960) and many remnant populations occur throughout the western United States and Canada (Trefethen, 1975). *O. dalli* ranges throughout rugged mountains in British Columbia, Yukon, Northwest Territories, and Alaska from 59°30' to 69°40'N latitude (Anderson, 1938; Scott et al., 1950; Trefethen, 1975; Fig. 2). *O. d. dalli* is the northernmost subspecies (Rausch, 1950), but occurs in all four areas; *O. d. kenaiensis* is confined to the Kenai Peninsula, and *O. d. stonoi* is the southernmost subspecies and occurs only in British Columbia and the Yukon. Extant-continuous ranges of *O. d. dalli* and *O. d. stonoi* are more extensive than those of *O. canadensis*, though small remnant populations of *O. dalli* occur (Trefethen, 1975). In the southern part of their range this species often is restricted to isolated, alpine habitats (Hoefs, 1975; Lord and Luckhurst, 1974). There are about 70,000 *O. d. dalli* in Alaska, 9,000 in the Yukon Territory, 7,000 in the Northwest Territory, and 200 in British Columbia; *O. d. stonoi* number about 3,000 in the Yukon Territory, and 10,000–11,000 in British Columbia (Hoefs, 1985).

**FOSSIL RECORD.** *Ovis* is a Palearctic immigrant to the North American Rancholabrean fauna of the late Pleistocene (Kurtén and Anderson, 1980). The oldest remains of *Ovis* in North America have been located in Illinoian penultimate glacial deposits (about 100,000 years B.P.) near Fairbanks, Alaska (Péwé and Hopkins, 1967); yet, specific designations of those remains have not been established (Kurtén and Anderson, 1980). *Ovis* fossils from the Wisconsinian glacial (about 40,000–23,000 years B.P.) are common (Guthrie, 1968; Harington, 1978, 1980; Weber et al., 1981). Ancestral *O. dalli* were larger than their present-day counterparts (Guthrie, 1984). Use of *O. dalli* by prehistoric humans has been verified by detection of blood residues on tools from 6,000 to 1,000 years B.P. (Loy, 1983).

The fossil record has not been resolved with regard to the origin of *O. dalli*, or other contemporary species such as *O. nivicola* and *O. canadensis* (Cowan, 1940; Stokes and Condie, 1961; Sushkin, 1925). Korobitsyna et al. (1974) believed that pachyercine sheep evolved in ice-free Beringia during the Illinoian and speciated into *O. dalli* and *O. nivicola* during the Sangamonian Interglacial, when the Bering Sea isolated populations in North America and Asia. Further glacial isolation of early *Ovis* in western North America resulted in *O. canadensis*. Nevertheless, Cowan (1940) and Stock and Stokes (1969) concluded that *O. dalli* and *O. canadensis* were recent, specialized forms of *O. nivicola*. Geist (1971) agreed with Cowan (1940) that *O. dalli* differentiated from *O. canadensis* while confined to the Alaska-Yukon (Beringia) refugium during the glacial Wisconsinian.

**FORM AND FUNCTION.** Pelage of *O. dalli* consists of an undercoat of fine wool and stiff, long guard hairs that are hollow (Cowan, 1940; Geist, 1971). Winter coats may be >5 cm thick (Nichols, 1978a). A single molt occurs from March through July (Geist, 1971), but mature males molt earlier than females, young, and individuals in poor condition (Cowan, 1940). Skin is thickest on the rostrum and face (2–6 mm versus 1 mm elsewhere), particularly on males (Geist, 1971). As an additional adaptation for rutting behavior, skulls of adult males are highly pneumatized and constructed to absorb heavy concussions (Geist, 1971). Ossification of skull sutures occurs slowly throughout the life of both sexes (Cowan, 1940). *O. dalli* possess an interdental gland on each foot, and anal, caudal, inguinal, and preorbital glands; females possess two teats (Geist, 1971).

Males attain greater body mass (about 40% heavier than females) and sustain growth longer than females (4 years in females versus 6 years in males; Bunnell and Olsen, 1976). Growth rates (kg kg body wt.<sup>-1</sup> month<sup>-1</sup>) for males and females 0–5 years of age are estimated at 0.49 and 0.48, respectively (Bunnell, 1982). Length measurements are less disparate between sexes (Bunnell and Olsen, 1976). Mass and linear measurements (heart girth and body length) are correlated variously in both sexes (Bunnell, 1980).

Horns of *O. dalli*, as with all *Ovis* (Clark, 1964), are conspicuous, sexually dimorphic characteristics. Slender horns of females (Fig. 3) contrast with massive, flaring and curling horns of

males (Fig. 1); the latter can be 8–10% of the total body mass of a male (Geist, 1966a). Horns begin to grow 10 weeks after birth, and near continuous growth is evident in the first year; the first growth increment and 20–25% of the second increment are present when a male reaches 1 year of age (Hoefs and Nette, 1982). Horns grow annually in both sexes, but after 4–5 months of age (Cowan, 1940) annual growth increments are substantially larger in males than in females (Bunnell, 1978; Hemming, 1969). Annual horn growth is greatest in the first 4–5 years of the life of males (Bunnell, 1978; Hoefs and Nette, 1982) and normal growth can exceed 170 mm/year (Hoefs et al., 1982). Mean ( $\pm$ SD) density of horn sheaths was  $1.23 \pm 0.03$  g/cm<sup>3</sup>. Total horn volume increased from 30 cm<sup>3</sup> in one-year-old males to >3,000 cm<sup>3</sup> in 12-year old males; sheath volume increased from 25 cm<sup>3</sup> to 2,600 cm<sup>3</sup> for these same age classes (Konig and Hoefs, 1984).

The period of horn growth (April through September) shortens as males age (Bunnell, 1978; Hoefs and Nette, 1982). Gradual wearing of horn tips (brooming) may occur with age and no increase in horn length occurs in average males  $\geq 8$  years of age because horn wear equals or exceeds the small amount of growth (Hoefs and Nette, 1982). Horns grow from the base while the cores expand, and cessation of growth in winter leaves a deep ring around the base of each horn, which moves distally along the horn with succeeding years of growth (Cowan, 1940). Ring counts can be used as a reliable estimate of age, particularly for males (Geist, 1966b; Hemming, 1969), but reliability of this technique is lower for older female Dall's sheep (Hoefs, 1984b). Body size and horn growth are not correlated in males or females, but annual horn growth, particularly in males, increases as a function of precipitation and its presumed effect on forage quality (Bunnell, 1978). Condition of females during gestation appears to influence horn growth of her offspring after birth (Bunnell, 1978).

Data on basic hematology and blood chemistry of *O. dalli* (Foreyt et al., 1983; Franzmann, 1971) tend to correspond to those of *O. canadensis* (Shackleton, 1985). Mean  $\pm$  SD blood values for 73 *O. dalli* were: total white blood cells ( $7,600 \pm 3,200 \times 10^6/\mu$ l); mature neutrophils ( $49.6 \pm 11.9\%$ ); lymphocytes ( $33.9 \pm 11.9\%$ ); eosinophils ( $14.5 \pm 7.5\%$ ); basophils (rare); total red blood cells ( $13.8 \pm 2.8 \times 10^6/\mu$ l); total hemoglobin ( $14.3 \pm 1.6$  g/dl); hematocrit ( $46 \pm 5.2\%$ ); and total plasma protein ( $6.8 \pm 0.1$  g/dl; Foreyt et al., 1983). Additional blood values for 10 different *O. dalli* were: calcium ( $9.1 \pm 1.2$  mg/100 ml); phosphorus ( $3.8 \pm 1.2$  mg/100 ml); blood urea nitrogen ( $43.8 \pm 24.1$  mg/100 ml); cholesterol ( $104.5 \pm 15.2$  mg/100 ml); glucose ( $263 \pm 80.1$  g/100 ml); and total protein ( $6.9 \pm 2.8$  g/100 ml; Franzmann, 1971). Body condition and health, age and sex, handling, and excitability can cause variation in these data (Shackleton, 1985). Intrapopulation-transferring polymorphisms (Nadler et al., 1971) and hemoglobin-isoelectric points (Butcher and Hawkey, 1979) are similar in *O. dalli*, *O. canadensis*, and domestic sheep. Fatty acid composition of marrow in legs of *O. dalli* changes abruptly within the same bone; particularly the radius, and decreases in saturation distally, which may reduce loss of heat through thermal conduction (West and Shaw, 1975).

**ONTOGENY AND REPRODUCTION.** Relatively little is known about the reproductive physiology and anatomy of *O. dalli*, but it is thought to be similar to that of domestic breeds (Lawson and Johnson, 1982), which possess an estrous cycle of about 17 days (Asdell, 1964). Although timing of estrus is constrained by photoperiod, presence of an adult male and physical condition of the female may affect onset of estrus (Geist, 1971:208). Unlike domestic sheep, *O. dalli* are monestrous; rut typically occurs in November and December (Geist, 1971; Nichols, 1978b). Reproduction has not been reported for lambs, but three of four yearlings examined by Nichols (1978b) were pregnant, although this may be uncommon (Geist, 1971). Indeed, lamb: adult female ratios in interior Alaska range between 0.40:1 and 0.64:1, suggesting not all females reproduce each year (Murphy et al., 1990; Rachlow and Bowyer, 1991). Most females are sexually mature by 30 months of age. Males in good condition may attain sexual maturity by 18 months of age, but seldom mate until 5–7 years of age (Geist, 1971). One young typically is born after a gestation period of 171 days (95% confidence interval = 165–177 days; Nichols, 1978b). Twins are rare (Hoefs, 1978). Northern populations tend to exhibit a more synchronized birthing period than those occurring at southern latitudes (Bunnell, 1980, 1982), with mean dates of birth occurring in

mid to late May (Rachlow and Bowyer, 1991). Fetal sex ratios are skewed slightly in favor of males, but do not depart significantly from parity (Geist, 1971; Nichols, 1978b). Lambs are extremely precocial and are able to travel with their mothers within 24 h (Pitzman 1970). Weaning is completed by the time lambs are 3–5 months of age. Growth of young is rapid and body mass of 27–30 kg may be attained by 9 months of age (Bunnell and Olsen, 1976).

*Ovis dalli* possess all of their deciduous teeth at birth or 1 week thereafter (Cowan, 1940). Milk from seven females that ranged from 3 to 24 weeks postpartum averaged: 27.5% total solids, 72.5% water, 12.0% fat, 1.1% ash, 9.2% protein, and 4.7% lactose. Generally, concentrations of milk protein and fat increase as lactation progresses. Milk from a female 10 days prepartum had considerably more total solids (34.4%) and protein (29.9%) and less lactose (0.46%) than that of postpartum females (Cook et al., 1970). Milk casein from *O. dalli* is protein-rich (70.2%), and its primary amino acids are glutamic acid (15.5%), serin (6.19%), aspartic acid (6.19%), tryosine (5.34%), and leucine (5.14%; Lauer and Baker, 1977).

Nichols (1978a) concluded that density-dependent factors limited populations of *O. dalli*. On low-quality areas, adult females may reproduce only in alternate years. Mortality of lambs in populations near carrying capacity may be 40–50% by the end of their first winter (Nichols, 1978a). Localized declines in populations of Dall's sheep sometimes follow severe winters (Murie, 1944; Nichols, 1978a); lamb recruitment is inversely related to snow depth and conditions promoting wet snows that seal off winter foods (Murphy, 1974). Maximal annual rates of increase for unhunted populations of *O. dalli* are 11–18% (Hoefs and Bayer, 1983; Nichols, 1978a).

**ECOLOGY.** Extremes in photoperiod and weather in the high latitude ranges of *O. dalli* have limited winter observations of behavior and ecology. Generally, *O. dalli* inhabits dry, mountainous terrain and selects subalpine grass-low shrub communities (Geist, 1971; Hoefs, 1984a; Hoefs et al., 1975; Lord and Luckhurst, 1974; Murie, 1944). Most populations occupy distinct summer and winter ranges, although some are sedentary and do not migrate between seasonal ranges (Dixon, 1938; Geist, 1971; Hoefs and Cowan, 1979; Murie, 1944). Migrations are correlated with snow depth, temperature, and plant phenology; maximum migration distances of 8–48 km have been reported (Hoefs and Cowan, 1979). Because of climatic conditions at northern latitudes, *O. dalli* spend most of the year on their winter range (males, 271–303 days, females 240–263 days; Geist, 1971) and select wind-swept areas where forage is exposed and readily available (Dixon, 1938; Murie, 1944). *O. d. dalli* in Kluane National Park, Yukon, spent 49.2% of their winter feeding in areas with no snow, 21.4% where snow was <5 cm deep, 17.4% where snow was 5–10 cm deep, 8.7% where snow was 11–15 cm deep, and the remainder at snow depths >15 cm (Hoefs and Cowan, 1979). Primarily productivities of winter ranges (29.1–120.1 g/m<sup>2</sup>; Hoefs, 1984a) are critical to over-winter survival and lamb production (Hoefs and Bayer, 1983).

Adult males occupy as many as six seasonal home ranges: prerutting range, rutting range, midwinter range, late winter and spring range, salt-lick range, and summer range (Geist, 1971). Adult females generally have only four seasonal home ranges: winter, spring, lambing, and summer (Geist, 1971). Geist (1971) noted that midwinter ranges were smallest (minimum size about 0.8 km in diameter) and that spring and autumn ranges were largest (maximum size about 6 km in diameter). Young *O. dalli* inherit home ranges from older individuals; females generally from their mother or maternal group and males by a gradual disassociation with their mother and a gradual association with mature (>4 years old) males (Geist, 1971). *O. dalli* demonstrate a high degree of loyalty to their seasonal home ranges; male and female *O. d. stonoi* had 88 and 90% fidelity; respectively, to seasonal ranges (Geist, 1971).

Published studies on diets for *O. dalli* are limited, but like *O. canadensis* (Shackleton, 1985), they select grasses (*Calamagrostis*, *Festuca*, *Bromus*, *Agropyron*, *Poa*), sedges (*Carex*), *Dryas octopetala*, and forbs when available (Hoefs and Cowan, 1979; Nichols, 1978a; Whitten, 1975; Winters, 1980). Shrubs such as *Artemisia*, *Salix*, and *Vaccinium* can be seasonally important (Hoefs, 1974b; Hoefs and Cowan, 1979; Murie, 1944). The average annual diet of *O. d. dalli* in Yukon was 46.3% grasses (and grass-like), 36.8% forbs, 16.1% browse, and 0.8% lichens and mosses (Hoefs and Cowan, 1979). Winter diets are influenced by snow accumulations on restricted winter ranges (Murie, 1944). Mineral licks of high calcium-phosphate (Dixon, 1938), or calcium-magnesium concen-

trations (Jones and Hanson, 1985) can be important seasonally (Geist, 1971; Murie, 1944).

No documentation of competition between *O. dalli* and other ungulates exists. Persistent competition for food or space is not likely with wild ungulates within the range of *O. dalli*; caribou (*Rangifer tarandus*), moose (*Alces alces*), and mountain goat (*Oreamnos americanus*) use divergent habitats or select different diet components (Henshaw, 1970; Klein, 1953). *O. dalli* has displaced caribou from two feeding sites (Henshaw, 1970). Feral horses may compete with *O. dalli* when in sympatry (Hoefs and Bayer, 1983).

Wolves (*Canis lupus*) prey on *O. dalli* in areas of sympatry (Child et al., 1978; Hoefs and Cowan, 1979; Hoefs et al., 1986) and may limit populations of Dall's sheep when alternate prey are not readily available (Heimer and Stephenson, 1982; Murie, 1944). Wolf diets have contained 2–25% *O. dalli* (Gasaway et al., 1984; Murie, 1944). Predation by wolves and coyotes (*C. latrans*) can increase during heavy accumulations of snow (Burles and Hoefs, 1984). Other predators include golden eagles (*Aquila chrysaetos*), lynx (*Lynx canadensis*), grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), and wolverines (*Gulo gulo*; Hoefs and Cowan, 1979; Murie, 1944, 1981; Nette et al., 1984; Pitzman, 1970). Deaths from accidental falls and avalanches also have been noted (Burles and Hoefs, 1984; Hoefs and Cowan, 1979).

*Ovis dalli* harbor a variety of disease agents, some of which may influence population demography. Lungworm (*Protostrongylus* sp.), which causes hemorrhagic septicemia (Shackleton, 1985), has been reported in *O. dalli* (Goble and Murie, 1942); it may be most prevalent in Dall's sheep on low-nutrient intakes (Seip and Bunnell, 1985). Large scale die-offs from lungworm infestations have not been observed in *O. dalli* as they have in *O. canadensis* (Stelfox, 1971). *Meullerius* sp. has been reported in one population of *O. d. stonoi* (Seip and Bunnell, 1985). Gibbs and Fuller (1959) observed *Wyominia tetoni* in the bile and hepatic ducts and intestinal lumen of four males, but no pathological disfunctions were noted. Parasitic protozoan coccidia (*Eimeria ahsata*, *E. crandaillii*, and *E. dalli*) have been isolated from *O. dalli* feces (Clark and Colwell, 1974). High concentrations of leukocytic eosinophils, which can be associated with endoparasitism, have been noted (Kim, 1977). The symbiotic protozoan fauna in the rumen of *O. dalli* (142–155 × 10<sup>4</sup>/cc of rumen contents) is unique among Arctic ruminants and appears to lack holotrichs (Dehority, 1974). Common rumen protozoa include *Entodinium* sp., *Diplodinium* sp., and *Ophryoscolex* sp. (Dehority, 1974).

Positive titers in *O. dalli* sera have been reported for a variety of arboviruses (Zarnke et al., 1983a), contagious ecthyma virus (Dieterich et al., 1981; Foreyt et al., 1983; Heimer et al., 1982; Smith et al., 1982; Zarnke, 1983; Zarnke et al., 1983b), *Campylobacter feti*, *Brucella* sp., parainfluenza III virus (Foreyt et al., 1983; Heimer et al., 1982), Q fever rickettsia, and epizootic hemorrhagic disease virus (Zarnke, 1983). Epizootic hemorrhagic disease is similar to bluetongue and causes a pneumonia-like syndrome. Contagious ecthyma may limit the juvenile cohort of some populations (Zarnke, 1983; Zarnke et al., 1983b). Erythrocyte sickling occurs in a variety of *Ovis*, but has not been reported for *O. dalli* (Butcher and Hawkey, 1979). Secondary amyloidosis, an inflammatory internal disorder that can be associated with chronic pneumonia, was observed in captive *O. dalli* (Kingston et al., 1982).

Necroses of the horn cores (Bunch et al., 1984b; Hoefs et al., 1982) and mandible-tooth arcade (lumpy jaw; Glaze et al., 1982; Heimer et al., 1982; Hoefs and Cowan, 1979; Murie, 1944; Sheldon, 1932) are common in *O. dalli*. Causes of horn aberrations are unknown (Bunch et al., 1984b), but *Corynebacterium pyogenes*, *Fusobacterium necrophorum*, *Proteus*, *Micrococci*, and *Escherichia* have been isolated from lumpy jaw infections (Glaze et al., 1982; Heimer et al., 1983). Horn and cranial asymmetry have been attributed to osteoporosis in *O. canadensis* (Bleich et al., 1990). Mandibular diseases and excessive toothwear from wind-blown silt deposits on forages may limit the life span of some individuals and thereby influence population demography (Hoefs, 1975; Hoefs and Bayer, 1983).

Deep snow, low temperatures, high population density, disease, low-quality forage, and predation have been responsible for mortality among *O. dalli*, especially for lambs (Burles and Hoefs, 1984; Murphy and Whitten, 1976; Nichols, 1978a; Simmons et al., 1984). Specifically how these factors interact to affect survivorship is uncertain.

Various federal, state, and provincial governmental agencies

are responsible for management of *O. dalli* (Hoefs, 1985; Trefethen, 1975). Populations of *O. dalli* are managed variously for: (1) sustainable trophy harvest (rams with  $\geq 3/4$  curl horns that occur outside parks or preserves); (2) aesthetic and nonconsumptive values (25% of *O. dalli* in Alaska [Heimer, 1985] and 30% in Yukon [Hoefs and Barichello, 1985] are protected from hunting in parks or preserves); and, to a lesser extent, (3) subsistence hunting by native peoples (thought to be a small percentage of the total annual harvest in Alaska; Heimer, 1985). Except for two populations in Alaska where harvest of females is permitted and subsistence hunting for which there are limited restrictions, annual harvest of *O. dalli* is restricted to mature rams (7/8 to full curl in Alaska, [Heimer, 1985], full curl or more in British Columbia [Elliot, 1985] and Yukon [Hoefs and Barichello, 1985], and 3/4 curl or more in Northwest Territories [Poole and Graf, 1985]). In 1985, the harvest represented <2% of the total estimated number of extant *O. dalli*. Most adult males are harvested by nonresidents (72% in Yukon), who are required to pay special fees, hire guides and outfitters, and restricted to specific management areas (Alaska) or outfitter units (Canada).

In general, wild *Ovis* in North America is perturbed by human activities (Geist, 1971, 1975; Leslie and Douglas, 1980); specifically, mineral exploration, road construction, and aircraft harassment have been noted as potential pernicious impacts to *O. dalli* (Hoefs and Barichello, 1985; Nichols, 1975; Poole and Graf, 1985). In British Columbia, some subalpine ranges of *O. d. stonoi* are burned in the spring in an attempt to improve habitat and thus population quality (Elliot, 1985; Seip and Bunnell, 1985). Elliot (1985) reported that range burning can slow population declines by 50% and improve trophy quality (horn size of adult males). Nutrient quality of forage was not greater on burned subalpine ranges compared to unburned alpine ranges (areas used by sheep in spring and summer), but burned areas that were accessible relative to snowfall provided a greater quantity of forage in winter compared to unburned areas (Seip and Bunnell, 1985). Such habitat manipulation is unique within the range of *O. dalli*, most of which remains remote and pristine.

**BEHAVIOR.** *Ovis dalli* is gregarious and exhibits a polygynous mating system in which large, dominant males breed most often. Rutting groups of as many as 21 individuals have been observed ( $\bar{X} = 3.7$ ,  $n = 166$ ), but maximum group size declined to seven for males and 12 for females by midwinter (Geist, 1971).

Prior to rut, males gather into groups and begin interacting with relatively low-intensity behaviors. Males may kick one another with a foreleg, display their horns, and occasionally jump-threat and clash with one another; dominance mounting also may occur. Subordinate males sometimes rub and horn the face of dominants (Geist, 1971).

As rut approaches, males begin to associate regularly with females, interactions among males become more vigorous, and fights to establish dominance occur. Encounters typically are won by larger, older individuals and result in dominance relationships that affect breeding opportunities later in rut. Such fights involve low-stretches (an aggressive broad-side display), vigorous kicking, jump-threats, and clashes in which males slam the edge of their horns forcefully together. Males often display their horns, which serve as measures of social rank (Geist, 1971).

Interactions among males at the height of rut tend to lack ritualization and fights over estrous females can be fierce. Males deliver blows to the sides of opponents with their horns and may even push competitors off precipitous cliffs. Losers of such fights often take flight with the dominant male pursuing them closely for a short distance (Geist, 1971).

Males court females by approaching them in a low-stretch posture while flicking their tongues. Such males investigate the reproductive status of females by licking urine from the perianal region, while the female is urinating, or lapping it from the ground after she has urinated. Males then flehmen (lip curl), which presumably allows them to determine the female's state of estrus (Estes, 1973). Females may distract courting males by inducing them to investigate an area where the female recently urinated while she moves away (Geist, 1971).

If the female is in estrus, the male usually continues to court and attempts to defend her from other males. Females sometimes elicit courtship from the male by butting and rubbing against him. Copulation occurs when receptive females stand for mounts rather than walking forward, which thwarts the male's attempts to mate.

Males may kick the female with a stiff foreleg during courtship, presumably to assess her willingness to be mounted. Males guard receptive females for 2–3 days, which probably reflects the length of estrus (Geist, 1971). Males then cease defending the female and begin searching for additional mates. This tending-bond mating system is typical of *O. dalli*; harem mating and territoriality have not been documented (Nichols, 1978a). As rut wanes, males become more solitary and aggressive interactions are less frequent. Younger males still may attempt to court females, but females seldom are receptive to such efforts (Geist, 1971).

Females often seek secluded sites among high cliffs to give birth; activities of the female are centered about the birth site for 8–12 h postpartum (Pitzman, 1970). Mass of lambs at birth is 3–4 kg (Bunnell, 1980). Females lick and paw neonates soon after birth (Geist, 1971; Pitzman, 1970) and lambs first stand 15–32 min following parturition. Females pass the placenta about 3 h postpartum and consume it. Nursing begins about 3.5 h after birth (Pitzman, 1970).

**GENETICS.** *Ovis dalli* has a diploid chromosome number (2n) of 54. Its karyotype has three pairs of large metacentric autosomes and 24 pairs of acrocentric chromosomes, the largest pair being the X chromosomes (Nadler, 1971). *O. dalli* has an identical chromosome number and similar chromosomal morphology to *O. canadensis*, *O. musimon*, and *O. orientalis*, (Korobitsyna et al., 1974; Wurster and Benirschke, 1968). *O. nivicola*, however, possesses only 2n = 52 with four pairs of metacentric and 22 pairs of acrocentric chromosomes (Korobitsyna et al., 1974). Among sheep, *O. vignei* apparently possesses the largest chromosome number of 2n = 58; chromosomal evolution is thought to have proceeded via a descending series of Robertsonian fusions, making *O. nivicola* the most recently derived karyotype (Korobitsyna et al., 1974).

At least the first three pairs of metacentric autosomes are homologous among some European and North American sheep, as indicated by meiotic pairing during spermatogenesis and comparisons of G-band patterns in hybrids of *O. musimon* and *O. canadensis* (Nadler et al., 1973). Further, measurements of chromosomal size and arm length proportions of these three largest metacentric autosomes are similar for *O. dalli*, *O. canadensis*, and *O. nivicola* suggesting they may have been derived from a common ancestor (Korobitsyna et al., 1974). *O. dalli* sera proteins and antigenic characteristics differ little from other *Ovis* and related caprids, and therefore, immunological differences are not currently useful for phylogenetic separations among most Caprini (Hight and Nadler, 1976).

**REMARKS.** *Ovis d. dalli* and *O. d. stonei* were named for W. H. Dall and A. J. Stone, respectively (Nichols, 1978a). Nichols (1978a) considered *O. d. kenaiensis* synonymous with *O. d. dalli*. Dall's sheep on Kenai Peninsula, Alaska, are somewhat smaller than other populations (Cowan, 1940), this difference may represent clinal variation in *O. d. dalli* (Nichols, 1978a). The type locality for *O. d. stonei* (Che-on-ee Mountains) does not appear on official maps. This location probably was the Rainbow Mountains between the Stickine and Iskut Rivers in British Columbia (Cowan, 1940).

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