

Mountain Sheep

Ovis canadensis and *O. dalli*

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NOMENCLATURE

COMMON NAMES. Mountain sheep, bighorn sheep

SCIENTIFIC NAME. *Ovis canadensis*

SUBSPECIES. *O. c. auduboni*, Audubon's bighorn, Black Hills bighorn, or badland bighorn; *O. c. californiana*, California bighorn; *O. c. canadensis*, Rocky Mountain bighorn; *O. c. nelsoni*, *O. c. mexicana*, *O. c. cremnobates*, and *O. c. weemsi*, desert bighorn

It is unlikely all currently recognized subspecies will be maintained when bighorn taxonomy is revised (Wehausen and Ramey 1993; Jessup and Ramey 1995).

COMMON NAMES. Thinhorn sheep, Dall's sheep

SCIENTIFIC NAME. *Ovis dalli*

SUBSPECIES. *O. d. dalli*, Dall's or Alaskan white sheep; *O. d. stonei*, Stone's or black thinhorn sheep (Valdez and Krausman 1999).

Recent summaries of mountain sheep by the authors (Krausman et al. 1999; Valdez and Krausman 1999; Bowyer et al. 2000; Krausman and Shackleton 2000) were used to develop this account.

DISTRIBUTION

Distribution of Rocky Mountain bighorn sheep closely follows the Rocky Mountains, and extends from about 55° N in Alberta and British Columbia, south through Montana, Idaho, Utah, Wyoming, and Colorado, and into northern New Mexico at around 36° N (Stelfox 1971, Clark 1978). California bighorns historically ranged from the eastern slopes of the Coast Mountains in central British Columbia (51° N), south into Washington, Oregon, and Idaho as far as the Sierra Nevada in California (37° N) (Cowan 1940). Nevertheless, from 1900 until 1954, this subspecies was extirpated from much of its distribution, especially in the United States. Subsequently, California bighorn sheep have been translocated, mainly from British Columbia, to restock and reestablish populations in California, Oregon, Washington, Idaho, Nevada, and North Dakota (Demarchi and Mitchell 1973). Desert bighorn sheep formerly occupied ranges from Nevada (40° N) to Baja California, Mexico (24° N), and from western Texas, southern New Mexico and Arizona, and western Colorado and Utah to California (Monson 1980) (Fig. 51.1).

Dall's sheep range through rugged and steep mountains in Alaska, Northwest Territories, the Yukon, and British Columbia from 69°40' to 59°30' N latitude. Stone's sheep is distributed the farthest southward, with populations in British Columbia (Bowyer et al. 2000) (Fig. 51.1). Unlike bighorn sheep, populations of Dall's sheep have not been reduced markedly and still occur throughout much of their original range.

DESCRIPTION

Mountain sheep are in order Artiodactyla, suborder Ruminantia, and family Bovidae. True sheep of the genus *Ovis* are characterized by the presence of interdigital, inguinal, and preorbital glands and the absence

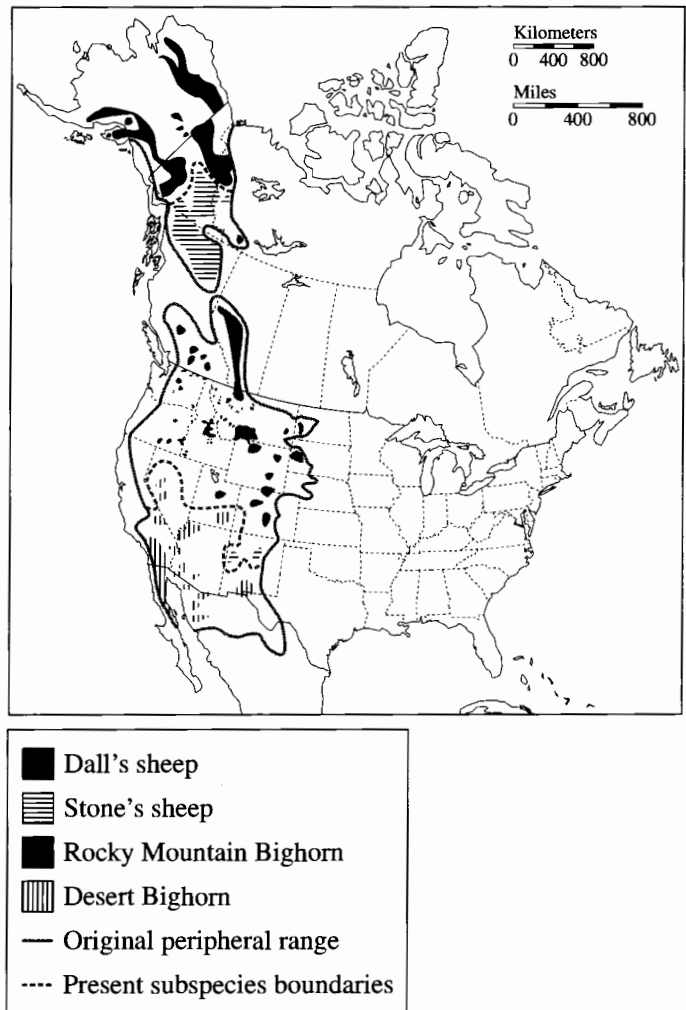


FIGURE 51.1. Distribution of mountain sheep. SOURCE: Data from Valdez and Krausman (1999).

of subcaudal glands and a chin beard (Valdez and Krausman 1999), which separates them from the genus *Capra*.

Horns. The most distinguishing feature of mountain sheep is the massive horns of adult males (Fig. 51.2). Bighorns possess more massive, less rugose, and usually more broomed (i.e., broken tips), and less widely expanded horns than thinhorn sheep. Desert bighorn exhibit more diverging horns than northern bighorn sheep. Horns of desert bighorn females are more expanded and curved than those of other subspecies (Valdez and Krausman 1999) (Table 51.1). Horns of Dall's sheep flair more widely than those of bighorn sheep.



FIGURE 51.2. Adult male bighorn sheep. SOURCE: Photo by V. Geist.

Weight. At birth, northern bighorn weigh 2.7–4.5 kg. Adult males average 79 kg (up to 145 kg). Females average 59 kg. At birth, desert bighorn weigh 2.7–4.1 kg. Adult males average 68 kg (up to 104 kg). Females average 52.2 kg. At birth, thinhorn weigh 3.2–4.1 kg. Adult males average 81.7 kg (up to 136.2 kg). Females average 56.8 kg (Valdez and Krausman 1999).

Adult External Measurements. Measurements for bighorn males (mm) are as follows: for males, total length, 1321–1956; tail, 102–152; hind foot, 356–483; shoulder height, 813–1118; for females, total length, 1168–1880; tail, 102–127; hind foot, 279–432; shoulder height, 76–91 (Valdez and Krausman 1999). Measurements for thinhorn males and females, respectively, are as follows (mm): total length, 1300–1780 and 1324–1620 (Cowan 1940; Bunnell and Olsen 1976; Hall 1981); tail, 8–13 and 8–10; hind foot, 38–46 and 28–41 (Valdez and Krausman 1999); and shoulder height, 916–1090 (Cowan 1940; Bunnell and Olsen 1976; Hall 1981) and 787–889 (Valdez and Krausman 1999).

Pelage. The back of the legs, distinct rump patch, and usually part of the muzzle are white. Bighorn are usually brown and have a stripe middorsally of dark body hair across the rump patch to the tip of their tail. Thinhorn are white (i.e., Dall's) or grayish to blackish (Stone's).

Markings on Stone's sheep are similar to those of bighorn sheep. Mountain sheep have unbanded awn-type guard hairs, which are round to oval (length ≤ 32.2 mm and diameter ≤ 4.8 mm) (Moore et al. 1974). The annual spring molt lasts approximately 1–2 months (Lawson and Johnson 1982). Dall's sheep are white or off-white, but sometimes have black tails. Stone's sheep are gray with white leg trimmings and rump patches similar to bighorn sheep. Fannin's sheep are intermediate in pelage color and markings between Dall's sheep and Stone's sheep, and is most common where the subspecies of thinhorns intergrade in distribution. However, it is not recognized as a subspecies.

Skull and Dentition. The mean skull mass of mature males excluding the lower jaw is 18 kg (Clark 1970). The lambdoidal suture forms a fairly straight line and the upper ends of the premaxillae do not meet the nasals and maxillae (Lawson and Johnson 1982). The infraorbital foramen is small with a well-defined rim, the braincase is pneumatic, and the occipital condyles are enlarged (Figs. 51.3 and 51.4).

Of all ruminants, wild sheep have the largest horns in proportion to body size, about 8–12% of an adult male's body mass (Geist 1966b). Horns begin to be visible at 2 months of age (Hansen 1965). At 5.5 months, the horns are 5–7 cm long (Jones 1959). At 12 months, the basal circumference of male horns is greater than that of female horns and increases at approximately the same growth rate as the length (Lawson and Johnson 1982). The horn is triangular in cross section during the first 2 years. During the third year, the base of the horn swells and the horn loses its flat-sided shape (Lawson and Johnson 1982). Growth is greatest during summer; differential yearly growth produces annual rings. During the first 3–4 years, horn rings are several inches apart and then occur closer and become harder to differentiate (Fig. 51.3) (Taylor 1962; Shackleton et al. 1999).

Female horns are smaller and shorter than those of males. Female horns are relatively thin and gently curved, whereas those of adult males are massive at the base, tapered, and curled in a spiral as they grow. Horn growth each year occurs when a new keratin horn sheath develops over the underlying bone horn-core, which is an extension of the frontal bone. The horn sheath grows beneath the preceding year's horn, so that each year, horn sheaths are grown one inside the other. Except for the first or lamb horn, only a part of the annual horn sheath is exposed (Taylor 1962; Shackleton et al. 1999). When horn growth stops, probably in autumn or early winter, and is then followed by growth of a new sheath the following spring, a distinct break or annual ring is formed.

Horns and horn growth are of value to wildlife biologists for several reasons. First, an individual's age can be determined by counting the horn rings or annuli that develop each year. With long-lived individuals,

TABLE 51.1. Mean, standard deviation (*SD*), and range (in inches; standard unit of measurement) of horn measurements of the 25 longest horned specimens of mountain sheep

	Horn Length		Basal Circumference		Tip-to-Tip Spread	Greatest Spread
	Right	Left	Right	Left		
Dall's sheep						
Mean	44.9	44.5	14.3	14.3	26.9	27.2
SD	2.9	2.6	0.6	0.6	4.0	3.6
Range	38.8–49.5	39.0–47.5	13.0–15.3	13.0–15.3	20.9–34.4	20.9–34.4
Stone's sheep						
Mean	45.0	44.9	14.8	14.8	24.5	26.6
SD	2.2	1.9	0.6	0.6	3.1	2.9
Range	42.1–50.1	41.9–51.6	13.5–16.3	13.5–16.3	19.0–31.4	22.0–31.5
Rocky Mountain and California bighorn						
Mean	43.7	43.7	15.9	15.9	22.0	23.4
SD	2.3	2.2	0.7	0.7	2.8	1.9
Range	39.1–49.5	40.5–49.3	14.8–17.5	14.8–17.4	18.1–28.9	21.5–28.9
Desert bighorn						
Mean	40.6	40.8	15.7	15.7	22.1	22.9
SD	2.1	2.3	0.6	0.6	2.9	2.2
Range	37.0–45.6	36.0–46.3	14.5–16.8	14.6–17.0	16.8–27.4	17.8–27.4

SOURCE: Data from Reneau and Reneau (1993).

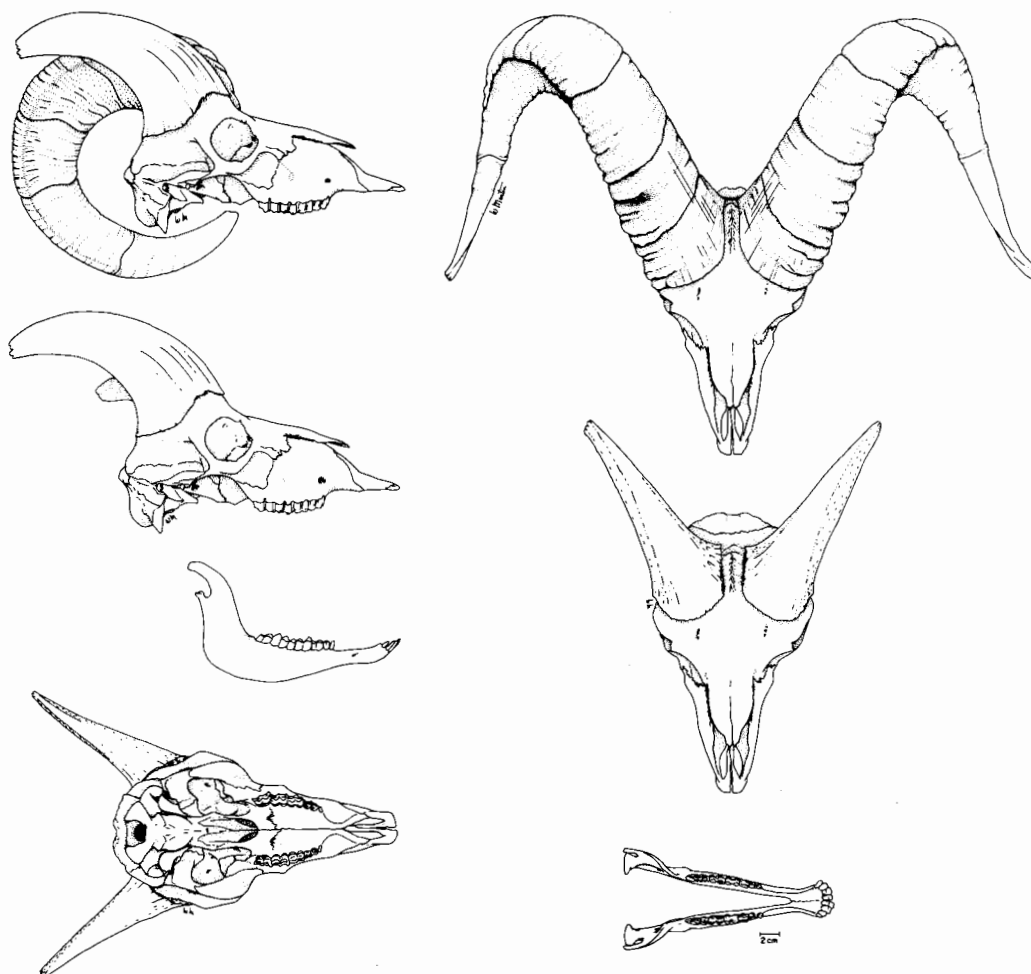


FIGURE 51.3. Skull of the thinhorn sheep (*Ovis dalli*). From top to bottom: (left) lateral view of cranium with one horn removed and (right) dorsal view of cranium with horns; (left) lateral view of cranium with both horns removed to show permanent bony core, and lateral view of mandible, and (right) dorsal view of cranium with horns removed; (left) ventral view of cranium with horns removed and (right) dorsal view of mandible.

however, it is usually easier to estimate the age of males than females. After about 4 or 5 years of age, female horns grow very little, probably because of reproductive costs, so their horn rings become very crowded and hard to distinguish. In males, the first 2 years or more of horn growth can be lost to "brooming" or breakage of the horn tips during fighting, making precise age determination problematic in older animals (Shackleton and Hutton 1971); brooming is less common in Dall's sheep because of the widely flaring tips of the horns. Although only relative measures of annual horn length are possible because all but the first year's horn are partially hidden by preceding ones, measuring annual horn growth can provide insights into an individual's and a population's status.

When the average lengths of the exposed annual horn sheaths are plotted (for males or females), the generalized pattern of horn growth is relatively consistent among bighorn sheep populations. The longest visible horn sheath almost always is grown in the second year of life, after which exposed horn length decreases rapidly. Maximum annual horn growth in the second year and rate of "decline" in annual horn length vary among populations, reflecting primarily environmental rather than genetic differences (Geist 1971; Shackleton 1973, 1976). Relative annual horn growth is initially greater in low-density populations on good range. This is because of rapid population growth, fast individual growth rates, early maturation, early mortality, intense social interaction, and high milk production, though it declines faster than in stable or declining populations at higher density relative to carrying capacity (Geist 1971; Shackleton 1973, 1976; Wishart and Brochu 1982).

Managers may be able to use the average pattern of annual horn sheath growth and body growth to compare populations and evaluate management options (Smith and Wishart 1978; Gilchrist 1992). This can be especially valuable for wildlife managers because size limits for trophy hunting are often described in terms of horn size (e.g., three-quarter curl and full curl) and hence are influenced by horn growth. Horn growth of rams is minimal after ages 7 or 8 years. Horns are fairly distinct between thinhorn and bighorn races of sheep (Table 51.1). Dall's and Stone's sheep exhibit the longest mean horn lengths, followed by Rocky Mountain bighorn and desert bighorn. Rocky Mountain bighorn exhibit the greatest mean basal circumferences, followed by desert bighorn, then Stone's and Dall's sheep. Dall's and Stone's sheep, however, exhibit the longest means of tip-to-tip spread and the greatest spread, followed by Rocky Mountain and desert bighorn (Table 51.1). The longest horns ever recorded in a North American wild sheep (right = 1273.2 mm, left = 1311 mm) are those of the Chadwick ram, a Stone's sheep shot by L. S. Chadwick along the Muskwa River, British Columbia, in 1936 (Valdez and Krausman 1999).

The largest number of record-sized Rocky Mountain bighorn rams recorded since 1975 originated from introduced populations in Montana (Boone 1988; Gilchrist 1992). Twenty-six of the 100 highest scoring Rocky Mountain bighorn rams listed in the 10th edition of the Boone and Crockett Club record book are from Montana (Reneau and Reneau 1993).

North American wild sheep have similar patterns of tooth development (Table 51.2). Deciduous dentition is complete within the first

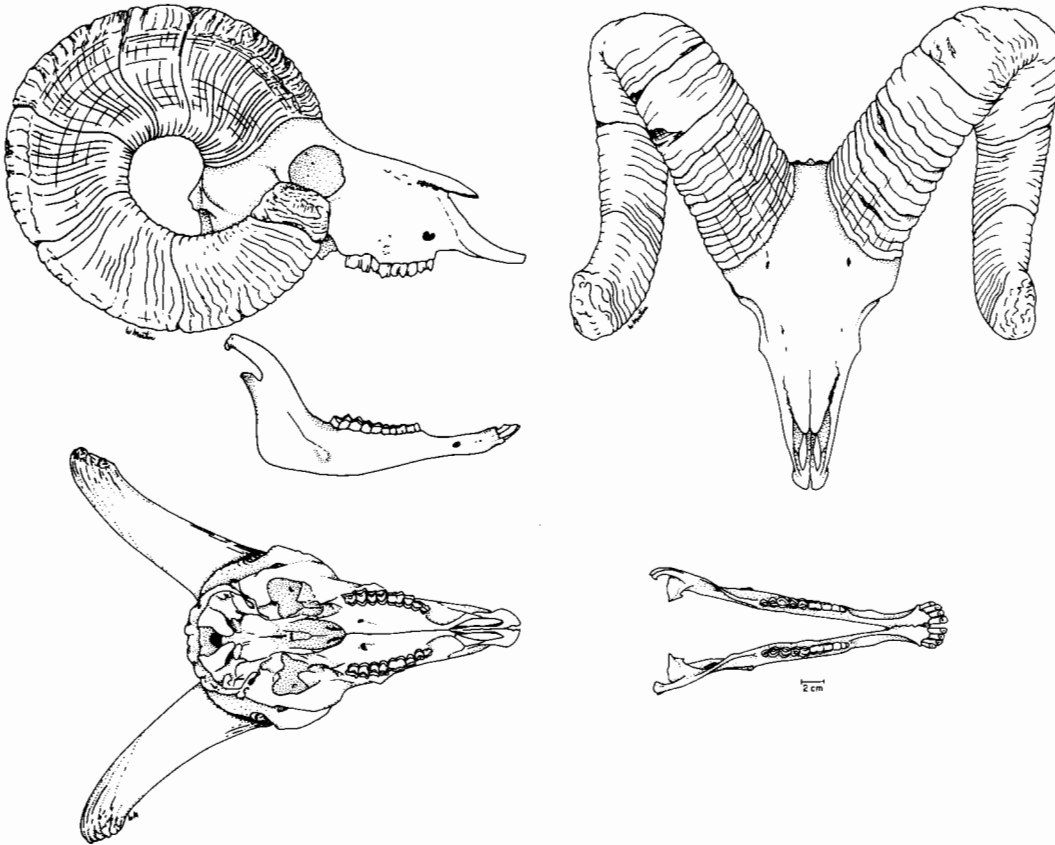


FIGURE 51.4. Skull of the bighorn sheep (*Ovis canadensis*). From top to bottom: (left) lateral view of cranium and lateral view of mandible and (right) dorsal view of cranium; (left) ventral view of cranium with horns removed and (right) dorsal view of mandible. Note the horn annuli, the normal corrugations, and the increment lost to brooming.

TABLE 51.2. Sequence of tooth eruption in the lower jaw of North American wild sheep

Age (months)	Incisors			Canine	Premolars				Molars		
	1	2	3	1	2	3	4	1	2	3	
6	D	D	D	D	D	D	D	(P)			
12	(P)	D	D	D	D	D	D	P	(P)		
18	P	D	D	D	D	D	D	P	P		
24	P	D	D	D	D	D	P	P	P		
36	P	P	(P)	D	P	P	P	P	P	(P)	
42	P	P	(P)	D	P	P	P	P	P	P	
44	P	P	P	P	P	P	P	P	P	P	

NOTE: D, Deciduous; P, permanent; (P), erupting.

week of life, but permanent dentition is not fully erupted until 4 years of age (Table 51.2). Incisors are spatulate, the lower canine is incisiform, and molars are subhypodont (i.e., long and broad); they do not contain an open pulp cavity throughout their life, (Geist 1971). Bighorn sheep and thinhorns have 32 teeth. The dental formula is I 0/3, C 0/1, P 3/3, M 3/3. Dental anomalies include deformations, lost teeth, malocclusions, incomplete sets of teeth, and vestigial upper canines (Murie 1944; Deming 1952; Welles and Welles 1961; Lawson and Johnson 1982).

PHYSIOLOGY

Temperature and Blood Chemistry. Lawson and Johnson (1982) reported the temperature and blood chemistry of mountain sheep. The

normal range of rectal temperature is 38.3–38.9°C, but it varies according to the ambient temperature, excitability, and diet. The cyclic nature of body temperature in mountain sheep appears to be related to metabolic factors that are physiological adaptations to conserve energy during winter (Franzmann and Hebert 1971).

Chappel and Hudson (1978) reported that the metabolic rate of Rocky Mountain bighorns is lowest at an ambient temperature of –10°C and the thermoneutral zone is –20°C to +10°C. Those authors also observed that moderate wind affected metabolic rate only at ambient temperatures below –20°C.

The blood transferrins and hemoglobins differed among *O. c. canadensis*, *O. c. mexicana*, *O. d. dalli*, and *O. d. stonei* (Nadler et al. 1971). Other physiological values, including blood proteins and minerals, white blood cell count, red blood cell count, and packed cell volume, were reported by Franzmann and Thorne (1970), Woolf and Kradel (1970), and Franzmann (1971, 1972).

Hematology and blood chemistry of Dall’s sheep are similar to those reported for bighorn (Franzmann 1971; Butcher and Hawkey 1979; Foreyt et al. 1983). Such data, however, may vary with sex, age, physical condition, season, handling, and numerous other factors (Shackleton 1985; Keech et al. 1998). Although some blood variables may correlate with physical condition, direct comparisons among populations using these values should be made with appropriate caution (Keech et al. 1998).

Neural. Mountain sheep depend more on their visual capabilities than on their auditory or olfactory senses. The mean hearing thresholds for desert bighorn sheep were 47, 47, 69, and 89 dB peak equivalent sound pressure level for click, 4000-, 2000-, and 1000-Hz tonebursts, respectively (De Young et al. 1993).

REPRODUCTION

Anatomy. The reproductive anatomy and physiology of wild sheep have not been thoroughly examined. Lawson and Johnson (1982:1038–39), however, summarized accounts from Blom (1968) and Hafez (1968) of domestic sheep anatomy and physiology as applicable to mountain sheep in North America:

The ovary, oviduct, and uterus are supported by a broad dorsolateral ligament in the region of the ilium. The bipartite uterus resembles a ram's horns with a convexity dorsal. The almond-shaped ovaries are located laterally and in close apposition to the fusion of the uteri in open ovarian bursae. The bursae are pouches derived from the same tissue as the ligament and attach the suspended oviducts to the uteri. The right ovary is most active. Mature corpora lutea are spheroid or oval and the oviduct is pigmented. The endometrium of the uterus is characterized by numerous pigmented caruncles, each generating many cotyledons during pregnancy. Annular folds form the lumen of the cervix, and the hymen is well developed.

There are two inguinal, functional mammarys; supranumerary teats, if present, are located anteriorly to the normal ones. Fine hair covers the teats, and the connective tissue closing the orifice is elastic.

The prostate gland of the ram is disseminate. The scrotum is pendulous and the testes inguinal. Rams have a fibroelastic penis with a filiform appendage, the precesses urethrae, located at the tip, which rotates rapidly during ejaculation to spray the semen in the vagina.

Physiology. Females are monoestrous. The rutting or mating season is that period in which mating activities result in 70% of the lamb production for the following season (Turner and Hansen 1980). Duration of the mating season is longer at lower elevations and southern latitudes, and shorter at higher elevations and more northern latitudes (Bunnell 1982; Thompson and Turner 1982). Rocky Mountain and northern populations of California bighorn mate in late autumn and early winter, with the mating season beginning as early as late October, or, as is typical for most Rocky Mountain populations, in early November (McCann 1956; Buechner 1960; Blood 1963; Geist 1971; Demarchi and Mitchell 1973). Sometimes mating extends into late December and early January, but usually peaks between mid-November and mid-December (Hones and Frost 1942; Smith 1954; Wishart 1958; Buechner 1960; Sugden 1961; Blood 1963; Morgan 1970; Geist 1971; Shackleton 1973). By contrast, desert bighorn exhibit an extended mating period, and births have been documented in the Sonoran Desert in all months except October (Wilson 1968; Leslie and Douglas 1979; Lenarz and Conley 1982; Witham 1983). This variation in mating seasons appears related to environmental conditions at the time of birth. Dall's sheep rut in November and December (Geist 1971; Nichols 1978a), timing reproduction so neonates can be provisioned successfully (Bowyer 1991; Rachlow and Bowyer 1991, 1994; Bowyer et al. 1998).

Before estrus, one to four Graafian follicles develop simultaneously. The estrous cycle in bighorns lasts 28 days, with a receptive period of around 48 hr (Turner and Hansen 1980). Gestation lasts 173–185 days in desert sheep, 173–175 days in California bighorn, 173–176 days in Rocky Mountain sheep (Blunt et al. 1972; Turner and Hansen 1980; Whitehead and McEwen 1980; Sandoval et al. 1984; Shackleton et al. 1984), and 171 days in Dall's sheep (Nichols 1978a). Females in all races usually produce a single lamb each year until old age or death overtakes them. Most males actively mate for only a few years, during which time they may inseminate many females. Successful mating is not entirely a function of sexual maturation, as social hierarchy and behavior play major roles (Geist 1971; Shackleton 1991).

If Dall's sheep are similar to domestic sheep, they have an estrous cycle of about 17 days (Asdell 1964). Photoperiod is likely an important cue in timing of reproduction, and the presence of an adult male and physical condition of the female are proximal stimuli that also affect onset of estrus, which is thought to last for 1 day (Geist 1971; Nichols 1978a).

Breeding. During mating, adult male and female–juvenile groups join for the duration of the rut, which usually takes place within the home range of females (Krausman and Shackleton 2000). An anestrous female may be courted throughout the year by young males, but the males are discouraged, as females avoid them and withdraw from mounting attempts (Welles and Welles 1961; Geist 1968, 1971). During estrus, females are more aggressive. Large-horned, older males are the most dominant and also those most likely to mate (Geist 1971; Hogg 1984, 1987; Shackleton 1991). Females do not show any clear relationships between physical attributes and social status; their dominance hierarchies appear less linear and more subtle than those of males (Eccles and Shackleton 1986; Festa-Bianchet 1991; Hass 1991; Zine and Krausman 2000). Only age and nursing rate have been related to social status in female bighorn, but there is no evidence that a female's status is related either to her reproductive fitness or to her differential investment in male and female offspring (Eccles and Shackleton 1986; Festa-Bianchet 1991; Hass 1991).

Mountain sheep are extremely gregarious and polygamous (Geist 1971). Males search for females in estrus (Smith 1954; McCann 1956; Leslie and Douglas 1979), and on finding a receptive female, dominant males attempt to chase away other males. Males examine females for estrus by sniffing the vulva and tasting urine.

Males often deliver a stiff foreleg kick to females in heat to stimulate a chase, or the ewe may initiate the chase. The chase may or may not be strenuous. If one of the pair tires, the partner usually waits until the other is ready to resume. When the female is sufficiently stimulated, she assumes a position of lordosis. If the male becomes exhausted, nearby subordinates may usurp his position at any time (Blood 1963; Geist 1971).

Dall's sheep possess a tending-bond mating system in which a dominant male guards, tends, and courts a female (Geist 1971; Hirth 1977). After copulation has occurred, the male leaves in search of additional mates.

Ovulation and spermatogenesis usually begin by 18 months of age, but wild bighorn do not become fully sexually active until they are older (Woodgerd 1964; Geist 1971; Blunt et al. 1972). Most females mate first when at least 2.5 years old, and male Rocky Mountain sheep usually do not begin to participate fully in the rut until 7–8 years old, well after puberty (Geist 1971). In expanding populations, however, or in rare instances, female bighorn have given birth to their first lamb at 18 months (Woodgerd 1964; Shackleton 1973; McCutchen 1976; Van Dyke 1978; Sandoval 1981; Morgart and Krausman 1983). Sexual activity can occur much earlier in captivity; captive desert bighorn male lambs began spermatogenesis at 26–28 weeks and exhibited a seasonal spermatogenetic cycle after 21 months of age. In other studies, captive yearling desert bighorn males inseminated all females living in their enclosure (Turner 1976; Blaisdell 1976; McCutchen 1976). Irvine (1969) reported no apparent decrease in spermatogenesis with increasing age and concluded that even the oldest males were capable of breeding.

Average climatic and forage conditions vary relatively predictably and seasonally in most areas inhabited by California and Rocky Mountain bighorn. Variation in these two factors is important for reproduction, especially for the timing of the birth season. Climatic conditions can affect the survival of newborn lambs and the forage quality and quantity that are important for lactation (Geist 1971; Festa-Bianchet 1988a, 1988b). Lambs, however, must also grow large enough to survive their first winter (Festa-Bianchet 1988c). Thus, for bighorns the birth season is a trade-off between young being born early enough for adequate prewinter growth and being born late enough to avoid the thermal stress and poor forage conditions of late winter (Sadler 1987).

Thompson and Turner (1982) assessed temporal variation in parturition seasons for 22 populations of bighorn sheep. In those from northern latitudes, parturition seasons were shorter, later, and cued to brief, relatively predictable periods of vegetation growth (Bunnell 1982).

The birth period of Rocky Mountain and California bighorn begins in early spring (late April or May) usually coinciding with initiation of spring vegetation growth and ameliorating climatic conditions.

Few lambs are born after June (Shackleton et al. 1999). The same factors, however, may operate differently for desert bighorn sheep due to low population density (Lenarz 1979). More importantly, Thompson and Turner (1982) reported poor correlation between the inception and duration of the vegetation growing season and the lambing period in desert bighorns. They, together with Lenarz and Conley (1982), concluded that an extended lambing season was a result of unpredictable precipitation patterns, and consequently plant regrowth, both of which appear essential for maternal and neonatal survival. For desert bighorns, seasonal fluctuations in resources are not as predictable from year to year. Throughout much of the range of desert bighorn, plant productivity is related directly to temporal and spatial precipitation patterns, and these vary considerably and unpredictably. Nonseasonal reproductive behavior may be an adaptive strategy of desert bighorn that ensures lamb survival during periods of varying and unpredictable forage production. An extended lambing period would increase the probability that late gestation and early lactation would coincide with a period of adequate precipitation and forage availability (Leslie and Douglas 1979; Sandoval 1979; Thompson and Turner 1982). Such reproductive responses to unpredictable resources are common in desert vertebrates (Sadler 1987).

There is increasing evidence that adjustment in gestation length may be under proximal control of female Dall's sheep (Rachlow and Bowyer 1991; Berger 1992; Bowyer et al. 1998). For instance, Dall's sheep in interior Alaska delayed onset of lambing 14 days when a spring storm deposited 25 cm of fresh snow during the peak lambing period of the previous year (Fig. 51.5) (Rachlow and Bowyer 1991). There is a trend for date of parturition to be earlier for populations of mountain sheep with increasing north latitude (Bunnell 1980, 1982). Nonetheless, marked interannual differences in the date of birth can occur. Rachlow and Bowyer (1991) reported that median date of birth in a normal year was 18 May, but was 27 May in the year with the late snowstorm. Synchrony of births also differed in these two disparate years. Evidence that birth synchrony in Dall's sheep is related to predation is lacking. Instead, synchronous births result from a limited time in which offspring can develop to a sufficient size in spring and summer to withstand harsh conditions in winter (Rachlow and Bowyer 1991).

Reproduction has not been reported for lambs (i.e., <6 months), but yearlings (>12 and ≥ 24 months) may become pregnant in highly

productive populations (Nichols 1978a). Females usually do not begin reproducing, however, until 30 months of age (Geist 1971). Indeed, young:adult female ratios at birth for Dall's sheep in interior Alaska varied from 0.4:1 to 0.6:1, indicating not all adult females reproduced each year, a pattern reported for other arctic ungulates (Murphy and Whitten 1976; Rachlow and Bowyer 1991; Cameron and Ver Hoef 1994). Males can become sexually mature at 18 months, but because of the polygamous mating system, they seldom gain an opportunity to breed until 5–7 years of age (Geist 1971).

Fetal sex ratios, although skewed slightly toward males in free-ranging populations, do not depart significantly from parity (Geist 1971; Nichols 1978). Captive females kept on a high nutritional plane, however, produced proportionally more daughters than sons (Hoefs and Nowlan 1994). Thus, nutritional condition of the female likely affects the rate of reproduction and the sex of her offspring.

Parturition. Most female mountain sheep give birth to only one lamb/year; however, twins do occur (Welles and Welles 1961; Spalding 1966; Geist 1971; Nichols 1978a; Hoefs 1978; Eccles and Shackleton 1979). Birth is relatively fast. Approximately 45 min before parturition, the placental membranes begin to appear, and 10 min before birth, the female begins to pant. Birth occurs in 10–15 min, at which time the female stands to facilitate the final expulsion (Lawson and Johnson 1982).

Females seek steep, rugged terrain where they seclude themselves from other sheep for 1–2 days to give birth (Pitzman 1970; Rachlow and Bowyer 1991, 1994, 1998). In the Little Harquahala Mountains, Arizona, individual females exhibited fidelity to parturition sites and sites did not overlap (Etchberger and Krausman 1999). Neonates are exceptionally precocial and stand within 30 min following parturition; young travel with their mothers within 24 hr of birth (Murie 1944; Pitzman 1970). Weaning generally is completed within 3–5 months (Bunnell and Olsen 1976).

Newborn. After birth, the mother licks the placental fluids from the neonate. Females usually consume the placental membrane (Lawson and Johnson 1982). Bighorn sheep weigh 2.7–4.5 kg at birth (Sugden 1961; Geist 1971; Blunt et al. 1972; McEwan 1975; Jorgensen and Wishart 1984). Dall's sheep weigh 3–4 kg at birth (Bunnell 1980).

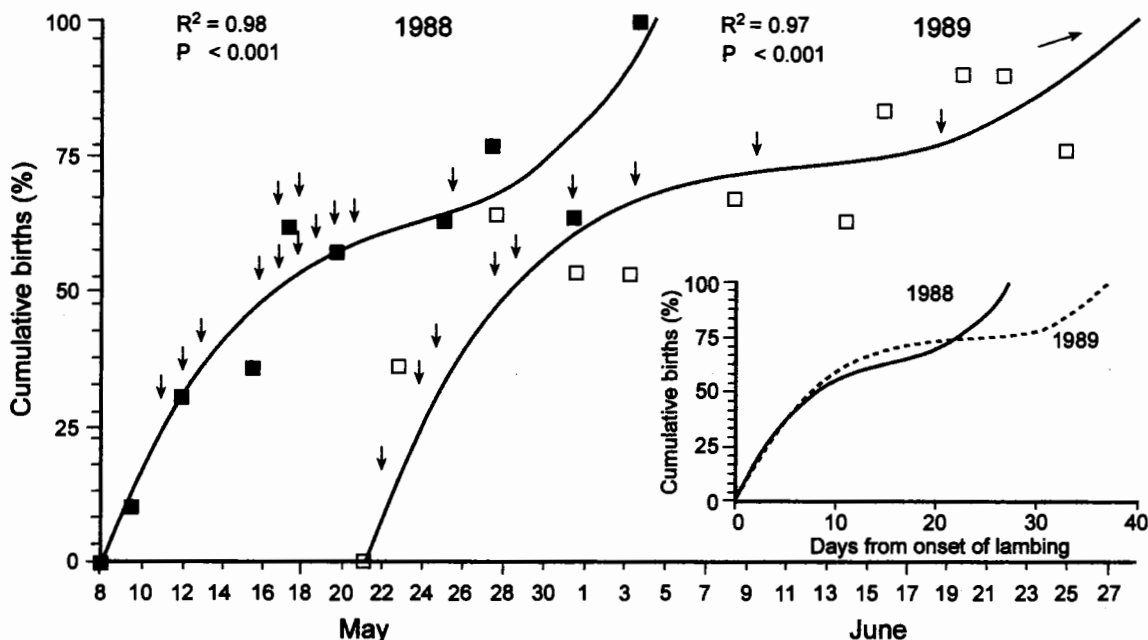


FIGURE 51.5. Cumulative percentage of births determined from young-to-female ratios showing differences in timing and synchrony (inset) of lambing in interior Alaska in 1988 and 1989. Arrows indicate date of birth observed or inferred. SOURCE: Rachlow and Bowyer (1991). Reproduced with permission from Alliance Communications Group.

ECOLOGY

HABITAT: BIGHORN SHEEP

Topography. The general name of "mountain sheep" reflects the bighorn's preference for steep, rugged topography typically found in mountains, though they can meet their requirements in other areas (Geist 1971; Adams et al. 1982; Risenhoover and Bailey 1985; Shackleton 1985). The range of habitat components they can use varies from steep or gentle slopes, broken cliffs, rock outcrops, and canyons and adjacent river benches to mesa tops (Buechner 1960; Sugden 1961; Wilson 1968; Welch 1969; Drewek 1970; Merritt 1974; Stelfox 1975; McQuiver 1978; Holl and Bleich 1983; Etchberger et al. 1989; Wakeling and Miller 1989). Alpine, related slopes, and river benches are mainly used for foraging, whereas cliffs and other precipitous ground supply bighorn with escape terrain (i.e., topography where sheep have a locomotive advantage over predators). These steep habitats provide sheep with their best defense against predators, and bighorns rarely occur far from such security cover (Oldemeyer et al. 1971; Erickson 1972; Pollister 1974; Shank 1979; Hansen 1982; Gionfriddo and Krausman 1986; Krausman and Leopold 1986). Though males may move further away than female–juvenile groups, escape terrain is especially important for females when giving birth (Blood 1961; Drewek 1970; Kornet 1978; Hall 1981; Akeson and Akeson 1992). Although specific characteristics of birth sites for Rocky Mountain and California bighorn have not been studied, parturition microsites for desert bighorn were made up of steep rugged terrain and had less barrel cacti for up to 8 weeks following parturition than sites used by females without lambs. Parturition site fidelity was strong among years with a mean distance between parturition sites for individual females of 450 m (Etchberger and Krausman 1999).

Bighorn occupy an extreme range of elevations. Desert sheep occur from 78 m below sea level in Death Valley, California, to more than 4267 m above sea level in the White Mountains, California. Other subspecies inhabit ranges from 450 to >3300 m above sea level (Welles and Welles 1961; Shackleton et al. 1999). Sheep in most populations make seasonal altitudinal movements, but a few remain at similar elevations year-round (Sugden 1961; Spalding and Bone 1970). Because of these variations, it is difficult to generalize about the elevational preferences of bighorn. A variety of exogenous and endogenous factors may influence elevational use of a particular range, and together reflect the animal's environmental, physiological, and behavioral preferences.

Climate. Areas inhabited by Rocky Mountain and California bighorn are relatively arid. Summers are warm or even hot with highs up to 35°C, and winters are usually cold with temperatures sometimes reaching -40°C (Jones 1959; Smith 1954; Schallenberger 1966). Extreme conditions also prevail in desert habitats, where temperatures as low as minus 29°C have been recorded in winter and >49°C in summer (Hansen 1980a; Sandoval 1980).

Desert bighorn activities are affected by temperature (Chillelli and Krausman 1981). In the Cabeza Prieta National Wildlife Refuge, Arizona, desert bighorn bedded in the shade an average of 7 hr each day when wet bulb temperatures were above 18°C (Simmons 1969). During the hot, dry summer months, heat stress is a serious obstacle to desert bighorn survival; they minimize its effect by limiting their activities, bedding in the shade during the hottest part of the day, and feeding and watering on shaded slopes. Conversely, wind, cold temperatures, and extremes of precipitation levels are limiting to Rocky Mountain bighorn.

Snow accumulation in winter limits habitat use by California and especially Rocky Mountain bighorn. Generally, areas with snow deeper than 30 cm are avoided because deep snow increases the cost of foraging and travel (Stelfox 1975). These activities also can be hampered by snow crusts that develop during freeze–thaw cycles (Sugden 1961; Petocz 1973). Consequently, most Rocky Mountain and California bighorn winter ranges are located in areas with low snow accumulation. Low snow depths can occur as a result of low precipitation, heat gains on south-facing aspects, high winds blowing snow away, or a combination of these factors.

Precipitation in desert ranges is low and unpredictable, ranging from <2.5 cm in the Mojave Desert to >251 cm in the White and San Gabriel Mountains, California (Hansen 1980a). Erratic rainfall patterns alter the significance of any precipitation measurements taken at a single locality. However, rainfall can determine the distribution and production of forage and is an important physical requisite for desert sheep survival in the Southwest (Russo 1956).

Vegetation Cover. Climate, elevation, and latitude vary widely throughout the geographic distribution of bighorn sheep. Such variation is naturally reflected in the structure and floristic composition of vegetation in their habitat (Demarchi 1965; Todd 1972; Goodson 1978; Dale 1987; Risenhoover and Bailey 1985; Krausman et al. 1989; Bleich et al. 1997). Different habitats can meet specific requirements of bighorn activities such as foraging, resting, mating, lambing, thermal regulation, and predator avoidance, so habitat use can vary daily and seasonally as requirements of sheep change (Hansen 1982; Risenhoover and Bailey 1985; Dale 1987).

Generally, bighorn use open habitats such as grasslands and shrub–steppe communities located at various elevations and on different slope gradients. Such open habitats provide bighorn with good visibility, improving their chances of detecting predators, but the sheep are usually not far from cliffs or other precipitous habitat. Open grasslands are used primarily for foraging. They contain grasses such as fescues (*Festuca* spp.), wheatgrasses (*Agropyron* spp.), and ricegrasses (*Oryzopsis* spp.), along with forbs and often shrubs at lower elevations, and sedges at the higher elevations used in summer (Jaeger 1957; Jorgensen and Turner 1975; Kovack 1979; Shackleton et al. 1999).

Throughout much of the desert bighorn's habitat, the vegetation associations are predominantly adapted to dry, rocky, or sandy soils, and plants characteristically have a thickened epidermis and reduced leaf surface (Jaeger 1957). In general, the vegetation is uniformly sparse. Plants are widely spaced by the demands of their root systems in the shallow soils, whereas a rounded canopy results from equal exposure to solar radiation from all sides (Douglas and White 1979; Kelly 1979; Leslie and Douglas 1979; Watts 1979; Krausman et al. 1989). Such plants must withstand severe drought lasting up to several years.

For most bighorn habitat in the Great Basin Desert, sagebrush (*Artemisia* spp.), shadscale (*Atriplex* spp.), blackbrush (*Coleogyne ramosissima*), and cliffrose (*Cowania* spp.) constitute the major browse species. The major grasses include wild rye (*Lolium* spp.), Indian rice (*Oryzopsis hymenoides*), galleta (*Hilaria rigida*), bluegrass (*Poa* spp.), and fescue (Bradley 1964; Hansen 1980a). In the lower elevations of the White, San Gabriel, San Jacinto, and Santa Rosa Mountains, California, their habitat is characterized by lowland browse types. Bighorn habitat extends through piñon (*Pinus* spp.)–juniper (*Juniperus* spp.) and ponderosa pine (*P. ponderosa*) associations. The summer range includes subalpine and alpine biotic communities (McQuiver 1978; DeForge 1980). In the Painted Desert, sagebrush, blackbrush, shadscale, galleta, and piñon–juniper constitute the major vegetation associations used by desert bighorn (Wilson 1968). Characteristic plants of desert bighorn habitat in the Sonoran Desert include paloverde (*Cercidium* spp.), ironwood (*Olynea testota*), saguaro (*Cereus giganteus*), and organpipe (*C. thurberi*) cactus. The major grass species include grama (*Bouteloua* spp.), galleta, and sacaton (*Sporobolus wrightii*) (Mendoza 1976; Seegmiller and Ohmart 1981). Bighorn habitat throughout the Chihuahuan Desert is characterized by few trees, agave (*Agave* spp.), yucca (*Yucca* spp.), small cacti, and numerous spring shrubs (Moore 1958; Sandoval 1979). In general, volcanic soils support relatively homogeneous grasslands, and sedimentary parent material produces creosote (*Larrea tridentata*), mesquite (*Prosopis* spp.), cactus savannas, and agave thickets. Much of the bighorn habitat in Baja California and Sonora in Mexico is characterized by agave, ocotillo (*Fouquieria splendens*), ironwood, cholla (*Opuntia* spp.), acacia, and numerous cacti (Flores et al. 1972; Alvarez 1976).

Bighorn rarely use densely forested areas, probably because forage and visibility are more limited, although trees may be used for shade when bedding or during cold days with high winds (Geist 1971).

Similarly, desert bighorn in the San Gabriel Mountains of California use vegetation for thermal cover (DeForge 1980). In the San Andres Mountains, New Mexico, the piñon-juniper community received little use by desert bighorn, except for a few occasions where they were traveling along established trails close to escape terrain (Sandoval 1979).

Visibility. For bighorn, structure of the vegetation probably is more important than the type of plant species present. Open habitats, with high visibility, were used most by Rocky Mountain bighorn to facilitate detection of predators (Risenhoover and Bailey 1985; Wakelyn 1987). Nonetheless, open habitat may not be used if escape terrain is not readily available (McCann 1956). Visibility is an important habitat feature for bighorn sheep because their predator-evasion strategy involves foraging diurnally in relatively large dispersed groups on open habitat close to escape terrain. Predators are detected visually, and a larger dispersed group of sheep may be more alert to potential predators over a relatively large area. Foraging efficiency was higher when sheep were in large groups and in habitats with greater visibility (Risenhoover and Bailey 1985).

Some areas of the Harquahala Mountains, Arizona, were not used, in part because large boulders obstructed vision (Krausman and Leopold 1986). Desert bighorn in Arizona have abandoned areas because fire suppression allowed vegetation to grow and obstruct visibility (Etchberger et al. 1989, 1990; Krausman et al. 1996). Similarly, DeForge (1980) observed that reduced visibility in maturing chaparral lowered its suitability for bighorn, thus decreasing carrying-capacity potential, and eventually resulting in the total loss of bighorn range.

HABITAT: THINHORN SHEEP

Dall's sheep generally inhabit wind-swept, dry, steep, and rugged mountains characterized by subalpine-grass and low-shrub communities typical of high elevations and high latitudes (Murie 1944; Lord and Luckhurst 1974; Hoefs 1984; Rachlow and Bowyer 1998). Most populations of Dall's sheep are migratory and occupy different ranges in summer and winter, although a few populations are relatively sedentary (Dixon 1938; Geist 1971; Hoefs and Cowan 1979). Typical of other polygynous and sexually dimorphic ruminants, the sexes of adult Dall's sheep spatially segregate around the time of parturition (Bowyer 1984; Bleich et al. 1997; Weckerly 1998; Rachlow and Bowyer 1998). Movements of Dall's sheep between seasonal ranges have been related to plant phenology, temperature, and depth of snow (Hoefs and Cowan 1979). Seasonal movements from 8 to 48 km have been reported. Because summers are short at northern latitudes, Dall's sheep spend most of the year on winter range (males 271–303 days, females 240–263 days; Geist 1971). Wind-swept areas with sufficient forage and suitable escape terrain to elude predators are likely the key elements of winter habitat for Dall's sheep. For instance, Dall's sheep in Kluane National Park, Yukon, spent 70% of their time foraging in areas with <5 cm snow depth and <10% of their time in areas with snow depths >15 cm (Hoefs and Cowan 1979). Primary productivity of plants on winter range (29–120 g/m²) is an important component of overwinter survival and for production of young (Hoefs and Bayer 1983; Hoefs 1984).

Adult males may occupy a variety of ranges throughout the year including areas inhabited during prerut, early to midwinter, late winter, spring, and summer. They also may move to areas with salt licks (Geist 1971). Ranges were smallest in midwinter (about 0.8 km in diameter) and largest in spring and summer (6 km). Adult females inhabited seasonal ranges in spring, for lambing, during summer, and in winter (Geist 1971). Estimates of home-range size from modern, quantitative methods, however, are unavailable (Kie et al. 1996).

Because of the severity of winters in the Arctic and subarctic, growth and development of young Dall's sheep and replenishment of female body reserves must occur during the short summer (Bunnell 1982; Rachlow and Bowyer 1991, 1994). Moreover, maternal females are likely constrained in their selection of habitat because of the vulnerability of young to predators and to exposure and hypothermia from severe climatic conditions (Frid 1977; Rachlow and Bowyer 1998).

Consequently, suitable lambing habitat may be a crucial component affecting the productivity of sheep populations.

Lambing habitat for Dall's sheep in interior Alaska was characterized by steep, rugged terrain intermixed with forage including grasses and dryas (*Dryas* spp.) (Rachlow and Bowyer 1998). Lambing sites typically occurred above 1180 m and were free of snow. A suite of variables is useful in discriminating lambing sites from random sites, including distance to escape terrain, cover of grasses, cover of dryas, slope aspect, slope brokenness, slope steepness, and presence of snow (Fig. 51.6) (Rachlow and Bowyer 1998). Moreover, maternal females altered selection of habitat with the chronology of lambing, with additional variables becoming important at peak lambing that related to climate (windchill and cover from wind provided by browse). Additionally, females selected terrain features more strongly in a year with adequate food, but selected forages in a year with reduced availability of food (Rachlow and Bowyer 1998).

Young Dall's sheep likely acquire home ranges from adults. Females typically have ranges that are similar to those of their mother (or maternal group), whereas males gradually disassociate from their mothers and begin associating with groups of mature males. As with many large mammals, males are the initial dispersers (Geist 1971). Nonetheless, Dall's sheep exhibit a high degree of fidelity (males, 88%; females, 90%) to seasonal ranges (Geist 1971).

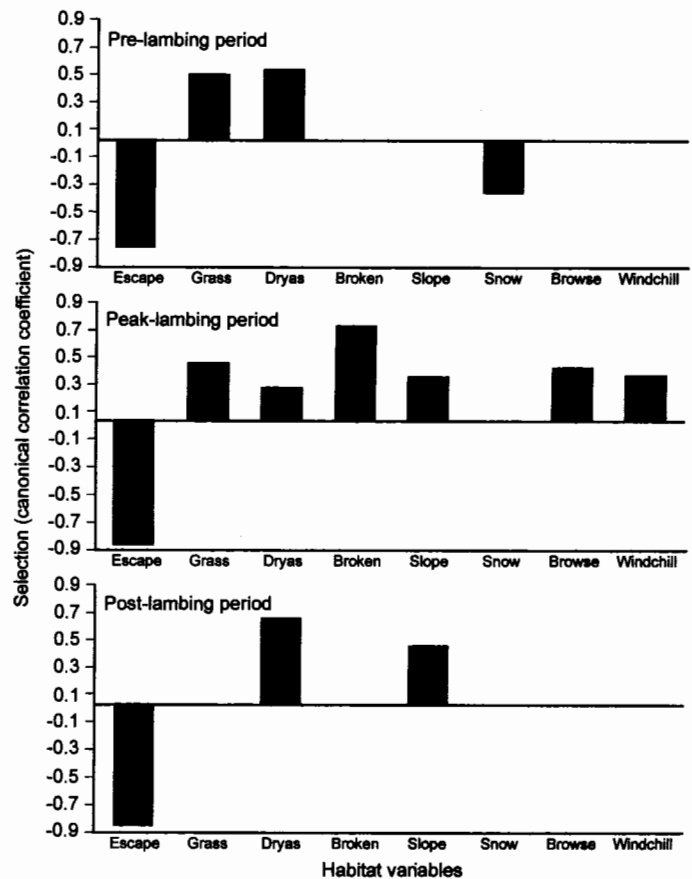


FIGURE 51.6. Selection of habitat by female Dall's sheep during pre-, peak, and postlambing periods in interior Alaska, 1988–1989. Escape, Distance to escape terrain; grass, percentage cover of grasses; dryas, percentage cover of dryas; broken, brokenness of terrain; slope, percentage slope; snow, presence or absence of snow; browse, percentage cover of browse; and windchill, temperature \times wind. Canonical correlations indicate the strength and direction of selection. For instance, the negative correlation for distance to escape terrain indicates females used sites closer to such terrain than randomly located sites. The positive correlation for grass indicates there was more of this forage at sites used by females than at random sites. SOURCE: Rachlow and Bowyer (1998).

Activity. The activities of mountain sheep are determined to a large extent by day length, energy demands (Nichols and Bunnell 1999), and availability of forage and water (Krausman et al. 1999; Shackleton et al. 1999). It is difficult to generalize about daily activities for all mountain sheep, but they are basically diurnal. The general pattern of activity involves alternating peaks of foraging and resting or loafing; other activities contribute little to the daily activity budgets (Blood 1963; Augsburg 1970; Geist 1971; Olech 1979; Chillemi and Krausman 1981; Eccles 1983; Seip and Bunnell 1985). Foraging is most frequent around dawn and dusk. In winter, however, the proportion of daylight hours spent feeding increases while resting decreases (Van Dyke 1978) to maintain foraging activity during shorter winter days (Shackleton et al. 1999). This relative increase in foraging activity may be a response to the shorter day length reducing foraging time, winter plants being in poorer nutritional condition and less available, especially for northern populations, or thermal stress in winter, which requires more energy consumption (Van Dyke 1978; Shackleton et al. 1999).

In the Arctic Brooks Range, Dall's sheep were active during all 24 hr of summer daylight, but after darkness began in late summer, activity was confined to the limited daylight hours. Nocturnal activity was reported for desert bighorn as a mechanism for avoiding solar radiation, minimizing water needs, and still obtaining sufficient forage (Simmons 1969). During the hottest and driest part of the year in western Arizona, desert bighorn were active 34% of any hour (Krausman et al. 1985). Diel activity of females relative to the moisture content of forage was not correlated; moisture content of forage was high during each hour of the day for all seasons (Alderman et al. 1989). Others have also documented nocturnal activity of desert bighorns (Monson 1964; Sandoval 1979; Elenowitz 1983), and in the Arctic, where the sun does not rise in midwinter, Dall's sheep have to feed in the dark or very dim twilight (Nichols and Bunnell 1999).

Desert bighorn and northern sheep exhibit similar behavior patterns (Augsburger 1970; Geist 1971). Desert bighorn exhibit similar activity patterns across their range (Wilson 1968; Lopez and Orihuela 1976; Olech 1979; Sandoval 1979; Chillemi and Krausman 1981). Daily activity patterns change seasonally, especially those related to foraging and bedding. In winter, foraging is the primary activity in crepuscular hours, but from 0900 to 1055 hr and from 1200 to 1355 hr, bedding made up more than 50% of winter activity. During summer, more feeding occurred before 0800 hr and after 1600 hr.

Social interactions between desert bighorn sheep were less intense than interactions described by Geist (1971), Olech (1979), and Chillemi and Krausman (1981) for northern sheep. Sexual aggression, contact greeting, dominance display, and resource competition were <1% of the activity of any hour (Chillemi and Krausman 1981). This lower behavioral activity level was likely caused by smaller group sizes, less social facilitation, and reduced play among lambs (Berger 1978).

Beds. Sheep bed in areas with loose surface material, which is cleared away by several swipes of the forefeet (Lawson and Johnson 1982). An oval depression is formed (0.6 × 0.4 m) from a few centimeters to >0.3 m deep (Jones 1959; Clark 1970), and a new bed is made each time a sheep lies down. The "new" bed may simply be a pawed-out "old" bed (Jones 1959; Welles and Welles 1961). Likely bed sites during the day are along ridges, out in the open, or in caves where visibility is maximized. Toward evening, bed sites are near rugged terrain with protection from cliffs and large rocks (Smith 1954; Jones 1959; Geist 1968; Nichols and Erickson 1969).

Movements. With few exceptions, males and females in most populations migrate between different areas at different seasons of the year, and there are usually at least two seasonal ranges for Rocky Mountain and California bighorn (i.e., winter and summer) and three for desert bighorn (summer, fall-winter, and spring) (Eustis 1962; Geist 1971; Bates et al. 1976; King and Workman 1982; Elenowitz 1983; Krausman et al. 1989). Seasonal movements of bighorn are not attributable to any one specific factor, probably because animal movements are dictated by an individual's response to a variety of stimuli (Leslie 1977).

Behavioral, physiological, and environmental factors seem to influence these migrations, including home range knowledge, water and forage availability, lambing and mating activities, season, topography, and age and sex class.

Female desert bighorn have a relatively small home range, especially compared to those occupied by adult male groups (Krausman et al. 1989; Scott et al. 1990). Most desert bighorn populations are restricted to small areas during hot summer months due to suboptimal distribution of resources. As a result, local rainfall patterns significantly affect seasonal range size and movement patterns of desert bighorn. Summer showers that fill natural water catchments allow sheep to use areas not normally available during dry periods.

For most Rocky Mountain and some California bighorn populations, seasonal movements are not just changes in location, but also involve vertical (elevation) migrations. Annual elevational movements between ranges have been examined from a functional and adaptive viewpoint. Hebert (1973) concluded that upward movements in spring and summer allowed bighorn to maintain or prolong a diet composed mainly of new, growing vegetation because the onset of plant phenology is retarded by increased elevations. New-growing vegetation provides high-quality, readily digestible forage; thus, sheep prolong the period of high forage quality by making vertical migrations from low to high elevations in spring and summer. Differences between bighorn populations in the elevation ranges used may affect development of individuals and populations (Klein 1965; Shackleton 1973, 1976).

Factors other than vegetation are also involved in migrations. If suitable lambing grounds are separate from the winter range, the primary stimulus for pregnant females is to move to more secure habitat just before birth to avoid predators. This drive for security from predators can even override selection of forage conditions. Females left areas with good forage and gave birth in areas of lower forage quality but with greater security cover (Festa-Bianchet 1988c). Similar trade-offs have been documented for desert bighorn sheep (Berger 1991; Bleich et al. 1997; Etchberger and Krausman 1999). Traditional use of parturition sites in rugged terrain outweighed the increased need for water by lactating females (Etchberger and Krausman 1999). Climatic factors such as snow accumulation are also believed to stimulate Rocky Mountain and California bighorns to return to lower elevations in late summer and early fall (Sugden 1961; Blood 1963). Avoidance of biting insects may cause movements to more exposed areas (Blood 1963). Availability and distribution of mineral licks may also affect space use by bighorns (Smith 1954).

In general, most Rocky Mountain and many California bighorn populations return to winter ranges in October and November (Woolf et al. 1970; Geist 1971; Becker et al. 1978). Similarly, most sheep leave their winter range in May and June, which for females is most likely a response to lambing and foraging requirements. Perhaps not surprisingly, distances sheep move between seasonal ranges vary (some move up to 70 km), most probably in relation to the availability and distribution of suitable ranges (Blood 1963; McCullough and Schneegas 1966; Berwick 1968; Festa-Bianchet 1986; Hengel et al. 1992). Migratory patterns of desert bighorn also vary considerably, with most populations remaining in isolated areas, whereas others move between mountain ranges, including elevational movements and dispersal from water sources, and movement to seasonally available water sources (McQuivey 1978).

Competition. Exploitation competition arises when two species use common resources that are in short supply or, if the resources are not in short supply, competition arises when the animals seeking those resources nevertheless harm each other in the process (Pianka 1978). Exploitation competition may result in reduced population quality of one or both species through increased mortality, increased dispersal, or decreased reproduction.

Overgrazing by domestic livestock may result in competition for forage, water, and space. Competition is an important factor in the historical decline of populations of desert bighorn in western North America. The effects of diseases, human encroachment, and poaching

can be documented more convincingly than the detrimental effects of overgrazing by livestock (Gallizioli 1977).

Overgrazing by livestock results in large-scale changes in plant composition and density, reduction of important plant species used by bighorn, and permanent reduction in the overall carrying capacity for bighorn sheep populations. In addition to reducing bighorn numbers, conversion of primarily grassland communities into predominantly homogeneous shrub communities provides better habitat for increasing deer populations.

Spatial and forage competition between cattle and desert bighorn continues to be a major problem that limits increased sheep population density. Overgrazed ranges also may be the major obstacle to the reintroduction of desert bighorn to historical habitats (Gallizioli 1977; Sandoval 1979). In Nevada, grazed areas supported significantly lower bighorn sheep densities than ungrazed areas. Grazed areas supported an average of 2.3 bighorn/km², whereas densities in ungrazed areas averaged 6.6 bighorn/km² (McQuivey 1978).

Microscopic analysis of fecal samples from desert bighorn and cattle in the Big Hatchet Mountains, New Mexico, revealed 12 of 18 major forage species were common to both bighorn and cattle. Winter fat (*Ceratoides lanata*) constituted an average of 17.9% and 15.4% of the annual diet of bighorn and cattle, respectively (Bavin 1975). Bavin (1975) concluded that cattle could be serious competitors with bighorn sheep for available forage, especially during years of limited forage production. A 32% dietary overlap (the percentage use in common of shared forage plants) between desert bighorn and cattle in the Peloncillo Mountains, New Mexico, was documented by Elenowitz (1983).

Wilson (1968) reasoned that spatial competition resulted in the displacement of a herd of desert bighorn in Utah. A recognizable group of bighorn occupying an ungrazed study area had been under observation for 5 years. A herd of 30 cattle was introduced into the area for 2 weeks. The bighorn sheep left the area and did not return for 8 months. Similar patterns of livestock and bighorn interactions have been reported by Jones (1980) and Steinkamp (1990). Steinkamp (1990) experimentally introduced cattle into bighorn core areas; the sheep responded by relocating.

In Aravaipa Canyon, Arizona, diet and spatial overlap were low between cattle and desert bighorn, primarily due to cattle preference for level slopes and bighorn use of steep slopes (Dodd and Brady 1986). However, plans were under consideration to redistribute cattle grazing to include areas with moderate slopes, which might have increased overlap and competition (Dodd and Brady 1986). Diets of desert bighorn and cattle in Carrizo Canyon, California, did not overlap because the populations were not sympatric; however, competition could arise if cattle were introduced to bighorn range (Cunningham and Ohmart 1986).

Historically, the most serious ecological competitors with desert bighorn have been domestic sheep and goats. These species have similar feeding habits, forage preferences, and affinities for rough topography, and they harbor parasites and other disease agents detrimental to bighorn. Extirpation of desert bighorn from numerous ranges in California (Weaver 1972), Arizona (Russo 1956; Gallizioli 1977), Nevada (McQuivey 1978; Kelly 1979), New Mexico (Gross 1960; Sandoval 1979), Utah (Wilson 1968; Dean and Spillet 1976), western Texas (Davis and Taylor 1939; Kilpatrick 1982), and northwestern Mexico (Mendoza 1976) has been attributed to competition for forage and space and to the transmission of diseases from domestic sheep and goats (Bunch et al. 1999).

Concurrent with introduction of the first domestic sheep in western North America, bighorn sheep died off on a large scale, ostensibly from psoroptic scabies (*Psoroptes ovis*) (Buechner 1960). Mortalities caused by scabies reduced populations of bighorn sheep at the time domestic sheep were introduced at Greybull River, Wyoming (Honest and Frost 1942; Honess and Winter 1956); Rocky Mountain National Park, Colorado (Wright et al. 1933; Packard 1946); Sierra Nevada, California (Jones 1959); and the Owyhee River, Oregon (Bailey 1936). Psoroptic mites on desert bighorn sheep have been reported from the Desert National Wildlife Range, Nevada (Carter 1968; Decker 1970);

the San Andres Mountains, New Mexico (Lange et al. 1980; Sandoval 1980); southeastern Utah (Irvine 1969); and western Arizona (deVos et al. 1980; Remington 1981).

Existence of free-ranging, exotic ungulates on occupied or potential bighorn habitat poses a serious threat to desert bighorn sheep survival. The feral burro (*Equus asinus*), aoudad (*Ammotragus lervia*), and Persian wild goat (*Capra aegagrus*) currently occupy historical bighorn habitat or are rapidly radiating into habitat vital to desert bighorn (Sandoval 1979).

The habitat requirements of aoudad (Simpson and Krysl 1981) and Persian wild goats (Bavin 1975) are similar to those of desert bighorn. Seegmiller and Simpson (1979) reported that the initial competition between two ecologically similar species consists of niche overlap and/or behavioral intolerance, shortage of limited resource, and reduced population fitness.

Hardin (1960) proposed the competitive exclusion principle, which states that two species cannot coexist on the same limited resources. Therefore, competition results in reduced population fitness for one or both species through decreased natality, decreased recruitment, increased mortality, or increased dispersal. The survivor is the species able to perpetuate itself under competitive interactions, whereas the other is excluded from the area of sympatry (Seegmiller and Simpson 1979).

Competition between feral burros and desert bighorn has attracted much attention and has been a source of controversy. Many argue that feral burros are disrupting the desert ecosystem and propose strong control and elimination measures. Others consider feral burros to have significant aesthetic value and support their preservation.

Feral burros efficiently use coarse, low-quality forage, but are not primarily browsers by preference. They are opportunistic and prefer grasses when available (Douglas and Norment 1977). McMichael (1964), Walters and Hansen (1978), and Seegmiller and Ohmart (1981) substantiated an overlap of burro and bighorn sheep range and competition for available forage in the Black Mountains, Grand Canyon, and Bill Williams Mountains, Arizona, respectively. McMichael (1964) showed a 50–58% similarity index in burro and desert bighorn diets, Walters and Hansen (1978) indicated a 52% overlap, and Seegmiller and Ohmart (1981) reported a 64% overlap. Based on fecal analysis, Hansen and Martin (1973) found that grasses dominated the diet of feral burros in Grand Canyon, Arizona. Browse species dominated feral burro diets in Death Valley, California (Browning 1960; Moehlman 1974), and the Chemehuevi Mountains, California (Woodward and Ohmart 1976). Douglas and Norment (1977) demonstrated the impact of burros on shrubby species in the Panamint Mountains, Death Valley, California. Of all shrubs, 46% exhibited some evidence of use and the survival of 12% was threatened by severe browsing.

Geist (1985) presented evidence that suggests current species in lower North America survive because of the absence of more capable competitors, and that most Siberian forms have been excluded for thousands of years. Bailey (1980) argued that large mammals in North America may not be robust competitors. As competitors (i.e., burros) return, they can be expected to outcompete bighorn sheep for resources.

Competition between Dall's sheep and other large herbivores with sympatric distributions has not been documented (Bowyer and Leslie 1992). Caribou (*Rangifer tarandus*), moose (*Alces alces*), and mountain goats (*Oreamnos americanus*) use different habitats or select diets different than those of Dall's sheep (Klein 1953; Henshaw 1970; Miquelle et al. 1992).

DIETS

Bighorn sheep diets have been well studied, and research has focused on their nutritional requirements, foraging impacts on vegetation, and competition and dietary overlap with native and exotic herbivores. Various methods were used to study bighorn diets including analysis of rumen contents of collected animals, direct observations of feeding, laboratory studies of captive animals, and detailed analyses of monthly and seasonal diets. Despite all this work, it is difficult to make more

than the broadest generalizations about bighorn diets because of the differing methodologies employed (Shackleton et al. 1999).

The general consensus is that bighorn are relatively opportunistic in their diet selection, using whatever palatable species are available to them (Sugden 1961; Todd 1972; Browning and Monson 1980; Shackleton et al. 1999). For example, more than 267 plant species were eaten by California bighorn (Wikeem 1984). Browning and Monson's (1980) review of desert bighorn diets showed they used more than 470 species throughout their distribution. Forbs are most frequently eaten by Rocky Mountain and California bighorn, followed by grasses and lastly browse, whereas browse dominates desert bighorn diets, followed by grasses or forbs, depending on precipitation patterns (Shackleton et al. 1999). Perhaps not surprisingly, the relative amounts of these three forage classes vary significantly in bighorn diets, among populations, within subspecies, and among age-sex classes and individuals (Blood 1967; Sanchez 1976; Brown et al. 1977; Shank 1982).

Besides geographic, taxonomic, and individual variation, diets of bighorn exhibit strong seasonal variation. Most probably this reflects changes in the availability and palatability of forage species and in the nutritional requirements of the animals, although forage nutrient quality does not correlate well with what bighorn eat (Shackleton et al. 1999). In desert regions, seasonal use of different forages has been attributed to precipitation patterns and the effects of soil moisture on vegetation classes (Brown et al. 1977; Krausman et al. 1989). Nonetheless, observed declines in their use of browse could be due to declines in palatability when twigs become coarse and woody, and possibly when they exceed an acceptable diameter (Sandoval 1979).

Studies on the diet of Dall's sheep are not numerous, but there is general agreement that these ungulates feed mostly on graminoids (Luckhurst 1973; Hoefs and Cowan 1979; Seip and Bunnell 1985; Hansen 1996; Bowyer et al. 2000). Nonetheless, Hoefs and Cowan (1979) recorded 110 different plant species in the diet of these herbivores. In the southwest Yukon, Canada, Hoefs and Cowan (1979) noted that reedgrass (*Calamagrostis* spp.) was the most common grass in the diet of sheep, whereas fescue was eaten most often in Alaska (Nichols 1978b, Hansen 1996). Other important grasses eaten by Dall's sheep include brome grass, bluegrass, and wheatgrass.

Dall's sheep also eat a variety of forbs, especially during late spring and summer (Hoefs and Cowan 1979; Hansen 1996). Browse consumed by Dall's sheep was principally sagebrush in the southern part of their range and willow (*Salix* spp.), dryas, and blueberry (*Vaccinium* spp.) in the north (Hoefs and Cowan 1979; Hansen 1996). Sheep sometimes move to lower elevations in early spring to obtain browse and do so again in early autumn when frost curtails growth of forbs and graminoids at higher elevations.

Hansen (1996) reported strong selection (use greater than availability) for grasses during all seasons, and selection for forbs in spring and summer and for sedges in winter; browse was avoided (use less than availability) throughout the year in the Brooks Range, Alaska. Hansen (1996) cautioned, however, that interannual patterns of diet selection could be affected by 10–15 cm of snow cover. Similarly, Rachlow and Bowyer (1998) noted that a cool summer that limited growth of forage resulted in differences in selection of habitat by Dall's sheep in interior Alaska. Mineral licks also can be important seasonally to Dall's sheep (Geist 1971; Jones and Hansen 1985).

Diet quality, as indexed by fecal crude protein, increased rapidly during early spring, peaked in June, and then began declining by July. Hansen (1996) reported a continued decline in fecal crude protein to prespring levels by October and levels remained low throughout the winter. This same general pattern was evident for digestible nitrogen, digestible energy, and *in vitro* dry matter digestibility of sheep forages. The growing season in arctic and subarctic environments is very short. The number of days between the last freeze in spring and the first freeze in autumn was 79 days in 1988, but only 33 days in 1989 for Dall's sheep in interior Alaska (Rachlow and Bowyer 1994). The cool, short growing season in 1989 resulted in a marked decrease in grasses and dryas available to Dall's sheep (Rachlow and Bowyer 1998). Thus, Dall's sheep must acquire the resources necessary to meet their need for reproduction

and to cope with harsh winter conditions in a narrow window that varies markedly among years (Rachlow and Bowyer 1994). In addition, forage generally was more plentiful as distance from steep, precipitous terrain preferred by Dall's sheep increased (Frid 1997; Rachlow and Bowyer 1994). Hence, diet selection was affected by risk of predation in these mountain ungulates (Rachlow and Bowyer 1998).

BEHAVIOR

Social Organization. Bighorn are highly social animals that spend their life in groups with other sheep, although group integrity remains flexible to some degree throughout the year (Geist 1971; Leslie and Douglas 1979). In general, group composition consists of spatially and sexually segregated units of all-male groups and female-juvenile groups made up of adult females, lambs, and offspring from the previous 1–2 years (Geist 1971). Sandoval (1979) described another group type in desert bighorn: groups of barren adult females, yearlings, and socially mature males.

Group sizes vary by group type, seasonally, and geographically, and range from 2 to >100 individuals (Geist 1971; Ashcroft 1986; Shackleton et al. 1999). Lone bighorns, most often males, are uncommon and probably only transitory (Shackleton 1973; Ashcroft 1986). Groups appear to provide two main advantages over individuals in many species: improved foraging efficiency and predator avoidance (Pulliam and Caraco 1984). In bighorns, predation is probably a major selective force in the formation and maintenance of groups (Jarman 1974; Jarman and Jarman 1979; Berger 1991).

Males and females in most bighorn populations occupy separate, seasonal ranges, although spatial and temporal overlap does occur (Geist and Petocz 1977; Morgantini and Hudson 1981; Krausman et al. 1989; Bleich et al. 1997). Several explanations have been offered for sexual segregation in bighorn (Geist and Petocz 1977; Bleich et al. 1997). The most probable, which also applies to other ungulates, is that these differences in habitat use are most likely due to females selecting secure areas for raising their young and males choosing areas for maximizing body condition (Main and Coblenz 1990; Main et al. 1996). Bleich et al. (1997) supported this and concluded that sexual segregation in mountain sheep most probably results from different reproductive strategies of the sexes. To optimize their fitness, male bighorn grow large bodies and horns to improve their chances in intrasexual competition and hence mating success. As a result, they need high-quality food resources, and because of their larger size can use areas with a higher predation risk. Females are smaller than males and are accompanied by highly vulnerable young, so they cannot afford to use areas with high predation risks. Thus, females may forgo foraging quality for higher security.

All but young males are socially dominant over adult females. Among males, it seems that age, horn size, and probably body size and fighting behavior are positively correlated with dominance status (Geist 1971; Hass and Jenni 1991).

Social Behavior. Social relations begin at birth when a female bighorn and her young must learn to recognize each other. Lactation is costly and females cannot afford to squander scarce resources on strange offspring, whereas the young need to be able to find their mother for food and protection. This mutual recognition, or mother-young bond, seems to develop during the first 1–2 days following birth when the female is mostly isolated from other group members (Shackleton and Haywood 1985; Etchberger and Krausman 1999). Females rely more on their neonate's smell for recognition, invariably sniffing its rear when it begins to suckle. Lambs, by contrast, quickly learn the sound of their mother's voice, and it is interesting to watch when a female gives an alarm bleat. Her young invariably runs straight to her, often briefly suckling, and the female sniffs its rear. The suckle probably reinforces the young's response to the alarm call (Shackleton and Haywood 1985).

Researchers have measured several variables related to nursing in bighorn and reported changes with the lamb's age. General trends are similar, but significant differences occur within and among populations

(Horejsi 1976; Berger 1979a, 1979b; Festa-Bianchet 1988a; Hass 1990). Length of suckling bouts, suckling rates, and total time spent suckling decrease with age as the lamb spends time grazing (Berger 1979a; Festa-Bianchet 1988b). Times spent nursing are also affected by whether they follow bedding periods, and by maternal age, condition, and lungworm loads, but not by sex of offspring.

Adult male bighorn have a diverse repertoire of social behaviors they perform toward females and other males (Geist 1971). Fighting is their most spectacular and well-known behavior. Just before rut, and sometimes in spring, males gather to interact and fight with each other, presumably to determine relative dominance. Fights are usually between pairs of males, but sometimes small groups or "huddles" of three or more males will interact (Geist 1971). When fighting, males rear up on their hind legs and run bipedally toward each other, lunging headfirst at the last moment to clash horns. These echoing clashes can be repeated many times before one of the males is defeated.

The social behavior pattern most often used by bighorns is the "low stretch." An animal, usually a male, approaches or passes another with head low, neck extended, and nose pointed upward. This pattern is used in many social situations, and especially in the rut, when males use it to approach and test females. Females usually respond by squatting and urinating, then the male sniffs the urine and lip curls (flehmen) to test whether the female is coming into estrus. Once a female comes into heat, she is guarded and courted by a dominant male, though the pair is often surrounded by eager, but subordinate, males of various ages (Geist 1971).

Rocky Mountain bighorn use as many as three mating tactics. The most typical is the tending pair (i.e., male defending and copulating with a single female), less frequent is "coursing" (i.e., fighting tending males for temporary access to defended females), and an even rarer tactic is "blocking" (i.e., moving and holding females away from other males beyond the periphery of a traditional tending area) (Geist 1971; Hogg 1987; Shackleton 1991). During actual courtship of an estrous female, the tending male uses a variety of behavior patterns including nosing the female's flank and rear, usually while twisting the top of the head to one side and accompanied by flicking the tongue and vocalizing, gently kicking her with his foreleg, pushing his chest against her rump; and finally attempting to copulate (Geist 1971; Shackleton 1991).

Dall's sheep are an extremely gregarious species and exhibit a high degree of polygamy, with large, dominant males mating most often (Geist 1971). Competition among males for mates has led to the evolution of marked dimorphism in body mass and size of horns between the sexes (Bowyer and Leslie 1992).

Rutting groups of Dall's sheep were composed of as many as 21 individuals, with an overall mean of 3.7 for 166 groups; however, group size declined for males and females by midwinter (Geist 1971). The mean size of 139 maternal bands ranged from about 4 to 10 individuals from prelambling through postlambling in spring and early summer. Group size is related to foraging efficiency. Larger groups spend more of their active time feeding than smaller ones, and spend less time in vigilance or alarm behaviors than smaller groups (Rachlow and Bowyer 1998). Similarly, group size increases with increasing distance to escape terrain, ostensibly an adaptation to lower the risk of predation (Hamilton 1971; Rachlow and Bowyer 1998).

The sexes of Dall's sheep spatially segregate from each other during spring and summer (Rachlow and Bowyer 1998). Causes of sexual segregation in bighorn sheep have been more thoroughly studied than in Dall's sheep, but the explanation is likely similar (Bleich et al. 1997). Females are confined to steep, rugged terrain where they and their neonates can reduce the risk of predation, but where forage is less abundant and of lower quality than on areas inhabited by males. Larger males are less susceptible to predation than females with young, forage in areas with more predators, and obtain the forage required to attain large body size necessary to be effective in combat for mates.

The sexes begin to associate as rut approaches. By that time, males already have formed groups and begun to sort out dominance interactions with relatively low intensity behaviors, which include foreleg kicks, horn displays, and, more rarely, jump-threats and clashes. Males

also mount other males in dominance interactions, but the notion that dominant males treat all subordinates as if they were females may not be correct. For instance, dominant males seldom direct courtship behaviors such as tongue flicks toward subordinate males or lick their perianal region, and do not flehmen in response to smaller males or their urine. Dominance mounting is simply a common form of aggression among ungulates (Geist 1971).

Aggressive interactions during rut are vigorous and tend to lack ritualization. Such behaviors include low-stretch postures, vigorous kicking, jump-threats, and forceful clashing of horns. The skulls of males have undergone pneumatization to help absorb such forceful horn clashes. Males often display their horns, which serve as indicators of social rank. Aggressive interactions determine which males mate, and such behavior between males over estrous females can be fierce; large males may strike opponents in the side of the body with their horns and even push rivals off cliffs. Vigorous rutting activities by these large males exhaust their energy reserves, and survivorship drops markedly in older age classes of males (Geist 1971).

Geist (1971) provided excellent descriptions of courtship behaviors in mountain sheep. Dominant males approach females in a low-stretch posture while flicking their tongues. Males ascertain the reproductive status of females by licking the perianal region of the female or lapping urine from the ground where a female has urinated. Males then flehmen to determine whether the female is in estrus and receptive (Estes 1973). Courting males may be distracted by females inducing them to investigate an area where a female has urinated, and then moving away while the male flehmens (Geist 1971). Estrous females sometimes elicit courtship from a male by butting and rubbing against him. Males may kick a female with a stiff foreleg during courtship, ostensibly to determine if she is willing to stand for mounting. Copulation cannot occur if a female moves forward, which prevents the male from mating successfully. Males may tend females for 2–3 days before copulation. Some smaller males may continue to direct courtship behaviors toward females, but females typically are not receptive to such advances (Geist 1971). No evidence exists of territoriality in Dall's sheep or bighorn sheep.

Communication. Wild sheep vocalize with more vibrato and in a deeper tone than domestic sheep (Lawson and Johnson 1982). Bleating is a mechanism to maintain contact between sheep, especially females and lambs (Welles and Welles 1961).

Play. Lambs play more with each other or their mothers than adults play (Murie 1944; Jones 1959). Contact play involves similar-aged lambs butting each other, and in locomotor play, all age classes chase each other (Berger 1978). Most play occurs during crepuscular hours (Welles and Welles 1961).

Wariness. Sheep respond to disturbances by assuming an attention posture or an alarm posture, or, if startled at close range, they run. In the attention posture, they stare in the direction of the disturbance (Lawson and Johnson 1982). When alarmed, they may snort, paw the ground, bow their head, or, in the presence of wolves (*Canis lupus*), huddle in a tight circle facing out (Murie 1944; Geist 1971). Females with young lambs are the most wary (Murie 1944). If not hunted, some populations are tolerant of humans and easily become habituated to their presence (Geist 1971).

MORTALITY

Reported mortality for bighorn sheep during their first year of life is as high as 90% (Blood 1961; Morgan 1970; Akeson and Akeson 1992). Most lambs are lost during their first few weeks, often due to predation (Spraker 1974; Stewart 1980; Hoefs et al. 1986; Festa-Bianchet 1988c; Hass 1989). Coyotes (*Canis latrans*) are usually cited as the main predator, but other causes of lamb mortality also occur and seem to be interrelated (Hebert and Harrison 1988). Besides predation, these causes may include pneumonia, weather, inbreeding depression, poor maternal nutrition, poor mothering, and human disturbance (Hass 1989;

Akeson and Akeson 1992). The effect of these mortality agents also may be influenced by underlying factors including birth date, range condition, population density, and quality of security cover (Shackleton et al. 1999).

Predation also may affect the population dynamics of Dall's sheep. These mountain ungulates inhabit steep, rugged terrain, which they readily negotiate to elude, avoid, and outdistance predators. Nonetheless, wolves prey on Dall's sheep, and diets of this canid contained 2–25% of Dall's sheep. Predation by wolves and coyotes may increase during periods of deep snow. Other predators of Dall's sheep include grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), wolverines (*Gulo gulo*), lynx (*Lynx canadensis*), and golden eagles (*Aquila chrysaetos*). Dall's sheep also may perish from accidental falls and be killed by avalanches (Burler and Hoefs 1984). We concur with Nichols (1978b) that predation does not exert an important influence on populations of Dall's sheep under most circumstances.

Published mortality data are limited for subadult bighorn. For males, Geist (1971) reported no mortality among yearlings and only 3% among 2-year-olds. However, others have found yearling mortality rates of 33% in males and 41% in females, and 16–18% and 41% for 2-year-old males and females, respectively (Stewart 1980; Festa-Bianchet 1989).

With males in most populations, death rates between 3 and 5 years old were similar, ranging from 3% to 14% (Shackleton et al. 1999). For older males, age-specific death rates were higher, but the slope of the increase depended on whether or not the population was hunted. Without hunting, age-specific mortality rates in stable populations increased slowest, reaching more than 60% by age 15 years, and life expectancy was high. In hunted populations living on high-quality ranges and increasing in numbers, male mortality rates increased more rapidly with increasing age, and life expectancy was shorter.

Only limited mortality data are available for females, partly because it is difficult to determine age of females older than 5 years by horn annuli counts. Adult female mortality rates seem to be higher than those of males, and have been estimated to be around 11% (Hansen 1980b; Hengel et al. 1992).

In desert bighorn sheep, Hansen (1980a) reported that the highest adult mortality of 47% occurred in age classes 10–12 years. By contrast, McQuivey (1978) reported that the average age structure of males in Nevada declined gradually through successive years of life, indicating relatively constant mortality rates. Also, he found no single mortality factor affected any age group for males >1 year old. These results closely agree with those of Leslie and Douglas (1979), who noted relatively constant mortality rates for males from the River Mountains, Nevada. Those authors hypothesized that increased mortality of young males could be due to involvement in rutting activities, especially during the prerut period. High levels of prerut activity of socially immature males also were observed by Sandoval (1979).

Survivorship of desert bighorn females did not differ between the Little Harquahala and Harquahala Mountains, Arizona (Krausman et al. 1989). The probability of survival for males, however, was consistently higher in the Harquahala Mountains. Mortality factors were similar between the study areas, except that predation by mountain lion (*Puma concolor*) was higher for female sheep in the Harquahala Mountains.

Disease can be a major mortality factor for bighorn sheep, and large (>50%), sudden population die-offs are common (Buechner 1960; Stelfox 1971; Ryder et al. 1992). Mortality from disease is likely related to stress that interacts with lungworm (*Protostrongylus* spp.) infestation (Ryder et al. 1992). It is unclear to what extent die-offs can be attributed to range conditions or domestic stock (Coggins and Matthews 1992; Dunbar 1992). Festa-Bianchet (1991) claimed lungworm infection is normal for bighorn and higher levels of infection do not predict epizootics or indicate poor population health.

Dall's sheep also are infected or infested with numerous disease organisms and parasites. Lungworm has been reported from Dall's sheep, but there have not been massive die-offs from this parasite and its associated pneumonias or hemorrhagic septicemia, as in bighorn sheep (Gable and Murie 1942; Stelfox 1971; Shackleton 1985). As with other

sources of mortality, this disease complex may be more prevalent in populations on a low nutritional plane (Seip and Bunnell 1985). Other nematodes have been reported in Dall's sheep, but caused no obvious pathology (Gibbs and Fuller 1959; Seip and Bunnell 1985). Perhaps low temperatures in winter or a short summer growing season at high latitudes helps limit direct transmission of parasite larvae or does not provide suitable conditions for intermediate hosts of pathogenic parasites that debilitate populations of bighorn sheep. Additionally, domestic sheep and cattle are uncommon throughout the range of Dall's sheep. Parasitic coccidia, however, have been isolated from feces of Dall's sheep (Clark and Colwell 1974). Furthermore, positive titers in blood sera have been reported for several arboviruses, contagious ecthyma, parainfluenza III, epizootic hemorrhagic disease, and Q fever (Zarnke et al. 1983). Serology also indicated that Dall's sheep were exposed to the bacteria *Brucella* spp. and *Campylobacter feti* (Heimer et al. 1982; Foreyt et al. 1983). *Mycoplasma ovipneumoniae* has killed captive Dall's sheep, but was not reported for free-ranging sheep (Zarnke and Rosedal 1989).

Necrosis of horn cores and the mandible are prevalent in Dall's sheep; *Corynebacterium pyogenes*, *Fusobacterium necroporum*, *Proteus* spp., *Micrococci* spp., and *Escherichia* spp. have been associated with infections of lumpy jaw (Glaze et al. 1982; Hoefs et al. 1982; Bunch et al. 1984; Hoefs and Bunch 1992). Causes of horn aberrations in Dall's sheep are uncertain, but may involve *Actinomyces* spp. (Hoefs and Bunch 1992). Skull asymmetry was caused by osteoporosis in bighorn sheep (Bunch et al. 1990). Dall's sheep may be predisposed to mandibular infections from excessive tooth wear because of wind-blown silt deposited on forage (Hoefs and Bayer 1983). There is no evidence that diseases play a major role in regulating or limiting populations of Dall's sheep.

AGE ESTIMATION

Age of mountain sheep up to 1 year old can be determined based on tooth eruption (Fig. 51.7), size, and external criteria (Hansen 1965). After 1 year, age of wild sheep is determined by horn annuli (Fig. 51.4) up to 7 years. Horn annuli on older males and females are not distinct and often are covered with hair (Geist 1966a; Hemming 1969). Tooth replacement patterns are useful up to 4 years (Table 51.2), but this method is not commonly used (Murie 1944; Hemming 1969).

The sex and age of sheep older than lambs are generally classified by body size and horn length (Fig. 51.7) (Geist 1966a). The horns of males become longer at the base than those of females and develop a curl with increased age. Horns on females retain the shape of lamb horns (Fig. 51.7) and grow a little each year (Lawson and Johnson 1982).

STATUS AND MANAGEMENT

Seton (1929) estimated that in pristine times there were about 2 million mountain sheep in the contiguous United States and another 2 million in Canada and Alaska combined. Seton's (1929) estimate of 4 million sheep is often cited as a reliable approximation of mountain sheep numbers. Valdez (1988), however, doubted wild sheep numbers ever exceeded 500,000 for all North America. Mountain sheep are highly selective in their habitat preferences, and it is probably a misconception that sheep were uniformly distributed throughout the mountains of western North America.

The present distribution ranges of all races of bighorn sheep seem considerably reduced; sheep may be occupying habitats in the most remote portions of their historical distribution (Sugden 1961). Bighorn sheep were quite well adapted to habitats far from the rugged terrain more often considered typical for the species (Buechner 1960; Shackleton 1985; Krausman 1993). Valdez and Krausman (1999) and Krausman (1997a) estimated the number of bighorns in North America in 1991. At that time, Canada supported 12,700 Rocky Mountain bighorn, and 3000 California bighorn sheep. Mexico supported 3500 desert bighorn, and in the contiguous United States there were 25,219 Rocky Mountain bighorn sheep, 4901 California bighorn, and 17,450

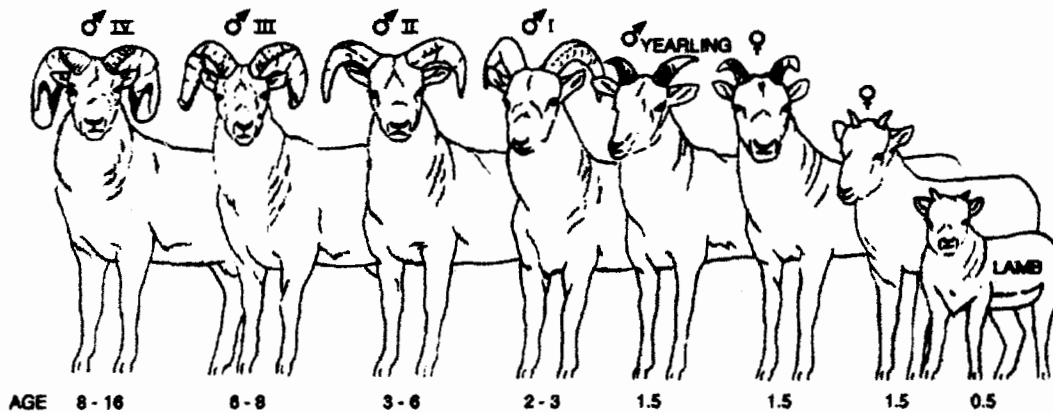


FIGURE 51.7. Age classes of bighorn sheep. Note that the classes form a cline in body and horn size. SOURCE: Redrawn from Geist (1968).

desert bighorn. The total number of bighorn sheep in North America has not changed significantly since the 1991 survey (Krausman 1997a).

Dall's sheep far outnumber all others, with over 100,000; there are 9000 in the Yukon, 500 in British Columbia, 14,000 in the Northwest Territories, and > 72,000 in Alaska (Bowyer et al. 2000). There are about 14,500 Stone's sheep (Valdez and Krausman 1999). Dall's and Stone's sheep populations have remained relatively unimpacted by humans and have retained their historical distribution and abundance.

Population Management. Bighorn sheep populations have declined significantly since 1900 with a subsequent reduction in their geographic distribution (Buechner 1960; Bailey 1980; Hansen 1980b). Declines in density and distribution have been attributed to a wide range of human-induced factors, which include overgrazing by livestock and feral burros, diseases transmitted by livestock, road construction, housing developments, canals, fire suppression, and recreational activities (Gallizioli 1977; Krausman et al. 1989; Harris 1992; Krausman 1996). As a result, population management has been directed at reducing human-caused decimating factors and at learning more about other population-limiting factors. Understanding limiting factors is especially important for resource managers charged with managing bighorns because many sheep populations are small and susceptible to extirpation (Berger 1990; Fitzsimmons and Buskirk 1992; Krausman et al. 1993, 1996).

Management efforts have been directed at eliminating domestic stock from bighorn habitat, understanding the effects of diseases on populations, eliminating competition with species such as feral burros, and minimizing human disturbance. One of the most active management programs for bighorn sheep, however, has been the translocation of animals to various locations within their historical ranges. In general, translocations have been successful and many populations have been returned to historical habitats. Human disturbance of translocated and other herds, however, needs to be closely monitored. In general, bighorn are intolerant of human activities, especially outside protected areas, and can have difficulty adjusting to human encroachment. These sheep have traditional range use and movement patterns that are probably passed from adults to young; consequently, bighorn do not adjust well when these patterns are disrupted (Geist 1971). Disturbances, whether specifically directed toward bighorn or not, have adverse effects on sheep populations. They may abandon ranges following increased levels of human activity (Leslie 1977; Hamilton et al. 1982; Krausman et al. 1989).

Currently, there is no reason to attempt to manage populations of Dall's sheep using predator control or by intervening in disease processes; predators or diseases do not regulate their populations often enough to be of consequence. Effective management, then, is restricted largely to regulating sport and subsistence harvest and providing viewing opportunities for aesthetic and other nonconsumptive uses (Bowyer and Leslie 1992).

Dall's sheep are managed by different state, federal, and provincial government agencies within their distribution. In general, Dall's sheep are managed to furnish trophies for hunters; subsistence harvest is thought to be small (Nichols 1978b; Heimer 1985). Although some harvesting of females was permitted in the past, harvests now are restricted mostly to three-fourths- or full-curl males (Elliot 1985; Hoefs and Barichello 1985; Poole and Graf 1985). Total harvest relative to the total size of populations is typically <2% (Bowyer and Leslie 1992). Most large males are harvested by nonresident hunters, who are required to follow a set of regulations that includes hiring guides or outfitters, payment of special fees, and hunting only in specified areas (Bowyer and Leslie 1992).

Nichols (1978a,b) concluded that the harvest of large males did not influence reproduction in populations of Dall's sheep, and this practice was not sufficient to reduce herd numbers. This is not surprising, because large males only use the same ranges as females during rut, and one consequence of sexual segregation is a reduction in competition of large males with females and young for much of the year. Thus, only the harvest of females can affect populations in a density-dependent manner. Density, interacting with climatic conditions, is the primary factor regulating productivity of Dall's sheep populations.

This interaction between density and climate also plays an important role in determining horn size in males and hence the quality of trophies available to harvest. For instance, Bunnell (1978) reported a strong positive relationship between precipitation (an index to primary productivity) and horn growth for male Dall's sheep. Moreover, depressed recruitment was in years in which growth of horns also was diminished (Bunnell 1978). The quality (i.e., growth) of horns of young males is mediated through the physical condition of the females, and this effect can be observed for up to 5 years of age. Annual growth of horns is much greater in males than females, and there is marked interannual variation in growth. Annual growth of horns and body mass were not correlated significantly for males (Bunnell 1978). This analysis, however, was complicated by the horns composing 8–12% of body mass in large males and the fact that some brooming (wear) of horn tips occurred (Geist 1971). Bunnell (1978) interpreted this lack of significance to mean that a male could recover from a period of nutritional deprivation and reattain its body mass, but that this period of hardship was recorded in horns. That the cause of differences in horn size was related to nutrition was demonstrated by greater growth of horns in a male held on a game farm than for individuals in a free-ranging population from which the captive male was obtained (Bunnell 1978). Finally, Bunnell (1978) calculated an index to horn quality, which varied markedly among years. Clearly, there are not populations of high and low quality. Instead, changes in quality within a population vary through time depending on nutrition and environmental conditions.

One manner in which the harvest of large males might affect population demography was proposed by Geist (1971). He argued that young males (i.e., less than a three-quarter curl) would experience high rates

of mortality if large males were harvested heavily, because younger individuals would begin participating in rutting activities that lead to high rates of mortality in larger males. Heimer et al. (1982) offered some support for Geist's (1971) hypothesis, but in a reanalysis of those data, Whitten (2001) reached the opposite conclusion. Murphy et al. (1990) reported no relationship between the ratios of old or younger males to females among a number of populations throughout Alaska, and concluded that a reduction in older males via hunting did not affect survivorship of younger males.

One additional way in which the harvest of large males might affect the demographics of a population is via the role of large males in initiation of estrus in females. The presence of a rutting male can hasten onset of estrus in bovids and cervids (Coblentz 1976). Whether young, but sexually mature, males can fulfill this role in Dall's sheep is unknown. Even if estrus is delayed in populations without a sufficient number of large males, whether this would markedly affect timing or synchrony of parturition is uncertain because of the apparent ability of females to adjust the length of gestation (Rachlow and Bowyer 1991; Berger 1992). Moreover, whether there might be a cost (e.g., low mass of a neonate) from adopting such a strategy requires more study. Indeed, this is one of the least known aspects of the biology of Dall's sheep.

Habitat Management. Because bighorn sheep exist in arid environments, habitat-related management generally has been limited to prescribed burns and the provision of water. Prescribed burns are used to control forest and heavy shrub encroachment on bighorn ranges in an attempt to mimic natural fires and maintain open grasslands for foraging and visibility (McWhirter et al. 1992). Water sources have been developed in many areas, but their value to bighorn sheep has been questioned because there is limited empirical evidence demonstrating the benefit of such artificial sources of water (Burkett and Thompson 1994; Broyles 1995; Krausman and Etchberger 1995; Krausman and Czech 1998). However, more research is needed in this area.

The relationship between food supply and population density is recognized as a basic concept of wildlife management. Management of renewable resources is based on the knowledge that there is a limit to the intensity of harvest that each species can tolerate. If this critical level is exceeded, the species will decline and the future annual harvest will diminish. Notwithstanding lower forage production in desert mountain ranges, it is probable that sufficient food supply exists to support more sheep than are currently present. When a certain population has a number of different requirements, the one in shortest supply relative to the demand obviously will be the limiting factor (Leopold 1933). The apparent excess of one life requirement, such as rough topography, cannot make up for the scarcity of another, such as suitable interspersions of food and water.

Until recently, bighorn sheep were often managed on a population-by-population basis, usually within a mountain range. The flatter areas between mountains, however, may act as corridors for sheep to gain access to other ranges for lambing and foraging (Bleich et al. 1990, 1996; Krausman 1997b). Bleich et al. (1990) proposed a model for the conservation of desert bighorn sheep. Schwartz et al. (1986) were among the first to suggest a management strategy based at the landscape level. Overall, they suggested that management should address intermountain travel corridors for bighorn and, where necessary, take steps to minimize potential barriers. Habitat for bighorn sheep still exists in the West, but managers (and the public) have to ensure that sufficient habitat is protected, movement corridors remain open, human disturbance is reduced or kept to a minimum, and transmission of diseases from livestock is eliminated. Only if these are accomplished will efforts to enhance viable populations of bighorn have a chance to be successful.

Because of the remote and rugged terrain occupied by Dall's sheep, manipulation of habitat is rare. Subalpine ranges in British Columbia, Canada, were burned in spring to improve habitat (Elliot 1985; Seip and Bunnell 1985). Elliot (1985) noted that such burning was capable of slowing population declines and enhancing horn size in males. Nutrient quality of burned areas was not superior to that of unburned ranges in

spring and summer, but burned areas had a greater quantity of forage than unburned areas in winter (Seip and Bunnell 1985).

Mineral exploration and extraction, road construction, harassment by low-flying aircraft, and other human disturbances of Dall's sheep, especially on lambing grounds, have the potential to affect populations (Nichols 1975; Hoefs and Barichello 1985; Poole and Graf 1985). Nonetheless, most of the range of Dall's sheep remains remote, pristine, and relatively unaffected by human developments or other activities.

Compared with other large mammals in North America, our understanding of the biology of Dall's sheep is incomplete. Much remains to be learned about these unique ungulates, which inhabit mountainous areas of the far north.

RESEARCH NEEDS

In 1957 and 1978, the Desert Bighorn Council and the Northern Wild Sheep and Goat Council were established, respectively. Since then, scientists have regularly published an array of life history data on mountain sheep. These efforts continue, and ideas and concepts are being refined, sharpened, and revised as technology advances and society changes. Radiotelemetry has been a significant tool in ascertaining movement, home range, site fidelity, sexual segregation, and other important information. Satellite telemetry and global positioning systems are the latest technology assisting with these types of data collection and others important to the management of mountain sheep.

Although biologists have acquired a wealth of data, more needs to be obtained. Some of the types of earlier data collection are still needed and will continue, but future and novel research is also necessary toward a better understanding of the ecology of mountain sheep. This should include studies of taxonomy, landscape use, anthropogenic forces, predation, competition, exploitation, translocations, small populations, and natality.

LITERATURE CITED

- Adams, L. G., K. L. Risenhoover, and J. A. Bailey. 1982. Ecological relationship of mountain goat and Rocky Mountain bighorn sheep. Proceedings of the Biennial Symposium of the Northern Sheep and Goat Council 3:9-22.
- Akeson, J. J., and H. A. Akeson. 1992. Bighorn sheep movements and summer lamb mortality in central Idaho. Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council 8:14-27.
- Alderman, J. A., P. R. Krausman, and B. D. Leopold. 1989. Diel activity of female desert bighorn sheep in western Arizona. Journal of Wildlife Management 52:264-71.
- Alvarez, T. 1976. Status of bighorns in Baja, California. Desert Bighorn Council Transactions 20:18-21.
- Asdell, S. A. 1964. Patterns of mammalian reproduction. Cornell University Press, Ithaca, NY.
- Ashcroft, G. E. W. 1986. Sexual segregation and group sizes in California bighorn sheep. M.S. Thesis, University of British Columbia, Vancouver, Canada.
- Augsburger, J. G. 1970. Behavior of Mexican bighorn sheep in the San Andres Mountains, New Mexico. M.S. Thesis, New Mexico State University, Las Cruces.
- Bailey, J. A. 1980. Desert bighorn, forage competition and zoogeography. Wildlife Society Bulletin 8:208-16.
- Bailey, J. A. 1936. The mammals and life zones of Oregon. North American Fauna 55:1-416.
- Bates, J. W., Jr., J. C. Pederson, and S. C. Amstrop. 1976. Bighorn sheep range, population trend and movement. Desert Bighorn Council Transactions 20:11-12.
- Bavin, R. L. 1975. Ecology and behavior of the Persian ibex in the Florida Mountains, New Mexico. M.S. Thesis, New Mexico State University, Las Cruces.
- Becker, K., T. Varcalli, E. T. Thorne, and G. B. Butler. 1978. Seasonal distribution patterns of Whiskey Mountain bighorn sheep. Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council 1:1-16.
- Berger, J. 1978. Group size, foraging, and antipredator ploys: An analysis of bighorn sheep decisions. Behavioral Ecology and Sociobiology 4:91-99.
- Berger, J. 1979a. Social ontogeny and behavioural diversity: Consequences for bighorn sheep *Ovis canadensis* inhabiting desert and mountain environments. Journal of Zoology (London) 192:251-66.

- Berger, J. 1979b. Weaning conflict in desert and mountain sheep (*Ovis canadensis*): An ecological interpretation. *Zeitschrift für Tierpsychologie* 50:188–200.
- Berger, J. 1990. Persistence of different sized populations: An empirical assessment of rapid extinctions in bighorn sheep. *Conservation Biology* 4:91–98.
- Berger, J. 1991. Pregnancy incentives, predation constraints and habitat shifts: Experimental and field evidence for wild bighorn sheep. *Animal Behavior* 41:61–77.
- Berger, J. 1992. Facilitation of reproductive synchrony by gestation adjustment in gregarious mammals: A new hypothesis. *Ecology* 73:323–29.
- Berwick, S. H. 1968. Observations on the decline of the Rock Creek, Montana, population of bighorn sheep. M.S. Thesis, University of Montana, Missoula.
- Blaisdell, J. A. 1976. The Lava Beds bighorn: So who worries? *Desert Bighorn Council Transactions* 20:50.
- Bleich, V. C., J. D. Wehausen, and S. A. Holl. 1990. Desert-dwelling mountain sheep: Conservation implications of a naturally fragmented distribution. *Conservation Biology* 4:383–90.
- Bleich, V. C., J. D. Wehausen, R. R. Ramey II, and J. L. Rechel. 1996. Metapopulation theory and mountain sheep: Implications for conservation. Pages 353–73 in D. R. McCullough, ed. *Metapopulations and Wildlife Conservation*. Island Press, Washington, DC.
- Bleich, V. C., R. T. Bowyer, and J. D. Wehausen. 1997. Sexual segregation in mountain sheep: Resources or predation? *Wildlife Monographs* 134:1–50.
- Blom, E. 1968. Male reproductive organs. Pages 27–37 in E. S. E. Hafez, ed. *Reproduction in farm animals*. 2nd ed. Lea & Febiger, Philadelphia.
- Blood, D. A. 1961. An ecological study of California bighorn sheep (*Ovis canadensis californiana* Douglas) in southern British Columbia. M.S. Thesis, University of British Columbia, Vancouver, Canada.
- Blood, D. A. 1963. Some aspects of behavior of a bighorn herd. *Canadian Field-Naturalist* 77:77–94.
- Blood, D. A. 1967. Food habits of the Ashnola bighorn sheep herd. *Canadian Field-Naturalist* 81:23–29.
- Blunt, M. H., H. A. Dawson, and E. T. Thorne. 1972. The birth weights and gestation in captive Rocky Mountain bighorn sheep. *Journal of Mammalogy* 58:106.
- Boone, J. P. 1988. Historical review of exceptional sheep trophies. Pages 121–142 in R. Valdez, ed. *Wild sheep and wild sheep hunters of the new world*. Wild Sheep and Goat International, Mesilla, NM.
- Bowyer, R. T. 1984. Sexual segregation in southern mule deer. *Journal of Mammalogy* 65:410–17.
- Bowyer, R. T. 1991. Timing of parturition and lactation in southern mule deer. *Journal of Mammalogy* 72:138–45.
- Bowyer, R. T., and D. M. Leslie, Jr. 1992. *Ovis dalli*. *Mammalian Species* 393:1–7.
- Bowyer, R. T., V. Van Ballenberghe, and J. G. Kie. 1998. Timing and synchrony of parturition in Alaskan moose: Long-term versus proximal effects of climate. *Journal of Mammalogy* 79:1244–1332.
- Bowyer, R. T., D. M. Leslie, Jr., and J. L. Rachlow. 2000. Dall's and Stone's sheep. Pages 491–516 in S. Demarais and P. R. Krausman, eds. *Ecology and management of large mammals in North America*. Prentice-Hall, Upper Saddle Ridge, NJ.
- Bradley, W. G. 1964. The vegetation of the Desert Game Range with special reference to the desert bighorn. *Desert Bighorn Council Transactions* 8:43–67.
- Brown, B. W., D. D. Smith, and R. P. McQuivey. 1977. Food habits of desert bighorn sheep in Nevada 1956–1976. *Desert Bighorn Council Transactions* 21:32–61.
- Browning, B. 1960. Preliminary report on the food habits of the wild burro in the Death Valley National Monument. *Desert Bighorn Council Transactions* 4:88–90.
- Browning, B. M., and G. Monson. 1980. Food. Pages 80–99 in G. Monson and L. Sumner, eds. *The desert bighorn*. University of Arizona Press, Tucson.
- Broyles, B. 1995. Desert wildlife water developments: Questioning use in the Southwest. *Wildlife Society Bulletin* 23:663–75.
- Buechner, H. K. 1960. The bighorn sheep in the United States, its past, present, and future. *Wildlife Monographs* 4:1–174.
- Bunch, T. D., M. Hoefs, R. L. Glaze, and H. S. Ellsworth. 1984. Further studies in Dall's sheep (*Ovis dalli dalli*) from Yukon Territory, Canada. *Journal of Wildlife Diseases* 20:125–33.
- Bunch, T. D., R. M. Mitchell, and A. Maciulis. 1990. G-banded chromosomes of the Gansu orgali (*Ovis ammon jubata*) and their implications in the evolution of the *Ovis* karyotype. *Journal of Heredity* 81:227–30.
- Bunch, T. D., R. S. Hoffmann, and C. F. Nadler. 1999. Cytogenetics and genetics. Pages 263–76 in R. Valdez and P. R. Krausman, eds. *Mountain sheep of North America*. University of Arizona Press, Tucson.
- Bunnell, F. L. 1978. Horn growth and population quality in Dall sheep. *Journal of Wildlife Management* 42:764–75.
- Bunnell, F. L. 1980. Factors controlling lambing period of Dall's sheep. *Canadian Journal of Zoology* 58:1027–31.
- Bunnell, F. L. 1982. The lambing period of mountain sheep: Synthesis, hypothesis, and tests. *Canadian Journal of Zoology* 60:1–14.
- Bunnell, F. L., and N. A. Olsen. 1976. Weights and growth of Dall sheep in Kluane Park Reserve, Yukon Territory, Canada. *Canadian Field-Naturalist* 90:157–62.
- Burkett, D. W., and B. C. Thompson. 1994. Wildlife association with human-altered water sources in semi-arid vegetation communities. *Conservation Biology* 8:682–90.
- Burles, D. W., and M. Hoefs. 1984. Winter mortality of Dall sheep (*Ovis dalli dalli*), in Kluane National Park, Yukon. *Canadian Field-Naturalist* 98:479–84.
- Butcher, P. D., and C. M. Hawkey. 1979. The nature of erythrocyte sickling in sheep. *Comparative Biochemistry and Physiology* 64A:411–18.
- Cameron, R. D., and J. M. Ver Hoef. 1994. Predicating parturition rate of caribou from autumn body mass. *Canadian Journal of Zoology* 71:480–86.
- Carter, B. H. 1968. Scabies in desert bighorn sheep. *Desert Bighorn Council Transactions* 12:76–77.
- Chappel, R. W., and R. J. Hudson. 1978. Winter bioenergetics of Rocky Mountain bighorn sheep. *Canadian Journal of Zoology* 56:2388–93.
- Chilelli, M. E., and P. R. Krausman. 1981. Group organization and activity patterns of desert bighorn sheep. *Desert Bighorn Council Transactions* 25:17–24.
- Clark, G. W., and D. A. Colwell. 1974. *Eimeria dalli*: A new species of protozoan (Eimeriidae) from Dall sheep, *Ovis dalli*. *Journal of Protozoology* 21:197–99.
- Clark, J. L. 1970. *The great arc of the wild sheep*, 3rd ed. University of Oklahoma Press, Norman.
- Clark, J. L. 1978. *The great arc of the wild sheep*, 4th ed. University of Oklahoma Press, Norman.
- Coblentz, B. E. 1976. Functions of scent urination in ungulates with special reference to feral goats (*Capra hircus*). *American Naturalist* 110:549–57.
- Coggins, V. L., and P. E. Matthews. 1992. Lamb survival and herd status of the Lostine bighorn herd following a *Pasteurella* die-off. *Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council* 8:147–54.
- Cowan, I. M. 1940. Distribution and variation in the native sheep of North America. *American Midland Naturalist* 24:505–80.
- Cunningham, S. C., and R. D. Ohmart. 1986. Aspects of the ecology of desert bighorn sheep in Corizzo Canyon, California. *Desert Bighorn Council Transactions* 30:14–19.
- Dale, A. R. 1987. Ecology and behavior of bighorn sheep, Waterton Canyon, Colorado, 1981–1982. M. S. Thesis, Colorado State University, Fort Collins.
- Davis, W. B., and W. P. Taylor. 1939. The bighorn sheep of Texas. *Journal of Mammalogy* 20:440–55.
- Dean, H. C., and J. J. Spillett. 1976. Bighorn in Canyonlands National Park. *Desert Bighorn Council Transactions* 20:15–17.
- Decker, J. V. 1970. Scabies in desert bighorn sheep in the Desert National Wildlife Range. *Desert Bighorn Council Transactions* 14:107–8.
- DeForge, J. R. 1980. Population biology of desert bighorn sheep in the San Gabriel Mountains of California. *Desert Bighorn Council Transactions* 24:29–32.
- Demarchi, R. A. 1965. An ecological study of the Ashnola bighorn winter ranges. M.S. Thesis, University of British Columbia, Vancouver, Canada.
- Demarchi, R. A., and H. B. Mitchell. 1973. The Chilcotin River bighorn population. *Canadian Field Naturalist* 87:433–54.
- Deming, O. V. 1952. Tooth development of the Nelson bighorn sheep. *California Fish and Game Journal* 38:523–29.
- De Vos, J., R. L. Glaze, and T. D. Bunch. 1980. Scabies (*Psoroptes ovis*) in Nelson desert bighorn of northwestern Arizona. *Desert Bighorn Council Transactions* 24:44–46.
- De Young, D. W., P. R. Krausman, L. E. Weiland, and R. C. Etchberger. 1993. Baseline ABRs in mountain sheep and desert mule deer. *International Congress on Noise as a Public Health Problem* 6:251–54.
- Dixon, J. S. 1938. Birds and mammals of Mount McKinley National Park, Alaska. U.S. National Park Service Fauna Series 3:1–236.
- Dodd, N. L., and W. W. Brady. 1986. Cattle grazing influences on vegetation of sympatric desert bighorn range in Arizona. *Desert Bighorn Council Transactions* 30:8–13.

- Douglas, C. L., and C. Norment. 1977. Habitat damage by feral burros in Death Valley. *Desert Bighorn Council Transactions* 21:23-25.
- Douglas, C. L., and L. D. White. 1979. Movements of desert bighorn sheep in the Stubbe Spring Area, Joshua Tree National Monument. *Desert Bighorn Council Transactions* 23:71-77.
- Drewek, J. R. 1970. Population characteristics and behavior of introduced bighorn sheep in Owyhee County, Idaho. M.S. Thesis, University of Idaho, Moscow.
- Dunbar, M. R. 1992. Theoretical concepts of disease versus nutrition as primary factors in population regulation of wild sheep. *Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council* 8:174-92.
- Eccles, T. R. 1983. Aspects of social organization and diurnal activity patterns of California bighorn sheep (*Ovis canadensis californiana* Douglas 1829) (Report R-6). British Columbia Ministry of Environment, Fish, and Wildlife, Victoria, Canada.
- Eccles, T. R., and D. M. Shackleton. 1979. Recent records of twinning in mountain sheep. *Journal of Wildlife Management* 43:974-76.
- Eccles, T. R., and D. M. Shackleton. 1986. Correlates and consequences of social status in female bighorn sheep. *Animal Behavior* 34:1391-1401.
- Elenowitz, A. S. 1983. Habitat use and population dynamics of transplanted desert bighorn sheep in the Peloncillo Mountains, New Mexico. M.S. Thesis, New Mexico State University, Las Cruces.
- Elliott, J. P. 1985. The status of thinhorn sheep (*Ovis dalli*) in British Columbia. Pages 43-47 in M. Hoefs, ed. *Wild sheep: Distribution, abundance, management and conservation of the sheep of the world and closely related mountain ungulates*. Special report. Northern Wild Sheep and Goat Council, Whitehorse, Yukon, Canada.
- Erickson, G. L. 1972. The ecology of Rocky Mountain bighorn sheep in the Sun River area of Montana with special reference to summer food habits and range movements (Federal Aid and Wildlife Restoration Project W-120-R-2 and R-3). Montana Fish and Game Department, Helena.
- Estes, R. D. 1973. The role of the vomeronasal organ in mammalian reproduction. *Mammalia* 36:315-41.
- Ethberger, R. C., and P. R. Krausman. 1999. Frequency of birth and lambing sites of a small population of mountain sheep. *Southwestern Naturalist* 44:354-60.
- Ethberger, R. C., P. R. Krausman, and R. Mazaika. 1989. Mountain sheep habitat characteristics in the Pusch Ridge Wilderness, Arizona. *Journal of Wildlife Management* 53:902-7.
- Ethberger, R. C., P. R. Krausman, and R. Mazaika. 1990. Effects of fire on desert bighorn sheep habitats. Pages 53-57 in P. R. Krausman and N. S. Smith, eds. *Managing wildlife in the Southwest*. Arizona Chapter, Wildlife Society, Phoenix.
- Eustis, G. P. 1962. Winter lamb surveys on the Kofa Game Range. *Desert Bighorn Council Transactions* 6:83-86.
- Festa-Bianchet, M. 1986. Site fidelity and seasonal range use by bighorn rams. *Canadian Journal of Zoology* 64:2126-32.
- Festa-Bianchet, M. 1988a. Seasonal range selection in bighorn sheep conflicts between forage quality, forage quantity, and predator avoidance. *Oecologia* 75:580-86.
- Festa-Bianchet, M. 1988b. Nursing behavior of bighorn sheep: Correlates of ewe age, parasitism, lamb age, birthdate and sex. *Animal Behavior* 36:1445-54.
- Festa-Bianchet, M. 1988c. Birthdate and survival in bighorn lambs (*Ovis canadensis*). *Journal of Zoology (London)* 214:653-61.
- Festa-Bianchet, M. 1989. Survival of male bighorn sheep in southwestern Alberta. *Journal of Wildlife Management* 53:259-63.
- Festa-Bianchet, M. 1991. The social system of bighorn sheep: Grouping patterns, kinship and female dominance rank. *Animal Behavior* 42:71-82.
- Fitzsimmons, N. N., and S. W. Buskirk. 1992. Effective population sizes for bighorn sheep. *Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council* 8:1-7.
- Flores, M. G., L. J. Jimenez, S. X. Madrigal, R. F. Moncayo, and R. F. Takaki. 1972. Tipos de vegetacion de la Republica Mexicana. Subsecretaria de Planeacion, Direccion General de Estudios, Direccion Agricola.
- Foreyt, W. J., T. C. Smith, J. F. Evermann, and W. E. Heimer. 1983. Hematologic serum chemistry and serologic values of Dall's sheep, *Ovis dalli dalli*, in Alaska, USA. *Journal of Wildlife Diseases* 19:136-39.
- Franzmann, A. W. 1971. Physiologic values of Stone's sheep. *Journal of Wildlife Disease* 7:139-41.
- Franzmann, A. W. 1972. Environmental sources of variation of bighorn sheep physiologic values. *Journal of Wildlife Management* 36:924-32.
- Franzmann, A. W., and D. M. Hebert. 1971. Variation of rectal temperature in bighorn sheep. *Journal of Wildlife Management* 35:488-94.
- Franzmann, A. W., and E. T. Thorne. 1970. Physiologic values in wild bighorn sheep (*Ovis canadensis canadensis*) at capture, after handling and after captivity. *American Veterinary Medical Association* 57:647-50.
- Frid, A. 1997. Vigilance by female Dall's sheep: Interactions between predation risk factors. *Animal Behavior* 53:799-808.
- Gable, F. C., and A. Murie. 1942. A record of lungworms in *Ovis dalli* (Nelson). *Journal of Mammalogy* 23:220-21.
- Gallizioli, S. 1977. Overgrazing on desert bighorn ranges. *Desert Bighorn Council Transactions* 21:21-23.
- Geist, V. 1966a. Validity of horn segment counts in aging bighorn sheep. *Journal of Wildlife Management* 30:634-35.
- Geist, V. 1966b. The evolutionary significance of mountain sheep horns. *Evolution* 20:558-66.
- Geist, V. 1968. On delayed social and physical maturation in mountain sheep. *Canadian Journal of Zoology* 46:899-904.
- Geist, V. 1971. Mountain sheep: A study in behavior and evolution. University of Chicago Press, Chicago.
- Geist, V. 1985. On Pleistocene bighorn sheep: Some problems of adaptation and relevance to today's American megafauna. *Wildlife Society Bulletin* 13:351-59.
- Geist, V., and R. G. Petocz. 1977. Bighorn sheep in winter: Do rams maximize reproductive fitness by spatial separation and habitat segregation from ewes? *Canadian Journal of Zoology* 55:1802-10.
- Gibbs, H. C., and W. A. Fuller. 1959. Record of *Wyominia tetoni* Scoot, 1941, from *Ovis dalli* in the Yukon Territory. *Canadian Journal of Zoology* 37:815.
- Gilchrist, D. 1992. Why is Montana the land of the giant rams? *Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council* 8:8-13.
- Gionfriddo, J. P., and P. R. Krausman. 1986. Summer habitat use by mountain sheep. *Journal of Wildlife Management* 50:331-36.
- Glaze, R. L., M. Hoefs, and T. D. Bunch. 1982. Aberrations of the tooth arcade and mandible in Dall's sheep from southwestern Yukon, Canada. *Journal of Wildlife Diseases* 18:305-10.
- Goodson, N. J. 1978. Status of bighorn sheep in Rocky Mountain National Park. M.S. Thesis, Colorado State University, Fort Collins.
- Gross, J. E. 1960. History, present, and future status of the desert bighorn sheep (*Ovis canadensis mexicana*) in the Guadalupe Mountains of southeastern New Mexico and northwestern Texas. *Desert Bighorn Council Transactions* 4:66-71.
- Hafez, E. S. E. 1968. Female reproductive organs. Pages 61-80 in E. S. E. Hafez, ed. *Reproduction in farm animals*, 2nd ed. Lea & Febiger, Philadelphia.
- Hall, E. R. 1981. *The mammals of North America*. 2nd ed. John Wiley, New York.
- Hamilton, K. S., S. A. Holl, and C. L. Douglas. 1982. An evaluation of the effects of recreational activity on bighorn sheep in the San Gabriel Mountains, California. *Desert Bighorn Council Transactions* 26:50-55.
- Hamilton, W. D. 1971. Geometry for the selfish herd. *Journal of Theoretical Biology* 31:295-311.
- Hansen, C. G. 1965. Growth and development of desert bighorn sheep. *Journal of Wildlife Management* 29:387-91.
- Hansen, C. G. 1980a. Habitat. Pages 64-79 in G. Monson and L. Sumner, eds. *The desert bighorn*. University of Arizona Press, Tucson.
- Hansen, C. G. 1980b. Population dynamics. Pages 217-35 in G. Monson and L. Sumner, eds. *The desert bighorn*. University of Arizona Press, Tucson.
- Hansen, M. C. 1982. Status and habitat preferences of California bighorn sheep on Sheldon National Wildlife Refuge, Nevada. M.S. Thesis, Oregon State University, Corvallis.
- Hansen, M. C. 1996. Foraging ecology of female Dall's sheep in the Brooks Range, Alaska. Ph.D. Dissertation, University of Alaska, Fairbanks.
- Hansen, R. M., and P. S. Martin. 1973. Ungulate diets in the lower Grand Canyon. *Journal of Range Management* 26:380-81.
- Hardin, G. 1960. The competitive exclusion principle. *Science* 131:1291-97.
- Harris, L. K. 1992. Recreation in mountain sheep habitat. Ph.D. Dissertation, University of Arizona, Tucson.
- Hass, C. C. 1989. Bighorn lamb mortality: Predation, inbreeding, and population effects. *Canadian Journal of Zoology* 67:699-705.
- Hass, C. C. 1990. Alternative maternal-care patterns in two herds of bighorn sheep. *Journal of Mammalogy* 71:24-35.
- Hass, C. C. 1991. Social status in female bighorn sheep (*Ovis canadensis*): Expression, development and reproductive correlates. *Journal of Zoology (London)* 225:509-23.
- Hass, C. C., and D. A. Jenni. 1991. Structure and ontogeny of dominance relationships among bighorn rams. *Canadian Journal of Zoology* 69:471-76.
- Hebert, D. M. 1973. Altitudinal migration as a factor in the nutrition of bighorn sheep. M.S. Thesis, University of British Columbia, Vancouver, Canada.

- Hebert, D. M., and S. Harrison. 1988. The impact of coyote predation on lamb mortality patterns at the Junction Wildlife Management Area. Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council 5:283-91.
- Heimer, W. E. 1985. Population status and management of Dall sheep in Alaska. Pages 1-15 in M. Hoefs, ed. Wild Sheep: distribution, abundance, management and conservation of the sheep of the world and closely related mountain ungulates. Special report. Northern Wild Sheep and Goat Council, Whitehorse, Yukon, Canada.
- Heimer, W. E., R. L. Zarnke, and D. J. Preston. 1982. Disease surveys in Dall sheep in Alaska. Symposium of the Northern Wild Sheep and Goat Council 3:188-97.
- Hemming, J. E. 1969. Cemental deposition, tooth succession, and horn development as criteria of age in Dall sheep. Journal of Wildlife Management 33:552-58.
- Hengel, D. A., S. H. Anderson, and W. G. Hepworth. 1992. Population dynamics, seasonal distribution and movement patterns of the Laramie Peak bighorn sheep herd. Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council 8:83-96.
- Henshaw, J. 1970. Conflict between Dall's sheep and caribou. Canadian Field-Naturalist 84:388-90.
- Hirth, D. H. 1977. Social behavior of white-tailed deer in relation to habitat. Wildlife Monographs 53:1-55.
- Hoefs, M. 1978. Twinning in Dall sheep. Canadian Field-Naturalist 92:292-93.
- Hoefs, M. 1984. Productivity and carrying capacity of a subarctic sheep winter range. Arctic 37:141-47.
- Hoefs, M., and N. Barichello. 1985. Distribution, abundance and management of wild sheep in Yukon. Pages 16-34 in M. Hoefs, ed. Wild sheep: Distribution, abundance, management and conservation of the sheep of the world and closely related mountain ungulates. Special report. Northern Wild Sheep and Goat Council, Whitehorse, Yukon, Canada.
- Hoefs, M., and M. Bayer. 1983. Demographic characteristics of an unhunted Dall sheep, *Ovis dalli dalli*. Canadian Journal of Zoology 61:1346-57.
- Hoefs, M., and T. D. Bunch. 1992. Cranial asymmetry in a Dall ram (*Ovis dalli dalli*). Journal of Wildlife Diseases 28:330-32.
- Hoefs, M., and Cowan. 1979. Ecological investigation of a population of Dall sheep (*Ovis dalli dalli* Nelson). Syesis 12(Supplement 1):1-81.
- Hoefs, M., and U. Nowlan. 1994. Distorted sex ratios in young ungulates: The role of nutrition. Journal of Mammalogy 75:631-36.
- Hoefs, M., T. D. Bunch, R. L. Glaze, and H. S. Ellsworth. 1982. Horn aberrations in Dall's sheep (*Ovis dalli*) from Yukon Territory, Canada. Journal of Wildlife Diseases 18:297-304.
- Hoefs, M., H. Hoefs, and D. Burtles. 1986. Gray wolf, *Canis lupus pambasilens*, in Kluane Lake Area, Yukon. Canadian Field-Naturalist 100:78-84.
- Hogg, J. T. 1984. Mating in bighorn sheep: Multiple creative male strategies. Science 225:526-29.
- Hogg, J. T. 1987. Intrasexual competition and mate choice in Rocky Mountain bighorn sheep. Ethology 75:119-44.
- Holl, S. A., and V. C. Bleich. 1983. San Gabriel mountain sheep: Biological and management considerations (San Bernardino National Forest Administration Report). U.S. Forest Service, San Bernardino, CA.
- Honess, R. F., and N. M. Frost. 1942. A Wyoming bighorn sheep study (Bulletin 1). Wyoming Game and Fish Department, Laramie.
- Honess, R. F., and K. Winter. 1956. Diseases of wildlife in Wyoming (Bulletin 9). Wyoming Game and Fish Department, Laramie.
- Horejsi, B. L. 1976. Suckling and feeding behavior in relation to lamb survival in bighorn sheep (*Ovis canadensis*). Ph.D. Dissertation, University of Calgary, Calgary, Alberta, Canada.
- Irvine, C. A. 1969. Factors affecting the desert bighorn in southeastern Utah. Desert Bighorn Council Transactions 13:6-13.
- Jaeger, E. C. 1957. The North American deserts. Stanford University Press, Palo Alto, CA.
- Jarman, P. J. 1974. The social organization of antelope in relation to their ecology. Behavior 48:215-67.
- Jarman, P. J., and M. V. Jarman. 1979. The dynamics of ungulate social organization. Pages 185-220 in A. R. E. Sinclair and M. Norton-Griffiths, eds. Serengeti: Dynamics of an ecosystem. University of Chicago Press, Chicago.
- Jessup, D. A., and R. R. Ramey II. 1995. Genetic variation of bighorn sheep as measured by blood protein electrophoresis. Desert Bighorn Council Transactions 39:17-25.
- Jones, F. L. 1959. A survey of the Sierra Nevada bighorn. Sierra Club Bulletin 35:29-76.
- Jones, F. L. 1980. Competition. Pages 197-216 in G. Monson and L. Sumner, eds. The desert bighorn. University of Arizona Press, Tucson.
- Jones, R. L., and H. C. Hanson. 1985. Mineral licks: Geography and biochemistry of North American ungulates. Iowa State University Press, Ames.
- Jorgensen, J. T., and W. D. Wishart. 1984. Growth rates of Rocky Mountain Bighorn sheep on Ram Mountain, Alberta. Northern Wild Sheep and Goat Council Proceedings 4:270-84.
- Jorgenson, M. C., and R. E. Turner. 1975. Desert bighorn of the Anza-Borrego Desert State Park. Desert Bighorn Council Transactions 19:51-53.
- Keech, M. A., T. R. Stephenson, R. T. Bowyer, V. Van Ballenberghe, and J. Ver Hoef. 1998. Relationships between blood-serum variables and depth of rump fat in Alaskan moose. Alces 34:173-79.
- Kelly, W. E. 1979. A comparison of 3 bighorn areas on the Humboldt National Forest. Desert Bighorn Council Transactions 23:37-39.
- Kie, J. G., J. A. Baldwin, and C. J. Evans. 1996. CALHOME: A program for estimating animal home ranges. Wildlife Society Bulletin 24:342-44.
- Kilpatric, J. 1982. Texas desert bighorn sheep status report, 1982. Desert Bighorn Council Transactions 26:102-4.
- King, M. M., and G. W. Workman. 1982. Desert bighorn on BLM lands in southeastern Utah. Desert Bighorn Council Transactions 26:104-6.
- Klein, D. R. 1953. A reconnaissance study of the mountain goat in Alaska. M.S. Thesis, University of Alaska, Fairbanks.
- Klein, D. R. 1965. Ecology of deer range in Alaska. Ecological Monographs 35:259-84.
- Kornet, C. A. 1978. Status and habitat use of California bighorn sheep on Hart Mountain, Oregon. Thesis, Oregon State University, Corvallis.
- Kovach, S. D. 1979. An ecological survey of the White Mountain Peak bighorn. Desert Bighorn Council Transactions 23:57-61.
- Krausman, P. R. 1993. The exit of the last wild mountain sheep. Pages 242-50 in G. P. Nabhan, ed. Counting sheep. University of Arizona Press, Tucson.
- Krausman, P. R. 1996. Problems facing bighorn sheep in and near domestic sheep allotments. Pages 59-64 in W. D. Edge, ed. Sustaining rangeland ecosystem symposium. Oregon State University, Corvallis.
- Krausman, P. R. 1997a. Regional summary. Pages 316-17 in D. M. Shackleton, ed. Conservation of wild sheep goats and their relatives: Status survey and conservation action plan for Caprinae. International Union for the Conservation of Nature, Gland, Switzerland.
- Krausman, P. R. 1997b. The influence of scale on the management of desert bighorn sheep. Pages 349-67 in J. A. Bissonette, ed. Primer in landscape ecology. Springer-Verlag, New York.
- Krausman, P. R., and B. Czech. 1998. Water developments and desert ungulates. Pages 138-54 in Symposium on environmental, economic and legal issues related to rangeland water developments. Center for the Study of Law, Science, and Technology, Arizona State University, Tempe.
- Krausman, P. R., and R. C. Etchberger. 1995. Response of desert ungulates to a water project in Arizona. Journal of Wildlife Management 59:292-300.
- Krausman, P. R., and B. D. Leopold. 1986. The importance of small populations of desert bighorn sheep. Transactions of the North American Wildlife and Natural Resource Conference 51:52-61.
- Krausman, P. R., and D. M. Shackleton. 2000. Bighorn sheep. Pages 517-44 in S. Demarais and P. R. Krausman, eds. Ecology and management of large mammals in North America. Prentice-Hall, Upper Saddle River, NJ.
- Krausman, P. R., S. Torres, L. L. Ordway, J. J. Hervent, and M. Brown. 1985. Diel activity of ewes in the little Harquahala Mountains, Arizona. Desert Bighorn Council Transactions 29:24-26.
- Krausman, P. R., B. D. Leopold, R. F. Seegmiller, and S. G. Torres. 1989. Relationships between desert bighorn sheep and habitat in western Arizona. Wildlife Monographs 102:1-66.
- Krausman, P. R., R. Etchberger, and R. M. Lee. 1993. Persistence of mountain sheep. Conservation Biology 7:219.
- Krausman, P. R., G. Long, and L. Tarango. 1996. Desert bighorn sheep and fire, Santa Catalina Mountains, Arizona. Pages 162-68 in P. F. Ffolliott, L. F. DeBano, M. B. Baker, Jr., G. J. Gottfried, G. Sols-Garza, C. B. Edminster, D. G. Neary, L. S. Allen, and R. H. Hamre, tech. coords. Effects of fire on the Madraean Province ecosystems (RM-GTR-289). U.S. Forest Service, Fort Collins, CO.
- Krausman, P. R., A. V. Sandoval, and R. C. Etchberger. 1999. Natural history of desert bighorn sheep. Pages 139-91 in R. Valdez and P. R. Krausman, eds. Mountain sheep of North America. University of Arizona Press, Tucson.
- Lange, R. E., A. V. Sandoval, and W. P. Meleney. 1980. Psoroptic scabies in bighorn sheep (*Ovis canadensis mexicana*) in New Mexico. Journal of Wildlife Disease 16:77-82.
- Lawson, B., and R. Johnson. 1982. Mountain sheep. Pages 1036-55 in J. A. Chapman and G. A. Feldhamer, eds. Wild mammals of North America. Johns Hopkins University Press, Baltimore.
- Lenarz, M. S. 1979. Social structure and reproductive strategy in desert bighorn sheep (*Ovis canadensis mexicana*). Journal of Mammalogy 60:671-78.

- Lenarz, M. S., and W. Conley. 1982. Reproductive gambling in bighorn sheep (*Ovis*): A simulation. *Journal of Theoretical Biology* 98:1-7.
- Leopold, A. 1933. *Game management*. Charles Scribner's Sons, New York.
- Leslie, D. M., Jr. 1977. Home range, group size, and group integrity of the desert bighorn sheep in the River Mountains, Nevada. *Desert Bighorn Council Transactions* 21:25-28.
- Leslie, D. M., and C. L. Douglas. 1979. Desert bighorn of the River Mountains, Nevada. *Wildlife Monographs* 66:1-56.
- Lopez, F. M. C., and V. M. Orihuela G. 1976. Behavior of the desert bighorn (*Ovis canadensis weemsi*) in Baja California. *Desert Bighorn Council Transactions* 20:24-25.
- Lord, T. M., and A. J. Luckhurst. 1974. Alpine soils and plant communities of a Stone sheep habitat in Northeastern British Columbia. *Northwest Science* 48:38-51.
- Luckhurst, A. J. 1973. *Stone sheep and their habitat*. M.S. Thesis, University of British Columbia, Vancouver, Canada.
- Main, M. B., and B. E. Coblentz. 1990. Sexual segregation among ungulates: A critique. *Wildlife Society Bulletin* 18:204-10.
- Main, M. B., F. W. Weckerly, and V. C. Bleich. 1996. Sexual segregation in ungulates: New directions for research. *Journal of Mammalogy* 77:449-61.
- McCann, J. L. 1956. Ecology of mountain sheep. *American Midland Naturalist* 56:297-324.
- McCullough, D. R., and E. R. Schneegas. 1966. Winter observations on the Sierra Nevada bighorn sheep. *California Fish and Game Department* 52:68-84.
- McCutchen, H. E. 1976. Status of Zion National Park desert bighorn restoration project 1975. *Desert Bighorn Council Transactions* 20:52-54.
- McEwan, E. H. 1975. The adaptive significance of the growth patterns in cervids compared with other ungulate species. *Zoologicheskii Zhurnal* 54:1221-32.
- McMichael, T. J. 1964. Relationships between desert bighorn and feral burros in the Black Mountains of Mohave County. *Desert Bighorn Council Transactions* 8:29-35.
- McQuivey, R. P. 1978. The desert bighorn sheep of Nevada (Bulletin 6). Nevada Department of Wildlife Biology, Las Vegas.
- McWhirter, D., A. Smith, E. Merrill, and L. Irwin. 1992. Foraging behavior and vegetation responses to prescribed burning on bighorn winter range. *Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council* 8:264-78.
- Mendoza, V. J. 1976. The bighorn sheep of the state of Sonora. *Desert Bighorn Council Transactions* 20:25-26.
- Merritt, M. F. 1974. Measurement of utilization of bighorn sheep habitat in the Santa Rosa Mountains. *Desert Bighorn Council Transactions* 18:4-17.
- Miquelle, D. G., J. M. Peek, and V. Van Ballenberghe. 1992. Sexual segregation in Alaskan moose. *Wildlife Monographs* 122:1-57.
- Moehlman, P. D. 1974. Behavior and ecology of feral asses (*Equus asinus*). Ph.D. Dissertation, University of Wisconsin, Madison.
- Monson, G. 1964. Long-distance and nighttime movements of desert bighorn sheep. *Desert Bighorn Council Transactions* 8:11-17.
- Monson, G. 1980. Distribution and abundance. Pages 40-15 in G. Monson and L. Sumner, eds. *The desert bighorn*. University of Arizona Press, Tucson.
- Moore, T. D. 1958. Transplanting and observation of transplanted bighorn sheep. *Desert Bighorn Council Transactions* 2:43-46.
- Moore, T. D., L. E. Spence, and C. E. Dugnon. 1974. Identification of the dorsal guard hairs of some mammals of Wyoming (Bulletin 4). Wyoming Game and Fish Department, Laramie.
- Morgan, J. K. 1970. Ecology of the Morgan Creek and East Fork of the Salmon River bighorn sheep herds and management of bighorn sheep in Idaho. M.S. Thesis, Utah State University, Logan.
- Morgantini, L. E., and R. J. Hudson. 1981. Sex differential in use of the physical environment by bighorn sheep (*Ovis canadensis*). *Canadian Field-Naturalist* 95:60-74.
- Morgart, J. R., and P. R. Krausman. 1983. Early breeding in bighorn sheep. *Southwestern Naturalist* 28:460-61.
- Murie, A. 1944. The wolves of Mount McKinley. U.S. National Park Service Fauna Series 5:1-238.
- Murphy, E. C., and K. R. Whitten. 1976. Dall sheep demography in McKinley Park and a reevaluation of Murie's data. *Journal of Wildlife Management* 40:597-609.
- Murphy, E. C., F. J. Singer, and L. Nichols. 1990. Effects of hunting on survival and productivity of Dall sheep. *Journal of Wildlife Management* 40:597-609.
- Nadler, C. F., A. Wolf, and Harris, K. E. 1971. The transferrins and hemoglobins of bighorn sheep (*Ovis canadensis*), Dall sheep (*Ovis dalli*) and mouflon (*Ovis musimon*). *Comparative Biochemical Physiology* 40B:567-70.
- Nichols, L. 1975. Report and recommendations of the Dall and Stone Sheep Workshop Group. Pages 208-66 in J. B. Trefethen, ed. *The wild sheep in modern North America*. Boone and Crockett Club and Winchester Press, New York.
- Nichols, L. 1978a. Dall sheep reproduction. *Journal of Wildlife Management* 42:570-80.
- Nichols, L., Jr. 1978b. Dall's sheep. Pages 173-89 in J. L. Schmidt and D. L. Gilbert, eds. *Big game of North America: Ecology and management*. Wildlife Management Institute and Stackpole Books, Harrisburg, PA.
- Nichols, L., and F. L. Bunnell. 1999. Natural history of thinhorn sheep. Pages 23-77 in R. Valdez and P. R. Krausman, eds. *Mountain sheep in North America*. University of Arizona Press, Tucson.
- Nichols, L., and Erickson, J. A. 1969. Dall sheep (Federal Aid in Wildlife Restoration Project W-15-R-3 and W-17-1; Work Plan N, Job Nos. 3, 4, 5, 6, 7). Alaska Department of Fish and Game, Fairbanks.
- Oldemeyer, J. L., W. J. Barmore, and D. L. Gilbert. 1971. Winter ecology of bighorn sheep in Yellowstone National Park. *Journal of Wildlife Management* 35:257-69.
- Olech, L. A. 1979. Summer activity rhythms of peninsula bighorn sheep in Anza-Barrego Desert State Park, San Diego County, California. *Desert Bighorn Council Transactions* 23:33-36.
- Packard, F. M. 1946. An ecological study of the bighorn sheep in Rocky Mountain National Park, Colorado. *Journal of Mammalogy* 27:3-28.
- Petocz, R. G. 1973. The effect of snow cover on the social behavior of bighorn rams and mountain goats. *Canadian Journal of Zoology* 51:987-93.
- Pianka, E. 1978. *Evolutionary ecology*. Harper and Row, New York.
- Pitzman, M. S. 1970. Birth behavior and lamb survival in mountain sheep in Alaska. M.S. Thesis, University of Alaska, Fairbanks.
- Pollister, G. L. 1974. The seasonal distribution and range use of bighorn sheep in the Beartooth Mountains, with special reference to the West Rosebud and Stillwater herds (Federal Aid Wildlife Restoration Project W-120-R-5). Montana Fish and Game Department, Helena.
- Poole, K. G., and R. P. Graf. 1985. Status of Dall's sheep in the Northwest Territories, Canada. Pages 35-42 in M. Hoefs, ed. *Wild sheep: Distribution, abundance, management and conservation of the sheep of the world and closely related mountain ungulates*. Special report. Northern Wild Sheep and Goat Council, Whitehorse, Yukon, Canada.
- Pulliam, H. R., and T. Caraco. 1984. Living in groups: Is there an optimal group size? Pages 122-47 in J. R. Krebs and N. B. Davies, eds. *Behavioral ecology: An evolutionary approach*, 2nd ed. Blackwell, Oxford.
- Rachlow, J. L., and R. T. Bowyer. 1991. Interannual variation in timing and synchrony of parturition in Dall's sheep. *Journal of Mammalogy* 72:487-92.
- Rachlow, J. L., and R. T. Bowyer. 1994. Variability in maternal behavior by Dall's sheep: Environmental tracking or adaptive strategy? *Journal of Mammalogy* 75:328-37.
- Rachlow, J. L., and R. T. Bowyer. 1998. Habitat selection by Dall's sheep (*Ovis dalli*): Maternal trade-offs. *Journal of Zoology (London)* 245:465-75.
- Remington, R. R. 1981. Arizona bighorn sheep status report. *Desert Bighorn Council Transactions* 25:44-46.
- Reneau, J., and S. C. Reneau, eds. 1993. *Records of North American big game*. Boone and Crockett Club, Missoula, MT.
- Risenhoover, K. L., and J. A. Bailey. 1985. Foraging ecology of mountain sheep: Implications for habitat management. *Journal of Wildlife Management* 49:797-804.
- Russo, J. 1956. The desert bighorn in Arizona (Bulletin No. 1). Arizona Game and Fish Department, Phoenix.
- Ryder, T. J., E. S. Williams, K. W. Mills, K. H. Bowles, and E. T. Thorne. 1992. Effect of pneumonia on population size and lamb recruitment in Whiskey Mountain bighorn sheep. *Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council* 8:136-46.
- Sadler, R. M. 1987. Reproduction in female cervids. Pages 123-44 in C. M. Wemmer, ed. *Biology and management of the cervidae*. Smithsonian Institution Press, Washington, DC.
- Sanchez, D. R. 1976. Analysis of stomach contents of bighorn sheep in Baja, California. *Desert Bighorn Council Transactions* 20:21-22.
- Sandoval, A. V. 1979. Preferred habitat of desert bighorn sheep in the San Andres Mountains, New Mexico. M.S. Thesis, Colorado State University, Fort Collins.
- Sandoval, A. V. 1980. Management of a psoroptic scabies epizootic in bighorn sheep (*Ovis canadensis mexicana*) in New Mexico. *Desert Bighorn Council Transactions* 24:21-28.
- Sandoval, A. V. 1981. New Mexico bighorn sheep status report. *Desert Bighorn Council Transactions* 25:66-68.

- Sandoval, A. V., R. G. Peterson, J. Haywood, and A. Bottrell. 1984. Gestation period in *Ovis canadensis*. *Journal of Mammalogy* 65:337-38.
- Schallenger, A. D. 1966. Food habits, range use and interspecific relationships of bighorn sheep in the Sun River area, west-central Montana. M.S. Thesis, Montana State University, Bozeman.
- Schwartz, O. A., V. C. Bleich, and S. A. Holl. 1986. Genetics and the conservation of mountain sheep. *Biology Conservation* 37:179-90.
- Scott, J. E., R. R. Remington, and J. C. de Vos, Jr. 1990. Numbers, movements, and disease status of bighorn in southwestern Arizona. *Desert Bighorn Council Transactions* 34:9-13.
- Seegmiller, R. E., and R. D. Ohmart. 1981. Ecological relationships of feral burros and desert bighorn sheep. *Wildlife Monographs* 78:1-58.
- Seegmiller, R. E., and C. D. Simpson. 1979. The Barbary sheep: Some conceptual implications of competition with desert bighorn. *Desert Bighorn Council Transactions* 23:47-49.
- Seip, D. R., and F. L. Bunnell. 1985. Nutrition of Stone's sheep on burned and unburned ranges. *Journal of Wildlife Management*. 49:397-405.
- Seton, E. T. 1929. The bighorn. Pages 519-73 in E. T. Seton, ed. *Lives of the game animals*. Vol. 3, Part 2. Doubleday, Garden City, NY.
- Shackleton, D. M. 1973. Population quality and bighorn sheep (*Ovis canadensis canadensis* Shaw). Ph.D. Dissertation, University of Calgary, Alberta, Canada.
- Shackleton, D. M. 1976. Variability in physical and social maturation between bighorn sheep populations. *Transactions of the Northern Wild Sheep Council* 4:1-8.
- Shackleton, D. M. 1985. *Ovis canadensis*. *Mammalian Species* 230:1-9.
- Shackleton, D. M. 1991. Social maturation and productivity in bighorn sheep: Are young males incompetent? *Applied Animal Behavior Science* 29:173-84.
- Shackleton, D. M., and J. Haywood. 1985. Early mother-young interactions in California bighorn sheep, *Ovis canadensis californiana*. *Canadian Journal of Zoology* 63:868-75.
- Shackleton, D. M., and D. A. Hutton. 1971. An analysis of the mechanisms of brooming in mountain sheep horns. *Zeitschrift für Säugetierkunde* 36:342-50.
- Shackleton, D. M., R. G. Peterson, J. Haywood, and A. Bottrell. 1984. Gestation period in *Ovis canadensis*. *Journal of Mammalogy* 65:337-38.
- Shackleton, D. M., C. C. Shank, and B. M. Wikeen. 1999. Natural history of Rocky Mountain and California bighorn sheep. Pages 78-138 in R. Valdez and P. R. Krausman, eds. *Mountain sheep of North America*. University of Arizona Press, Tucson.
- Shank, C. C. 1979. Sexual dimorphism and the ecological niche of wintering Rocky Mountain bighorn sheep. Ph.D. Dissertation, University of Calgary, Alberta.
- Shank, C. C. 1982. Age-sex differences in the diets of wintering Rocky Mountain bighorn sheep. *Ecology* 63:627-33.
- Simmons, N. M. 1969. Heat stress and bighorn behavior in the Cabeza Prieta Game Range, Arizona. *Desert Bighorn Council Transactions* 13:56-63.
- Simpson, C. D., and L. J. Krysl. 1981. Status and distribution of Barbary sheep in the Southwest United States. *Desert Bighorn Council Transactions* 25:9-15.
- Smith, D. 1954. The bighorn sheep in Idaho: (Wildlife Bulletin 1). Idaho Department of Fish and Game.
- Smith, K. G., and W. D. Wishart. 1978. Further observations of bighorn sheep non-trophy seasons in Alberta and their management implications. *Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council* 1:52-74.
- Spalding, D. J. 1966. Twinning in bighorn sheep. *Journal of Wildlife Management* 30:207.
- Spalding, D. J., and J. N. Bone. 1970. The California bighorn sheep of the south Okanagan Valley, British Columbia (Wildlife Management Publication 3). Fish and Wildlife Branch, Victoria, British Columbia, Canada.
- Spraker, T. R. 1974. Lamb mortality. *Transactions of the Northern Wild Sheep Council* 3:102-3.
- Steinkamp, M. J. 1990. The effect of seasonal cattle grazing on California bighorn sheep habitat use. M.S. Thesis, Utah State University, Logan.
- Stelfox, J. G. 1971. Bighorn sheep in the Canadian Rockies: A history, 1800-1970. *Canadian Field-Naturalist* 85:101-22.
- Stelfox, J. G. 1975. Range ecology of Rocky Mountain bighorn sheep in Canadian National Parks. Ph.D. Dissertation, University of Montana, Missoula.
- Stewart, S. T. 1980. Mortality patterns in a bighorn sheep population. *Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council* 2:313-30.
- Sugden, L. G. 1961. The California bighorn in British Columbia with particular reference to the Churn Creek herd. British Columbia Department of Recreation and Conservation, Victoria, Canada.
- Taylor, R. A. 1962. Characteristics of horn growth in bighorn rams. M.S. Thesis, University of Montana, Missoula.
- Thompson, R. W., and J. C. Turner. 1982. Temporal geographic variation in the lambing season of bighorn sheep. *Canadian Journal of Zoology* 60:1781-93.
- Todd, J. W. 1972. A literature review of bighorn sheep food habits (Special Report 27). Colorado Department of Game, Fish and Parks and Cooperative Wildlife Research Unit, Fort Collins.
- Turner, J. C. 1976. Initial investigations into the reproductive biology of the desert bighorn ram, *Ovis canadensis nelsoni*, *O. c. cremnobates*. *Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council* 4:22-25.
- Turner, J. C., and C. G. Hansen. 1980. Reproduction. Pages 145-51 in G. Monson and L. Sumner, eds. *The desert bighorn*. University of Arizona Press, Tucson.
- Valdez, R. 1988. Wild sheep and wild sheep hunters of the New World. *Wild Sheep and Goat International*, Mesilla, NM.
- Valdez, R., and P. R. Krausman. 1999. Description, distribution and abundance of mountain sheep. Pages 3-22 in R. Valdez and P. R. Krausman, eds. *Mountain sheep of North America*. University of Arizona Press, Tucson.
- Van Dyke, W. A. 1978. Population characteristics and habitat utilization of bighorn sheep, Steens Mountain, Oregon. M.S. Thesis, Oregon State University, Corvallis.
- Wakeling, B. F., and W. H. Miller. 1989. Bedsite characteristics of desert bighorn sheep in the Superstition Mountains, Arizona. *Desert Bighorn Council Transactions* 33:6-8.
- Wakelyn, L. A. 1987. Changing habitat conditions on bighorn sheep ranges in Colorado. *Journal of Wildlife Management* 51:904-12.
- Walters, J. E., and R. M. Hansen. 1978. Evidence of feral burro competition with desert bighorn sheep in Grand Canyon National Park. *Desert Bighorn Council Transactions* 22:10-16.
- Watts, T. J. 1979. Detrimental movement patterns in a remnant population of bighorn sheep (*Ovis canadensis mexicana*). M.S. Thesis, New Mexico State University, Las Cruces.
- Weaver, R. A. 1972. Conclusion of the bighorn investigation in California. *Desert Bighorn Council Transactions* 16:56-65.
- Weckerly, F. L. 1998. Sexual size dimorphism: Influence of mass and mating systems in the most dimorphic mammals. *Journal of Mammalogy* 79:33-52.
- Wehausen, J. D., and R. R. Ramey II. 1993. A morphometric reevaluation of the peninsular bighorn species. *Desert Bighorn Council Transactions* 37:1-10.
- Welch, R. D. 1969. Behavioral patterns of desert bighorn sheep in south-central New Mexico. *Desert Bighorn Council Transactions* 13:114-29.
- Welles, R. E., and F. B. Welles. 1961. The bighorn of Death Valley (Fauna Series 6). U.S. National Park Service.
- Whitehead, P. E., and E. H. McEwen. 1980. Progesterone levels in peripheral plasma of Rocky Mountain bighorn ewes (*Ovis canadensis*) during the oestrous cycle and pregnancy. *Canadian Journal of Zoology* 58:1005-1108.
- Whitten, K. R. 2001. Effects of horn-curl regulations on demography of Dall's sheep: A critical review. *Alces* 483-495.
- Wikeen, B. M. 1984. Forage selection by California bighorn sheep and the effects of grazing on an *Artemisia-Agropyron* community in southern British Columbia. Ph.D. Dissertation, University of British Columbia, Vancouver, Canada.
- Wilson, L. O. 1968. Distribution and ecology of desert bighorn sheep in south-eastern Utah (Publication No. 68-5). Utah Department of Natural Resources and Division of Fish and Game, Salt Lake City.
- Wishart, W. D. 1958. The bighorn sheep of the Sheep River Valley. M.S. Thesis, University of Alberta, Edmonton, Canada.
- Wishart, W. D., and D. Brochu. 1982. An evaluation of horn and skull characteristics as a measure of population quality in Alberta bighorns. *Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council* 3:127-42.
- Witham, J. H. 1983. Desert bighorn sheep in southwestern Arizona. Ph.D. Dissertation, Colorado State University, Fort Collins.
- Woodger, W. 1964. Population dynamics of bighorn sheep on Wildhorse Island. *Journal of Wildlife Management* 28:381-91.
- Woodward, S. L., and R. D. Ohmart. 1976. Habitat use and fecal analysis of feral burros (*Equus asinus*), Chemehuevi Mountains, California, 1974. *Journal of Range Management* 29:482-85.
- Woolf, A., and D. C. Kradel. 1970. Hematological values of captive Rocky Mountain bighorn sheep. *Journal of Wildlife Disease* 6:67-68.

- Woolf, A., T. O'Shea, and D. L. Gilbert. 1970. Movements and behavior of bighorn sheep on summer ranges in Yellowstone National Park. *Journal of Wildlife Management* 34:446-50.
- Wright, G. J., J. S. Dixon, and B. H. Thompson. 1933. A preliminary survey of faunal relations in National Parks of the U.S. (Fauna Series 1). U.S. National Park Service.
- Zanke, R. L., and S. Rosendal. 1989. Serologic survey for *Mycoplasma ovipneumoniae* in freeranging Dall sheep (*Ovis dalli*) in Alaska. *Journal of Wildlife Diseases* 25:612-13.
- Zanke, R. L., C. L. Calisher, and J. Kerschner. 1983. Serologic evidence of

arbovirus infections in humans and wild animals in Alaska, USA. *Journal of Wildlife Diseases* 19:175-79.

- Zine, M., and P. R. Krausman. 2000. Behavior of captive mountain sheep in a Mojave Desert environment. *Southwestern Naturalist* 45:184-95.

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