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Mountain Goat

Oreamnos americanus

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NOMENCLATURE

Common Names. Mountain goat, Rocky Mountain goat, snow goat, white goat
Scientific Name. *Oreamnos americanus*

Mountain goats belong to the family Bovidae, subfamily Caprinae, and tribe Rupicaprini (*Rupes* = rock, *capra* = goat). Despite their name, mountain goats are not a true goat and do not belong to the genus *Capra.* There is considerable disagreement about the phylogenetic position of *Oreamnos* (Hassanin et al. 1998). Some studies based on molecular and morphological characteristics place the mountain goat close to wild sheep (*Ovis* spp; Gatesy et al. 1997). Most taxonomists, however, classify the mountain goat in a clade grouping *Capricornis, Nemorhaedus,* and *Ovibos* (Cronin et al. 1996; Groves and Shields 1996; Hassanin et al. 1998). Other rupicaprins include the goral (*Nemorhaedus goral*), serow (*Capricornis sumatraensis*), and Japanese serow (*Capricornis crispus*) from Asia and two species of chamois (*Rupicapra rupicapra* and *R. pyrenaica*) from Europe, Turkey, and the Caucasus. *O. americanus* is the only rupicaprin in North America.

Mountain goats were classified into four subspecies (*americanus, kennedyi, missoulae,* and *columbiae*), but currently no subspecies of *O. americanus* are recognized (Cowan and McCrory 1970). A smaller species, *Oreamnos harringtoni,* went extinct about 11,000 years ago, at the end of the Rancholabrean (Mead and Lawler 1994).

DISTRIBUTION

The ancestors of mountain goats are thought to have come from Asia, crossing the Bering Land Bridge between Alaska and Siberia during the Pleistocene (Cowan and McCrory 1970; Rideout and Hoffmann 1975). They colonized the mountains during the glaciations and remained there when the glaciers withdrew. Ancestors of mountain goats apparently evolved specialized adaptations to mountainous environments at least 100,000 years ago. Fossil distribution is poorly documented, but was likely wider than historical distribution; for example, fossils have been recovered from Vancouver Island (Nagorsen and Keddie 2000).

Mountain goats use alpine and subalpine areas throughout northwestern North America. They occur primarily on the Rocky Mountains and foothills, as well as along the main coastal mountain ranges in British Columbia and southern Alaska (Fig. 49.1). Most native mountain goat populations are in British Columbia and Alaska (Table 49.1). Although their historical range has been reduced, native populations also exist in Washington, Montana, Idaho, Alberta, Yukon, and the Northwest Territories (Fig. 49.1 and Table 49.1). Goat populations have been introduced in some states outside their known historical range, including Colorado, Oregon, Nevada, South Dakota, Utah, and Wyoming, mostly during 1940–1970 (Johnson 1977). They have also been reintroduced in parts of Alaska, Idaho, Montana, Washington, and Alberta. Including native and nonnative herds, there are an estimated 75,000–110,000 mountain goats in North America (Table 49.1).

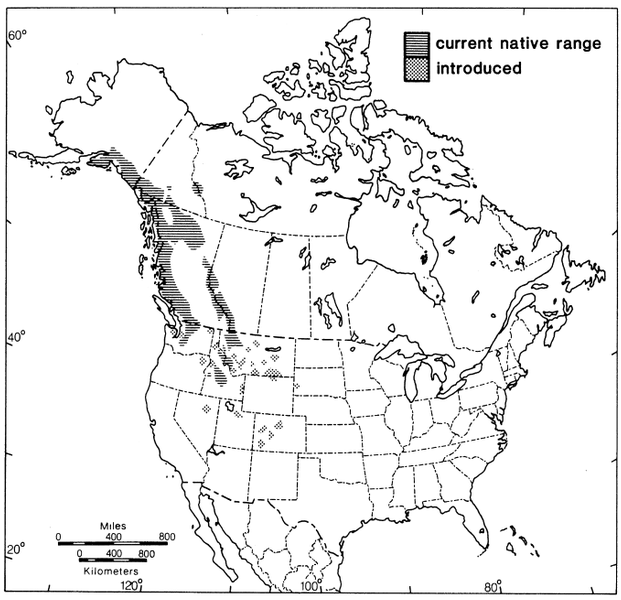

Figure 49.1. Distribution of mountain goats.

DESCRIPTION

Male and female mountain goats are alike in appearance and characterized by a stocky body with short legs, a coat of long and coarse white hairs, conspicuous sharp black horns, and a short tail (Fig. 49.2). Their forequarters are large, with massive muscles to help pull the animal up rocky ledges. Their paired hooves are separated by a large interdigital cleft and their dew claws are well developed. The hooves have a soft pad protruding beyond the outer cornified shell, which gives good traction in precipitous terrain (Brandborg 1955). The horns are conical in shape and slightly curved posteriorly. Black supraoccipital glands, swollen during the rut and more developed in males than in females, are located just behind the horns. The glands are thought to be used for scent marking during the rutting season, although no precise information exists on their role (Geist 1964).

Body Size and Growth. Although little information is available, mountain goat kids probably weigh 2.5–3.5 kg at birth (Brandborg 1955; Lentfer 1955; S. D. Côté, unpublished data.). Carl and Robbins (1988) reported an average mass of 4.1 kg for seven captive-born kids at 1 week of age. In the Caw Ridge mountain goat population in west-central Alberta, male and female kids weigh 13.9±2.9 and 13.2±2.7 kg, respectively, at 1.5 months of age (Table 49.2). Growth rate during the first summer is similar in both sexes, averaging 195 g/day (Fig. 49.3). On Caw Ridge, kid mass at weaning (approximately 4 months of age) was not affected by birthdate or maternal characteristics such as age and

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TABLE 49.1. Estimates of mountain goat abundance for jurisdictions with >100 individuals

Jurisdiction	Year 2000 Estimate	Source[a]
British Columbia	36,000–63,000	I. Hatter, pers. commun., 2000
Alaska	24,193–29,820	Alaska Department of Fish and Game 2000
Washington	4,000	Washington Department of Fish and Wildlife 2000
Montana	2,295–3,045	J. McCarthy, pers. commun., 2000
Idaho	2,700	D. Toweill, pers. commun., surveys conducted in 2000
Alberta Provincial Lands	1,650	Alberta Fisheries and Wildlife Management Division 2000
Alberta National Parks	800	G. Mercer and W. Glasgow, pers. commun., 2000
Colorado	1,620	J. Ellenberger, pers. commun., 2000 estimates
Yukon	1,400	Hoefs et al. 1977; J. Carey, pers. commun., 2000
Northwest Territories	400+	Johnson 1977; A. Veitch, A. Gunn, and R. Case, pers. commun., 2000
South Dakota	150–170	T. A. Benzon, pers. commun., 2000

[a]Named sources (excluding literature citations) are individuals on staff with the respective jurisdictional wildlife agencies.

social rank (Côté and Festa-Bianchet 2001a). Forage quality measured by fecal crude protein in late spring, however, affected kid mass: kids born in years when forage quality was high during early lactation were heavier in summer than kids born in years of poor-quality forage (Côté and Festa-Bianchet 2001a).

As yearlings, males are about 10% heavier than females and their skeletal size, as measured by total length and hind foot length, is about 4% larger (Table 49.2). Sexual dimorphism in body mass develops after weaning, increasing gradually up to at least 6 years of age (Table 49.2 and Fig. 49.4) (Houston et al. 1989). Females complete their mass gain at 6 years of age (Côté 1999), whereas males may continue to increase in mass with age. At ≥5 years of age, males are about 40–60% heavier than females (Houston et al. 1989; Côté 1999); midsummer body mass is about 95–115 and 60–75 kg for males and females, respectively (Table 49.2). Total lengths are about 155–180 cm for adult males and 140–170 cm for adult females (Table 49.2). At Caw Ridge, Alberta, shoulder height is about 5% and chest girth 7% larger in adult males than in adult females: Shoulder height for males is 96.3±8.0 (*SD*) cm ($n = 6$) and for females is 91.9±4.0 cm ($n = 43$); chest girth for males is 111.2±9.7 cm ($n = 32$) and for females is 103.9±6.5 cm ($n = 73$). Comparative data indicate differences among populations (Table 49.2). For example, mountain goats on Caw Ridge are larger than individuals from several populations in the United States. Comparisons, however, are difficult to make because only the Caw Ridge study accounted for the substantial effects of season on body mass. For goats of all sex–age classes, mass increases during the forage growing season and then decreases through the winter (Houston et al. 1989). In midsummer at Caw Ridge, adult males gain >400 g/day and adult females >200 g/day (S. D. Côté and M. Festa-Bianchet, unpublished data).

FIGURE 49.2. Adult female mountain goat in summer coat in August. SOURCE: Photo by S. D. Côté.

Pelage. Mountain goats have a long and shaggy white coat. The winter pelage consists of long and coarse guard hairs (often >20 cm) and an underlayer of wool about 3–5 cm thick. There is a manelike dorsal ridge of hair on the center of the back, and their pointed beard grows with age (B. L. Smith 1988). The winter coat is shed in May–August and the new hairs start growing before the molt is completed (Brandborg 1955). The summer coat is short (guard hairs 2–5 cm long), and hairs grow from June to autumn. Growth of the winter coat is completed by November or early December (Holroyd 1967; B. L. Smith 1988). Adult males finish shedding their coat before females. At Caw Ridge, males ≥3 years old completed their molt on 16 July ± 7 days ($n = 60$) on average, whereas females of the same age finished shedding on 9 August ± 12 days ($n = 270$). Adult females with kids completed their molt slightly later than nonlactating females (12 August ± 9 days, $n = 145$ compared to 4 August ± 14 days, $n = 114$). This later molt may reflect an energy or protein constraint imposed by a greater expenditure in lactating females (Robbins 1993; Byers 1997). In the same population, juvenile males and females (1- and 2-year-olds) completed their molt about a week before adult females with kids (males: 5 August ± 14 days, $n = 50$; females: 5 August ± 13 days, $n = 84$).

Mountain goats have thick dermal shields protecting their rump. Geist (1967) suggested that dermal shields were an adaptation to the high risk of injury caused by the goat's typical antiparallel circle fighting technique, during which the sharp horns of each goat aim for the opponent's flanks.

Skull and Dentition. The skull of mountain goats (Fig. 49.5) is light and bones are thin (Rideout and Hoffmann 1975). The horn cores are approximately one third the length of the horn sheath and are conical in shape and straight, with a round base and a sharp tip (Fig. 49.5). Rostral length is about 5% longer in adult males (193 mm) than in females (183 mm) (B. L. Smith 1988). The dental formula is I 0/3, C 0/1, P 3/3, M 3/3 (Rideout and Hoffmann 1975). Kids are born with 18 milk teeth, lacking deciduous incisiform canines (Rideout and Hoffmann 1975). The I1 incisors are replaced at 15–16 months of age, the I2 incisors at 2 years of age, the I3 at 3 years of age, and the incisiform canines at 4 or 5 years of age (Brandborg 1955; Rideout and Hoffmann 1975; Wigal and Coggins 1982). Premolars and molars are hypsodont and selenodont (Wigal and Coggins 1982). Goats >8 years of age often show severe tooth wear and can lose some or all of their incisors and canines (Brandborg 1955; B. L. Smith 1986; S. D. Côté, pers. obs.).

Horns. Both sexes have sharp black horns (Fig. 49.6) and use them prominently in social interactions (Geist 1967). Mountain goats display an unusually high level of female–female aggression (Fournier and Festa-Bianchet 1995; Côté 2000a). However, they do not fight through horn contact (Geist 1964), and the high level of female–female aggression may make horns just as useful for females as for males (Côté et al. 1998a). Horn growth starts at birth and continues throughout life, decreasing with advancing age and stopping during winter (Fig. 49.7)

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TABLE 49.2. Body mass, total length, and hind foot length in mountain goats of different age–sex classes

Location	Sex	Age (years)	Mass (kg)	Total Length (cm)	Hind Foot Length (cm)	Reference and Comments
Alberta[a] (Caw Ridge)	M	Kid	13.9 ± 2.9 (41)	92.4 ± 6.3 (13)	23.6 ± 1.4 (36)	S. D. Côté and M. Festa-Bianchet, unpublished data
	F	Kid	13.2 ± 2.7 (53)	90.2 ± 6.6 (33)	22.4 ± 1.4 (50)	
	M	1	35.7 ± 4.5 (51)	126.7 ± 6.4 (13)	30.4 ± 1.7 (45)	
	F	1	32.5 ± 3.7 (45)	124.4 ± 3.6 (13)	29.2 ± 1.3 (39)	
	M	2	53.0 ± 4.4 (37)	144.8 ± 6.0 (6)	33.8 ± 1.3 (29)	
	F	2	46.2 ± 3.6 (32)	140.0 ± 4.8 (10)	32.6 ± 1.5 (29)	
	M	3	65.3 ± 5.5 (12)	—	35.4 ± 1.6 (12)	
	F	3	55.9 ± 3.9 (14)	144.5 ± 5.3 (6)	32.9 ± 1.1 (14)	
	M	4	83.1 ± 6.7 (5)	—	36.7 ± 1.3 (6)	
	F	4	62.2 ± 8.4 (13)	146.1 ± 9.2 (9)	34.3 ± 1.6 (11)	
	M	≥5	102.3 ± 10.1 (16)	—	37.3 ± 1.4 (16)	
	F	≥5	70.6 ± 5.9 (47)	160.2 ± 11.9 (31)	34.5 ± 1.4 (49)	
Washington[b] (Olympic National Park)	M	Kid	12.6 ± 2.6 (11)	—	—	Calculated from Fig. 2 in Houston et al. (1989)
	F	Kid	13.6 ± 3.2 (17)	—	—	
	M	1	30.7 ± 6.7 (20)	—	—	
	F	1	33.1 ± 5.2 (16)	—	—	
	M	2	46.5 ± 9.3 (10)	—	—	
	F	2	40.3 ± 6.2 (15)	—	—	
	M	3	60.0 ± 8.9 (11)	—	—	
	F	3	52.3 ± 10.8 (8)	—	—	
	M	4	72.6 ± 14.4 (6)	—	—	
	F	4	57.6 ± 6.2 (17)	—	—	
	M	≥5	∼111.6 ± 4.8 (9)	—	—	
	F	≥5	∼61.9 ± 5.2 (40)	—	—	
Montana[c] (Sapphire Mountains)	M	Kid	16	90.8	23.9	Rideout (1978)
	F	Kid	15	85.1	24.8	
	M	1	33.6	119.4	29.2	
	F	1	32.4	118.2	28.0	
	M	2	41.5	134.3	29.7	
	F	2	38.6	128.6	29.5	
	F	3	49.6	136.3	31.6	
	M	≥4	68.6	154.0	32.8	
	F	≥4	56.5	141.0	30.8	
Montana (Crazy Mountains)	M	1	35 (5)	120.1 (5)	28.4 (5)	Lentfer (1955)
	F	1	30.5 (3)	114.3 (3)	28.7 (3)	
	M	2	46.8 (2)	143.5 (2)	32.8 (2)	
	F	2	44.5 (2)	142.2 (2)	31.8 (2)	
	F	3	62.3 (2)	148.8 (2)	32.0 (2)	
	M	≥4	82.0 (2)	178.6 (4)	36.6 (4)	
	F	≥4	71.6 (2)	154.4 (5)	32.0 (5)	
Idaho	M	≥4	69.9 (5)	153.7 (5)	—	Brandborg (1955)
	F	≥4	53.1 (6)	141.0 (6)	—	

NOTE: Means ± *SD* are shown with sample sizes in parentheses.

[a]The Caw Ridge data were collected from 1988 to 2000. Body mass was adjusted to midsummer (15 July) for each individual using age- and sex-specific growth rates (Côté 1999). Total length and hind foot length of kids and yearlings also were adjusted to 15 July using age- and sex-specific growth rates. Only means based on more than five individuals are presented.

[b]Goats were captured and weighed between 25 June and 16 July 1981–1984.

[c]Total sample size is 28, including all age–sex classes.

(Côté et al. 1998a). Goats complete about 93% of horn growth by 3 years of age (Côté et al. 1998a). B. L. Smith (1988) reported average horn lengths of 232 mm in adult males and 222 mm in adult females from Idaho and Montana. Males have longer first increments (grown from birth to 18 months of age) than females, whereas females grow more horn than males in their third year (Fig. 49.7C) (Cowan and McCrory 1970; Hoefs et al. 1977; Côté et al. 1998a). After 3 years of age, the annual horn increments of males and females are similar and very short (Fig. 49.7C). Males have larger horn circumference than females at all ages (Fig. 49.7B) (Hoefs et al. 1977; B. L. Smith 1988; Côté et al. 1998a).

Horns do not show directional asymmetry or antisymmetry in total length or base circumference (Côté et al. 1998a; Côté and Festa-Bianchet 2001b). Horn length, however, exhibits fluctuating asymmetry, which refers to small random deviations from perfect bilateral symmetry. Because symmetry reflects the ability of individuals to undergo stable development, fluctuating asymmetry may be a potential measure of individual quality (Møller and Swaddle 1997; Gangestad and Thornhill 1999). Absolute asymmetry increases with horn length in both sexes, but relative asymmetry in horn length does not vary with either sex or age (Côté and Festa-Bianchet 2001b). A study of fluctuating asymmetry in mountain goat horns indicated that asymmetry in horn length revealed individual quality in females, because those with highly symmetrical horns had a higher social rank, were heavier, and produced more young than asymmetrical females (Côté and Festa-Bianchet 2001b). In adult males, however, there was no strong

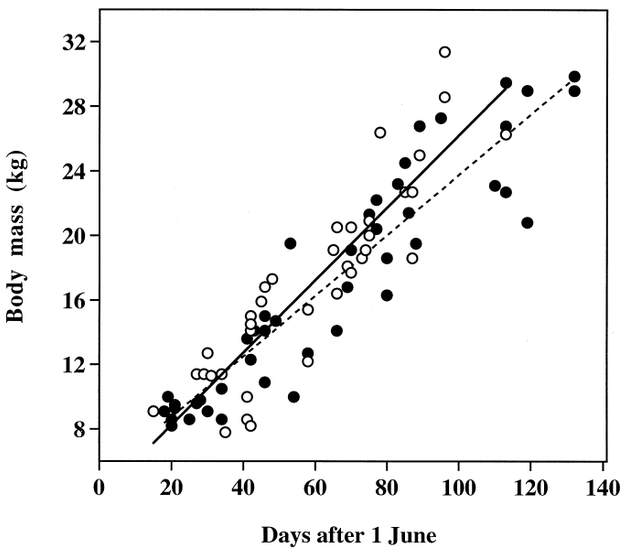

FIGURE 49.3. Summer mass gain by mountain goat kids at Caw Ridge, Alberta, 1988–1997. Males are indicated by open circles and solid line, females by closed circles and dashed line. Each point refers to an individual kid. SOURCE: Côté and Festa-Bianchet (2001a).

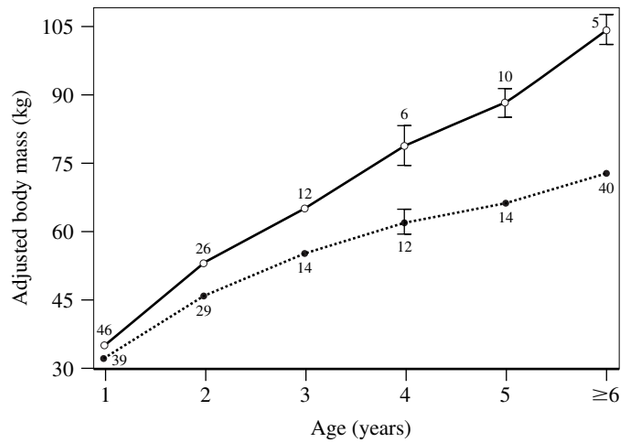

FIGURE 49.4. Development of sexual dimorphism in body mass of mountain goats from Caw Ridge, Alberta, 1988–1999. Body mass was adjusted to midsummer (15 July) using the sex-specific growth rate of each age class. Mean body mass (±*SE*) for males (open circles) and females (closed circles) is accompanied by sample size. SOURCE: Data from Côté (1999).

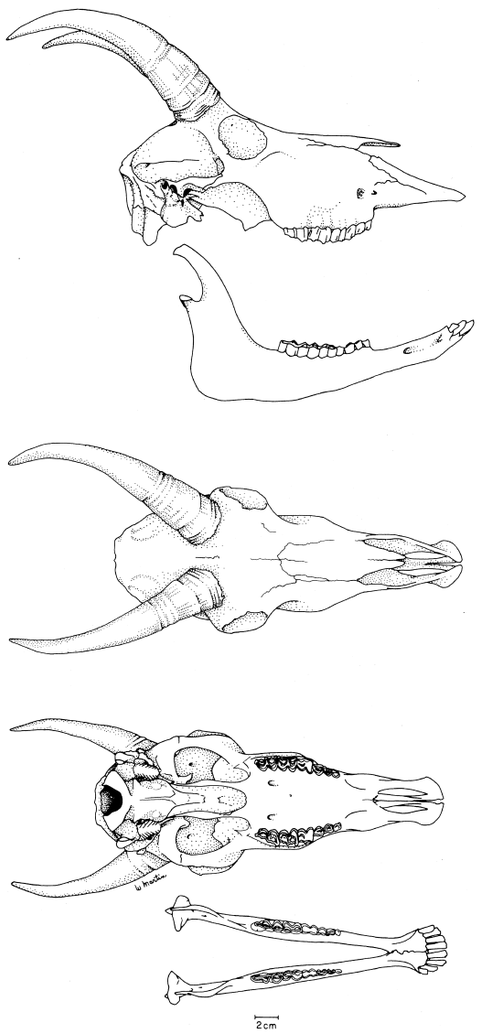

FIGURE 49.5. Skull of the mountain goat (*Oreamnos americanus*). From top to bottom: lateral view of cranium, lateral view of mandible, dorsal view of cranium, ventral view of cranium, dorsal view of mandible.

relationship between horn asymmetry and life-history traits (Côté and Festa-Bianchet 2001b).

SEX DETERMINATION AND AGE ESTIMATION

Compared to other ungulates, it is difficult to determine the sex and age of mountain goats. The most useful characteristic for determining the sex of mountain goats is horn shape. As stated in the previous section, males have larger horn base circumferences than females (also see Fig. 49.6). A useful rule is that horn base circumference is about the size of the eye in females, but is much bigger than the eye in males. In addition, horn curvature in the male is distributed regularly along the horn's entire length (see profile in Fig. 49.6) (Brandborg 1955; B. L. Smith 1988), whereas the female's horns are comparatively straight, but the tips often display a distinctive backward "crook" (Fig. 49.6) (B. L. Smith 1988). Two-year-olds have intermediate rostral length between yearlings and adults, and this characteristic can be used to identify them (B. L. Smith 1988). Males are larger than females, but differences in size are useful for field identification only if animals of different age–sex classes are present for comparison. Determining sex of kids from a distance is very difficult. Two criteria could be used: observation of the vulvar patch in females and urination posture. When urinating, females squat, whereas males stretch. Determining sex of yearlings is difficult, especially at 12–15 months of age, but is possible for an experienced observer familiar with the subtle differences in horn shape. Accuracy of classified counts obtained from aerial surveys is poor, and even experienced observers may confuse kids and yearlings (Gonzalez-Voyer et al. 2001). Most of the time, sex cannot be determined during aerial surveys.

Age of mountain goats can be estimated by counting the horn annuli (Brandborg 1955). The first distinct annual growth ring is formed at the beginning of the second winter, when the goat is ca. 1.5 years old; thereafter, each subsequent ring is formed in early winter (Brandborg 1955; B. L. Smith 1988). Age can be estimated by adding 1 year to the number of distinct rings observed at capture (Stevens and Houston 1989). Only the first seven to eight annuli can be measured because

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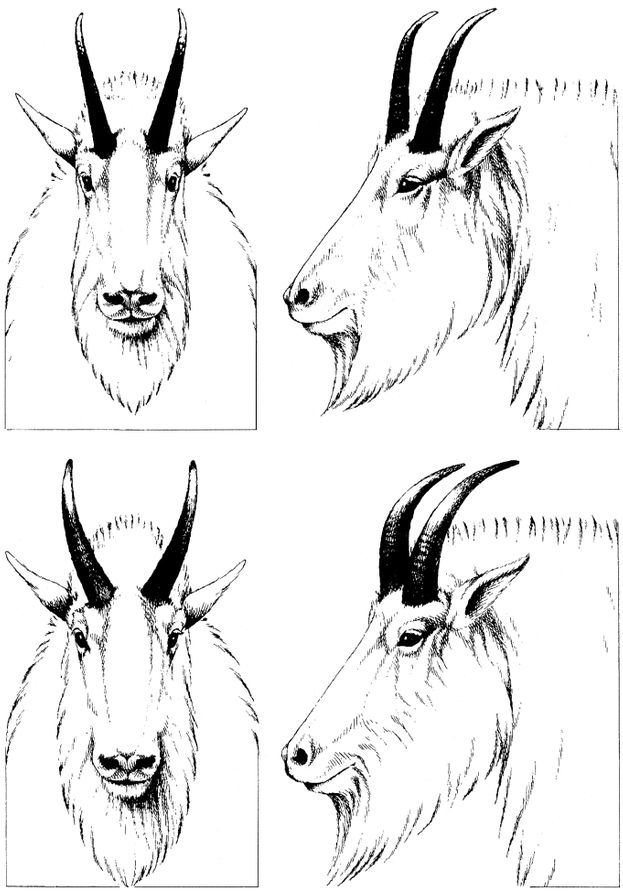

FIGURE 49.6. Variation in horn shape of (top) female and (bottom) male mountain goats (*Oreamnos americanus*). SOURCE: Adapted from B. L. Smith (1988).

later growth rings are often indistinct (Brandborg 1955; Stevens and Houston 1989).

Horn measurements also can be used for estimating body mass and size. Côté et al. (1998a) provided equations for estimating body mass, chest girth, and hind foot length from horn length and circumference. Relationships are approximately linear and correlations (r_p) averaged 0.83.

HABITAT

Foraging Sites. Mountain goats live in some of the most inhospitable terrain in North America, alpine areas close to cliffs or rocky ledges on which they depend to escape predators (Brandborg 1955; McFetridge 1977; Von Elsner-Schack 1986; Haynes 1992; Gross et al. 2002). Weather is typically very harsh, with snow on the ground for 8–9 months of the year and frequent high winds. Goats may seek shelter under rocky ledges and trees during extreme weather. They occur mainly from treeline to the highest alpine meadows (Haynes 1992). In the northern Rocky Mountains, typical elevation ranges from 1500 to 2700 m (Smith 1977), but goats can be seen at >4000 m in Colorado (Hibbs 1967). On the west coast of British Columbia and Alaska, some winter ranges are near sea level (Hebert and Turnbull 1977).

Typical foraging sites for mountain goats are alpine meadows near cliffs (Brandborg 1955; Von Elsner-Schack 1986). Female and juvenile groups rarely wander far from escape terrain or below treeline (McFetridge 1977). Adult males, however, often forage in coniferous forest below treeline (Hebert and Turnbull 1977; Risenhoover and Bailey 1982). Therefore, in some areas, bachelor groups may have access to new-growth forage before adult females in the spring.

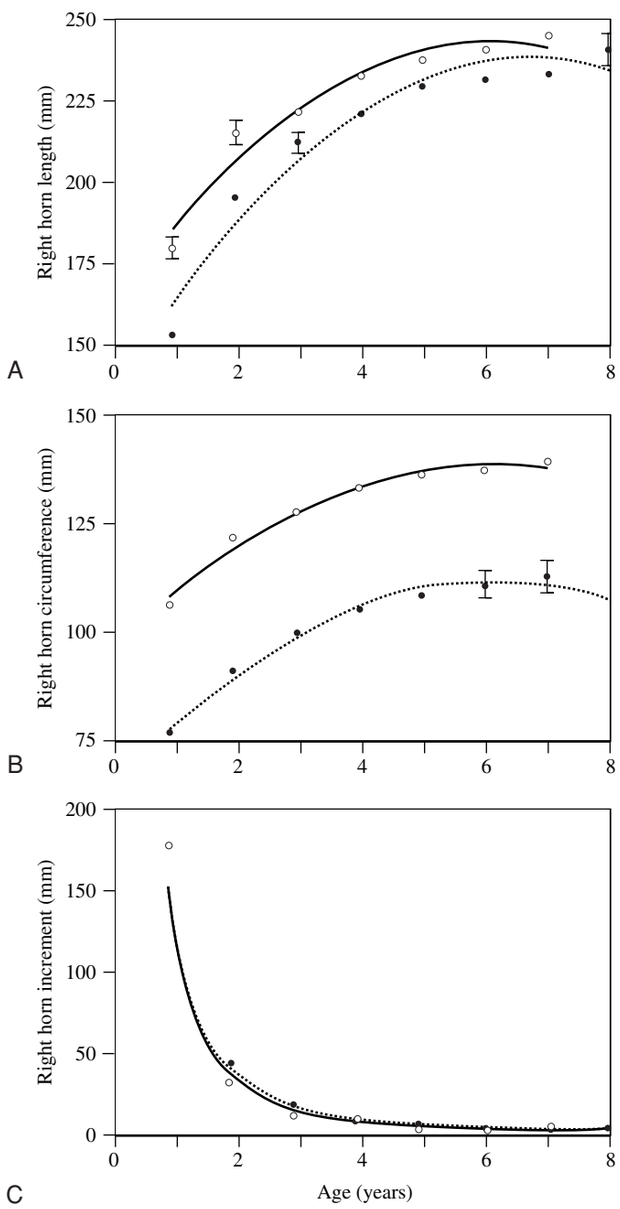

FIGURE 49.7. (A) Average horn length, (B) horn circumference, and (C) annual horn increment of mountain goats at Caw Ridge, Alberta ($n = 259$ individuals). Open circles and broken lines represent males; closed circles and continuous lines represent females. *SE* is shown when large enough for the figure's resolution; fitted lines are second-degree polynomial regressions (A, B) and a power function (C) through the averages and are included to visualize differences between males and females. SOURCE: Data from Côté et al. (1998a).

Bedding Sites. Selection of bedding sites is important for mountain goats. Areas near or on cliffs with a clear view of the surroundings are normally used (McFetridge 1977). Before lying down, goats often dig a bedding site with their front paws and sometimes throw dirt on themselves (Holroyd 1967). Bedding sites are used repeatedly by different animals. All individuals in the group normally use the same area to bed, and, most of the time, distances between neighbors are only

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1–4 m (Côté 1999). Good bedding sites are limited and situated near cliffs, are leveled, and contain 3–10 cm of soft ground (Rideout and Hoffmann 1975). Goats compete for these sites; about 36% ($n = 6775$) of all aggressive interactions occur at resting–ruminating sites, when goats displace each other to occupy the best bedding places (S. D. Côté, unpublished data).

Daily Movements. The extent of daily movements is variable and depends on season and sex. Not surprisingly, movements are shorter in winter when snow is deep (Geist 1964; Hjeljord 1973; Chadwick 1983). Rates of movements while foraging increase with group size (Risenhoover and Bailey 1985). Nursery groups (females, 1- and 2-year-olds of both sexes, and kids) have longer average daily movements than bachelor groups or solitary males. In general, males move <1 km/day, whereas females may move 2–5 km/day or more (S. D. Côté, unpublished data; Singer and Doherty 1985). Foster and Rahs (1985) reported average daily movements of 400 m for canyon-dwelling mountain goats in British Columbia. In contrast, Singer and Doherty (1985) reported hourly movements of 530 and 990 m in males and females, respectively. We hypothesize that females with kids travel more than males as an antipredator strategy, because longer displacements make their location less predictable to predators. Generally, males have small summer home ranges and do not travel much, although some studies have reported extended movements between intensively used areas (Rideout 1974). Conversely, nursery groups generally have larger home ranges than bachelor groups. At Caw Ridge, Alberta, for example, males have summer home ranges of about 5 km^2, whereas females have annual home ranges (100% of locations) of approximately 25 km^2 (S. D. Côté, unpublished data). Rideout (1977) reported annual home range sizes of 21.5 and 24 km^2 for males and females, respectively, in Montana. Although based on small sample sizes, Singer and Doherty (1985) reported annual home ranges of 6.3 km^2 for males and 8.9 km^2 for females in Glacier National Park, Montana. Differences in reported home range sizes could be due to topography. In certain areas, goats may use seasonal home ranges that are a considerable distance from each other. Males could also make extensive movements during the rut in some populations but not in others, depending on the distance between neighboring groups.

Seasonal Movements. Little is known about seasonal movements of mountain goats. Some populations remain in the same area throughout the year, whereas others have distinct summer and winter ranges. In summer, nursery groups normally use all foraging grounds near escape terrain from treeline to the limit of vegetation. Winter ranges, however, are restricted to wind-swept and west/south-facing slopes at treeline and just below treeline near escape terrain (Brandborg 1955; Hjeljord 1973; Smith 1976, 1977; Rideout 1977). Goats may use low-elevation habitats during winter, especially when snow is deep (Hjeljord 1973; Rideout 1974; Smith 1977). Male groups and solitary males use forested areas near treeline throughout the year and may perform important seasonal migrations in some populations (Rideout 1974; Risenhoover and Bailey 1982). Smith (1977) reported that in winter, males were found more often than female in sites with deep snow. On the coast of British Columbia and in Southeast Alaska, goats can winter in coniferous forests at sea level and summer in the mountains (Hebert and Turnbull 1977; Fox 1983). To our knowledge, mountain goats do not have specific rutting ranges.

Feeding Habits. Along the continuum from grazers to browsers, mountain goats are classified as intermediate browsers (Hofmann 1989). They eat a variety of forage (Saunders 1955; Laundré 1994). Diets are similar in summer and winter and are generally dominated by grasses (Saunders 1955; Hibbs 1967; Rideout 1974; Laundré 1994). Laundré (1994) summarized 10 studies on feeding habits of mountain goats and found that summer diet included 52% grass, 30% forb, and 16% browse. Based on averages of the values reported in technical literature, the preferred plant genera in summer were bluegrass (*Poa* sp., 14%), sedges (*Carex* sp., 10%), wheatgrass (*Agropyron* sp., 9%), bluebells (*Mertensia* sp., 6%), fescue (*Festuca* sp., 5%), and hairgrass (*Koeleria* sp., 5%) (Laundré 1994). However, feeding habits at the level of plant species vary tremendously among populations. Goats are generalist herbivores and seem to eat what is available. In the spring, they seek growing, young alpine herbaceous plants (Dailey et al. 1984). In the summer, they also eat large amounts of young leaves of common treeline shrubs such as willows (*Salix* spp., 4%) and dwarf birch (*Betula glandulosa*) (Laundré 1994). Some goats use forested areas in autumn, possibly because of seasonal changes in forage quality (Festa-Bianchet et al. 1994).

In winter, Laundré (1994) reported that the average diet shifted to 60% grass, only 8% forb, and 32% browse. The preferred plant genera were fescue (18%), sedges (8%), wheatgrass (4%), bluegrass (4%), sagebrush (*Artemisia* sp., 3%), hairgrass (1%), and willows (1%). Diet can also vary with snow conditions; Fox and Smith (1988) reported that forbs and ferns decreased in the diet of southeast Alaska goats as snow depth increased to >50 cm. When forage is limited in winter, goats also eat twigs and needles of coniferous trees such as Engelmann spruce (*Picea engelmanii*) and alpine fir (*Abies lasiocarpa*) (Saunders 1955; Geist 1971; Adams and Bailey 1983; Fox and Smith 1988). Harmon (1944) and Fox and Smith (1988) reported heavy use of lichens and mosses in winter by goats in South Dakota and southeast Alaska, respectively.

Salt Licks. Minerals are limited in alpine vegetation and a diet of succulent new-growth vegetation decreases sodium retention by herbivores (Hebert and Cowan 1971a). Mountain goats, therefore, use traditional salt licks where they return regularly during the summer (Singer and Doherty 1985; Hopkins et al. 1992). They normally start visiting the licks in April–May (males) or early June (females) and stop in early autumn (Hebert and Cowan 1971a). Goats sometimes travel long distances to reach mineral licks, sometimes crossing dangerous terrain such as forest or rivers in flood (Holroyd 1967; Hebert and Cowan 1971a; Hopkins et al. 1992). Rates of aggressive encounters are higher at mineral licks than elsewhere, presumably because licks are a limited and defensible resource (Chadwick 1977; Hopkins et al. 1992; Côté 2000b). Over 100 animals can concentrate in 150–200 m^2 and the outcome of social interactions at mineral licks may be different from that seen elsewhere (Côté 2000b).

BEHAVIOR

Activity Patterns. Like all ruminants, mountain goats alternate feeding and resting bouts. Goats typically have six to seven feeding-resting cycles/24 hr. There are peaks of activity in early morning and in the evening (Saunders 1955; Rideout 1974; Romeo and Lovari 1996), but goats also are active during the night (Rideout 1974; Singer and Doherty 1985). Daily activity patterns can be affected by weather conditions (Fox 1977). In the summer, Singer and Doherty (1985) reported increased movements in early morning and late afternoon. The proportion of time that goats spend feeding while active generally increases with group size, mainly because of reduced time spent vigilant (Risenhoover and Bailey 1985; Holmes 1988). During hot midsummer days, activity in the afternoon is often reduced. Long-distance movements (>5 km) can occur at any time of the day.

Social Organization. Male and females are spatially segregated except during the rut (Geist 1964; Chadwick 1977; Stevens 1983; Risenhoover and Bailey 1985). Males are solitary or form bachelor groups of two to six individuals (Risenhoover and Bailey 1982; Haviernick 1996). In late spring, however, bachelor groups can include up to 15 males (Chadwick 1977; S. D. Côté, unpublished data). As noted, females form nursery groups with kids, yearlings, and 2-year-olds of both sexes (Chadwick 1977). Numbers of goats in nursery groups vary substantially depending on population size and on season (Brandborg 1955; Holroyd 1967; Smith 1976, 1977; Chadwick 1977; Singer 1977; Hayden 1984; Masteller and Bailey 1988a).

The mother–kid bond is very strong. Yearlings, and sometimes 2-year-olds, may associate with their mother and occasionally suckle,

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especially if the mother does not have a kid at heel (Hutchins 1984; Dane 2002). Kids are normally physiologically weaned at about 4 months, and behaviorally weaned at about 1 year of age when the new kid is born (Brandborg 1955; Holroyd 1967; Côté 1999). Kids start eating vegetation when about 1 week old, and by 4–5 weeks of age they feed extensively on vegetation (DeBock 1970; S. D. Côté, pers. obs.). Suckling is greatly reduced by 5–6 weeks of age, although it continues, decreasing in frequency, until behavioral weaning (DeBock 1970; Hutchins 1984). Most males leave nursery groups when they are 2 or 3 years old, sometimes 4 years (Chadwick 1977; Romeo et al. 1997).

Females isolate themselves from other goats to give birth, sometimes tolerating the presence of their previous year's offspring. About 1 week after parturition, in early June, females start to form small groups. By July, nursery groups attain peak size, sometimes including >100 individuals in the largest populations (Hopkins et al. 1992; Côté 1999). In late autumn and winter, nursery groups rarely exceed 30 individuals (Brandborg 1955; Smith 1977; Masteller and Bailey 1988a).

Aggressive Interactions. Compared to other ungulates, mountain goats display a high frequency of intraspecific aggression (Chadwick 1977; Dane 1977; Côté 2000a), even though their dangerous horns can injure or even kill conspecifics (Geist 1964, 1967). Adult females at Caw Ridge, Alberta, had an average of 3.4 aggressive interactions/hr, the highest frequency of intraspecific aggression for any female ungulate for which aggressiveness has been measured in the wild (Fournier and Festa-Bianchet 1995).

Aggressive behaviors include present threat (broadside orientation with apparent size enhanced by arching the back), horn threat (display or aggressive movement of the horns), rush threat (sudden quick movement toward an antagonist) and orientation threat (a lower intensity form of rush threat involving walking) (see Geist 1964 and Chadwick 1977 for complete descriptions). Submissive behaviors include orientation avoidance (avoiding the opponent by walking or staring away from it) and rush avoidance (quickly moving away from the antagonist) (Chadwick 1977). Low-pitched grunts are sometimes associated with aggressive interactions (Rideout and Hoffmann 1975). Escalated fights are rare (Geist 1964). They made up only 1.9% of 4265 aggressive interactions during active bouts at Caw Ridge (S. D. Côté, unpublished data). Fights mostly occur as circle fights, where opponents in present threat circle in an antiparallel position, with the head facing the rump of the antagonist (Chadwick 1977). Body (or horn) contacts and high-intensity, bleatlike vocalizations occur in <0.5% of aggressive interactions (Côté 1999).

The presence of a kid does not affect the aggressive behavior of females (Côté 2000a), which suggests that aggressiveness probably did not evolve for offspring defense in mountain goats as previously suggested by Geist (1974). Females and kids nevertheless remain close to each other most of the time and if separated will bleat loudly to locate each other (Brandborg 1955; Holroyd 1967; Rideout and Hoffmann 1975). Most adult behavior patterns are performed by kids during play.

Dominance Hierarchy. Except during the rut, adult females are dominant over all other age–sex classes (Chadwick 1977; Irby and Fitzgerald 1994) and establish highly linear and stable hierarchies even within large groups (Côté 2000a). Adult females are also more aggressive than other age–sex classes (Risenhoover and Bailey 1985; Masteller and Bailey 1988b; Côté 1999). Female social rank is strongly related to age and does not decrease in the oldest females (Côté 2000a). When age is accounted for, social rank does not vary with body mass, horn length, or body size (Côté 2000a). Dyadic dominance relationships are likely established early in life, when a single year of difference in age results in an important difference in body size, and are thereafter maintained into adulthood even though by then some dominant individuals may be smaller or have smaller horns than their younger subordinates. Females interact more often with individuals of similar ranks than with individuals that are distant in the dominance hierarchy (Côté 2000a).

Rutting. Little information is available on the rutting behavior of mountain goats. Early work by Geist (1964) and Chadwick (1983) suggested that adult males establish a dominance hierarchy during the rut and defend estrous females from other males. Throughout the rut, males dig rutting pits, where they often urinate and paw dirt over their underside and hindquarters (Geist 1964; Holroyd 1967). They also mark grass or twigs by brushing their horns on the vegetation to spread secretions from the supraoccipital glands (Geist 1964; DeBock 1970). At the peak of the rut, males follow receptive females everywhere, often leading to perilous chases on cliff faces. According to Geist (1964), females are very aggressive toward courting males and can only be approached during estrus. Males use the low stretch posture (a slow and submissive approach, crouching and exposing the vulnerable part of their neck) to approach females and can sometimes be hit and injured by the sharp horns of females (Geist 1964, 1967). Males test the receptivity of a female by inhaling the scent of the female's urine in their vomeronasal organ (a behavior known as flehmen or "lip curl") and perform frequent tongue flicking when near females in estrus (Geist 1964; Chadwick 1977). Before mounting, males perform a front leg kick between or along the female's haunches (Geist 1964).

REPRODUCTION

Breeding. Mating season is from late October to early December, normally peaking in mid-November (Brandborg 1955; Geist 1964; Holroyd 1967; DeBock 1970; Chadwick 1983). Timing of the rut may vary according to latitude, but little information on geographic variation is available. Little is known about the mating system of mountain goats. During estrus, which is thought to last about 2 days, males follow females and defend them from other males (Geist 1964). It is not clear whether a male can defend more than one female at a time nor how long a male normally defends a female. Based on the short birth season observed (see below), it is likely that most females in a population attain estrus within a 2-week period. It is not known whether females copulate with more than one male. Large and dominant males likely secure most of the mating opportunities, but yearlings and 2-year-olds, which are fertile, may also mate if the opportunity arises (Henderson and O'Gara 1978). There are no data on male reproductive success, which could only be measured through molecular methods.

Birth Season. Mountain goats give birth from mid-May to early June, and about 80% of kids are normally born within 2 weeks of the first birth (Holroyd 1967; Rideout 1978; Côté and Festa-Bianchet 2001a). At Caw Ridge, the median birthdate ranged from 24 to 27 May and the time from first to last birth varied between 28 and 47 days over 5 years (Côté and Festa-Bianchet 2001a). Although the beginning of the birth season is highly synchronized, there are usually a few late births from mid-June to early July (Fig. 49.8). The gap in parturitions between 6 and 15 June

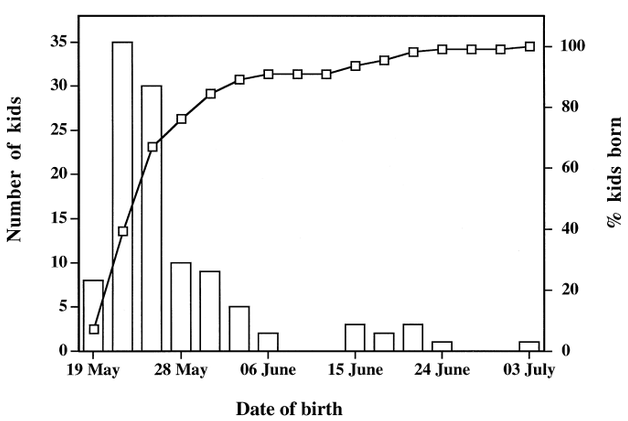

FIGURE 49.8. Birthdates of 109 mountain goat kids during 1993–1997 at Caw Ridge, Alberta. Histograms indicate the number of kids born every 3 days beginning on 15 May, and the solid line shows the cumulative percentage of kids born. SOURCE: Côté and Festa-Bianchet (2001a).

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(Fig. 49.8) may suggest that late births result from females that failed to conceive during their first estrus. Based on peak rutting activities and peak birth period, the gestation is approximately 190 days.

Females isolate themselves to give birth (Holroyd 1967). They normally select a site safe from predators in a rocky outcrop or a cliff where they give birth and remain for a few days with the newborn kid (Côté and Festa-Bianchet 2001a). Kids are of the "montane follower" type (Geist 1981) and at about 2–3 days of age they can follow their mother. Some females return to the same birth site every year, but most do not (S. D. Côté, unpublished data). Following birth, females normally eat the placental remains and lick blood drops from the ground and rocks surrounding the birth site (S. D. Côté, pers. obs.). By doing so, they make birth sites more difficult to detect by predators and likely gain a nutritional advantage by recovering proteins.

Primiparity. In the native population of mountain goats at Caw Ridge, Alberta, females produced their first kid at 3–7 years of age (average = 4.6 ± 0.9 years) (Festa-Bianchet et al. 1994; Côté and Festa-Bianchet 2001c). In introduced populations, females can produce their first kid at 2 years of age (Stevens 1983; Bailey 1991), but normally do so at 3 years (Houston and Stevens 1988; Bailey 1991). These results suggest that the physical development of females in native populations is slow (see also Fig. 49.4) (Côté 1999), and that the costs of reproducing at a young age are probably high. There is no evidence that population density or social rank affects age at first reproduction in mountain goats (Côté and Festa-Bianchet 2001c).

MORTALITY

Starvation. Starvation, particularly of kids, is a likely cause of mortality in late winter and spring. However, animals that die from starvation are difficult to find for two reasons. First, starvation is more likely to occur in late winter, when access to mountain goat habitats by researchers is very difficult and limited. Second, most carcasses are eaten by scavengers before they can be found. At Caw Ridge, for example, only three carcasses of non-radio-collared animals were found, but >200 animals disappeared. In the same study, we documented two kids <1 week old that died of starvation (S. D. Côté, unpublished data). Some deaths of starving animals may be attributed to predation because weak animals are more easily taken by predators.

Predation. In native mountain goat herds, predation is likely the most important mortality factor. The most important predators are grizzly bears (*Ursus arctos*), wolves (*Canis lupus*), and cougars (*Puma concolor*) (Table 49.3) (C. A. Smith 1986; Fox and Streveler 1986; Festa-Bianchet et al. 1994; Côté and Beaudoin 1997; Côté et al. 1997). Coyotes (*Canis latrans*) and black bears (*Ursus americanus*) are other potential predators (Brandborg 1955; Smith 1976), and wolverines (*Gulo gulo*) attack goats, especially young kids (Guiguet 1951; Côté et al. 1997). Brandborg (1955) and Smith (1976) reported golden eagles (*Aquila chrysaetos*) preying on kids in Idaho and Montana. Risk of predation appears higher in areas with trees or in krummholz (stunted forest/scrub), which provide cover for ambush predators (Festa-Bianchet et al. 1994; Côté and Beaudoin 1997). When goats cross forested valleys, they normally use traditional and well-marked trails and often run through areas with trees (S. D. Côté, pers. obs.).

Accidental Death. Although accidents are generally not a frequent mortality factor in goats, deaths due to climbing accidents have been repeatedly suggested (Chadwick 1983; Fox and Streveler 1986). Similarly, authors have reported goats being killed by avalanches (Brandborg 1955; Macgregor 1977; Chadwick 1983).

Fatal injuries can also be inflicted during fighting (Geist 1964, 1967), although this phenomenon appears to be rare. Road kills are not a serious concern for most mountain goats because of the scarcity of roads in their natural range.

Parasites and Diseases. Compared to other ungulates, relatively little is known about parasites and diseases in mountain goats. Kerr and Holmes (1966) identified two species of ticks, two species of cestodes, and nine species of nematodes including a species of lungworm (*Protostrongylus* sp.) in mountain goats from Alberta. They examined 10 goats >2 weeks old, and all were infected with parasites. Samuel et al. (1977) examined 53 goats from the same region and found 17 species of helminths (12 nematodes, 5 cestodes) and 1 species of tick. Brandborg (1955) and Boddicker et al. (1971) found a similar number of parasite species in goats from Idaho and Montana, and South Dakota, respectively. Overall, the nematode *Ostertagia circumcincta* had the highest prevalence (Samuel et al. 1977). Detrimental infections of lungworms and of the nematode *Nematodirus maculosus* were reported in introduced goats from South Dakota (Boddicker et al. 1971). Lungworms were common in mountain goats examined by Cooley (1977) in Colorado and Alberta. Protozoan parasites responsible for coccidiosis (*Eimeria* spp.) (Shah and Levine 1964; Todd and O'Gara 1968) and sarcocyst infections (*Sarcocystis* sp.) (Mahrt and Colwell 1980; Foreyt 1989) also occur in mountain goats. Although mountain goats are infected by several species of parasites, there is no evidence that parasitism has a strong effect on individual body condition, survival, or reproduction (Kerr and Holmes 1966). No study, however, has specifically examined the ecological effects of parasites on mountain goats. Indeed, there has been very little research on the parasites of mountain goats since 1980. Most mountain goat populations appear to be free of contagious ecthyma, a viral disease that is more common in bighorn sheep (*Ovis canadensis*) (but see Samuel et al. 1975; Hebert et al. 1977). To our knowledge, there is no clear evidence of disease transmission from domestic livestock to mountain goats, possibly because the opportunities for contact are few. Selenium deficiency myopathy, known as white muscle disease, has been reported in mountain goats from British Columbia (Hebert and Cowan 1971b), and respiratory syncytial virus, which predisposes to respiratory diseases, was isolated from goats in Washington (Dunbar et al. 1986).

TABLE 49.3. Date of death and predator species for marked mountain goats that were apparently killed by predators at Caw Ridge, Alberta, 1988–2000

Predator	Goat Sex	Goat Age (months)	Date Death Discovered (day/month/year)[a]
Grizzly bear[b]	F	4	03/10/1989
	F	5	10/10/1990
	M	5	23/10/1990 (?)
	M	12	11/06/1991
	F	16	29/09/1991
	F	4	23/09/1992
	M	39	13/09/1996
Wolf[b]	M	4	16/09/1989
	M	6	28/11/1989
	M	3	09/09/1990
	F	8	13/02/1992 (?)
	F	15	30/08/1995
	M	5	19/09/1996 (?)
	F	143	09/05/1999
Cougar	F	7	25/01/1991
	F	14	27/07/1991
	F	3	14/09/1991

SOURCE: Updated from Festa-Bianchet et al. (1994).

[a]Question marks indicate cases when >5 days elapsed between death and recovery of the remains; therefore the cause of death is not certain.

[b]In addition, we observed eight unsuccessful attacks by grizzly bears and three by wolves.

POPULATION DYNAMICS

Productivity. Most females in most populations produce a single kid, but varied frequencies of twinning have been reported. Twins constituted 18% of the kids observed in 1 year in the Stikine River population in British Columbia (Foster and Rahs 1985) and 25–33% over 2 years in

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the introduced Snake River population in Idaho (Hayden 1984). Triplets were reported during a phase of rapid population growth in the Crazy Mountains of Montana (Lentfer 1955). At Caw Ridge, only 2 cases of twinning were observed out of 300 parturitions. Bailey (1991) reported that only 9% of lactating females had twins in an introduced population in Colorado. In the Olympic Mountains, twinning rate among lactating females increased from 2% to 12% after population density was experimentally lowered (Houston and Stevens 1988). Therefore, litter size may be related to resource availability. The fragmentary information available suggests that twinning is more common in introduced and rapidly growing populations than in either native or established and stable populations.

Kid production increases with age during the first few years following primiparity, then remains stable until about 10 years of age, and finally declines in very old females. At Caw Ridge, kid production increased from 4% for females 3 years old to 50% at 4 years, 74% at 5 years, and 84% at 6 years, remained stable at about 84% until 10 years, then declined to 73% for females older than 10 years (Côté and Festa-Bianchet 2001c; M. Festa-Bianchet and S. D. Côté, unpublished data). Similar age-related patterns in productivity have been reported for other goat populations, although in regions with milder climates the plateau phase in kid production begins at an earlier age than at Caw Ridge. Bailey (1991) grouped adult females into three age classes: 3-year-olds, 4- to 9-year-olds, and 10 years of age and older. He reported respective kid production rates for each age class of 52%, 66%, and 53% for mountain goats introduced to Colorado and 77%, 69%, and 57% for those introduced in the Olympic Mountains. Therefore, age-specific productivity in mountain goats fits the typical, inverse-U shape reported for most ungulates (Gaillard et al. 2000). Kid production increases with social rank of the female, but the positive effect of rank on productivity is much stronger for females 3–5 years of age than for older females (Côté and Festa-Bianchet 2001c). Houston et al. (1989) reported that only females weighing at least 50 kg were lactating in the Olympic Mountains, and most nonlactating females were lighter than this threshold mass.

Partly because of differences in female age structure, kid production can vary considerably from year to year, and variability is presumably greater in populations with a variable frequency of twinning. At Caw Ridge, the proportion of females 3 years and older seen with a kid ranged from 45% to 85% and averaged 63% from 1991 to 2000. If 2-year-old females were included, the proportion with kids ranged from 39% to 71% and averaged 54.5% (Côté et al. 2001).

Other studies reported kid:female ratios in summer of 71:100 (Glacier Park, Montana, Rideout 1974), 77–84:100 (Sapphire Mountains, Montana; Rideout 1974), 55–79:100 (Red Butte Range, Montana; Brandborg 1955), 42–43:100 (Glacier National Park; Singer and Doherty 1985), and 92–100:100 (Flathead National Forest, Montana; Singer and Doherty 1985). Hayden (1984) reported kid:female ratios of 90–114:100 over 2 years in a rapidly growing population in Idaho. Because the sex of mountain goats is not easily distinguishable from a distance, some studies pooled the sexes to calculate age ratios. Swenson (1985) reported ratios of kid:100 adult goats varied from 21 to 60 over 9 years in the introduced Absaroka population in Montana. Unfortunately, age ratios are of extremely limited utility in predicting population changes (Gaillard et al. 2000).

Other than litter size, there is limited evidence of density dependence in mountain goat recruitment, possibly because no study has monitored the same population over a sufficiently wide range of densities. The experimental results obtained by Houston and Stevens (1988) suggest that density dependence is likely a threshold rather than a linear response. However, density dependence was not supported by their statistical analysis, possibly because of the limited number of years of study and imprecision of population counts. Swenson (1985) reported density dependence in population growth over 10 years in an introduced population in southern Montana, but his analysis did not account for harvest rates changing from 5.7% to 23.1%. Bailey (1991) found that kid:older goat ratios decreased with increasing population size in the introduced Sheep Mountain–Gladstone Ridge population in Colorado, but age ratios continued to decline after the population had stabilized. He suggested that there may be long-term effects of mountain goats on their forage base, but also commented that changes in population age structure could affect age ratios. Bailey's (1991) suggestion that mountain goats may have a negative long-term impact on the forage supply of their range is important because it may provide clues to the differences in reproductive performance between colonizing and established populations. At Caw Ridge, where the population in June ranged from 81 to 138 mountain goats, we found no evidence of density dependence in kid production or survival.

Survival. Survival from birth to 1 year of age is generally lower and much more variable than adult survival, as is typical of ungulates (Gaillard et al. 2000). By comparing kid:adult ratios to yearling:adult ratios the following year, Adams and Bailey (1982) estimated that an average of 57% of kids (range = 46–78%) annually survived during a period of 4 years. Smith (1976) estimated that 69% of kids survived to 1 year of age in the Bitterroot Mountains, Montana. At Caw Ridge, kid survival (calculated by comparing the number of kids born to the number of yearlings alive in June the following year) averaged 60%, but varied from 38% to 92% over 11 years (Côté and Festa-Bianchet 2001a, and unpublished data). Survival to 1 year of kids of known sex was 70% for males ($n = 99$) and females ($n = 93$). Kid survival varies according to winter weather. In particular, greater snow depth and longer duration of snow cover have a negative effect on kid survival (Brandborg 1955; Rideout 1974; Smith 1976; Chadwick 1983). The late summer ratio of kids to older goats was negatively affected by snow depth in May in two introduced populations in Colorado (Adams and Bailey 1982; Hopkins et al. 1992), suggesting a negative effect of deep snow in early spring on juvenile survival. Orphaned kids appear to have lower survival than nonorphaned kids, but some orphans survive at least to yearling age (Foster and Rahs 1982; Côté et al. 1998b; Côté and Festa-Bianchet 2001a).

Survival of yearling and adult mountain goats has only been estimated at Caw Ridge and in coastal Alaska (C. A. Smith 1986). Results from both studies (Table 49.4) suggest an age-specific survival pattern similar to that of other ungulates (Gaillard et al. 2000): Survival of yearlings is higher than kid survival but lower than adult survival, male survival is lower than female survival, and survival decreases in older goats of both sexes. Annual survival of adult females (≥2 years of age) on Caw Ridge varied from 89% to 97% (based on an average of 37 females/year), whereas it ranged from 50% to 94% for adult males, but the sample only averaged 16 males/year.

As with bighorn sheep (Ross et al. 1997), the effects of predation on a mountain goat herd may vary substantially according to the presence of individual predators that specialize on this species. Most mountain goat populations are too small to serve as prey base for a population of predators, and a single cougar, bear, or wolf pack that specialized on preying on mountain goats could have a very strong impact on a local herd. Consequently, the effects of predation on mountain goat population dynamics may be density independent.

TABLE 49.4. Annual survival rates of yearling and adult mountain goats in two populations

		Age		
Population	Sex	Yearling	2–8 Years[a]	9 Years or Older[a]
Alaska	both	0.71 (7)	0.95 (152)	0.68 (25)
Caw Ridge	females	0.82 (57)	0.94 (303)	0.84 (85)
Caw Ridge	males	0.73 (48)	0.78 (161)	0.71 (17)

SOURCE: Data for coastal Alaska are from C. A. Smith (1986), who did not report sex-specific survival rates.

NOTE: Sample sizes (number of goat-years) in parentheses.

[a]To compare with the C. A. Smith (1986) data, we report survival rates for the same age classes for the Caw Ridge, Alberta, population. If calculated for goats ≥10 years of age, survival decreases to 0.76 ($n = 59$) for females and 0.64 ($n = 11$) for males.

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Causes of death of mountain goats are very rarely known, except for those with radio-collars, and it is often impossible to distinguish between mortality and dispersal. We documented emigration of four males (2–3 years old) and three females (1–4 years old) from Caw Ridge over 11 years, but all four known immigrants were males, 2 to >5 years old (Côté and Festa-Bianchet 2001d, and unpublished data). Therefore, it is likely that a few of the young goats that disappeared from Caw Ridge, especially the males, may have emigrated, and some may have recruited into other populations. Dispersal of 2-year-old goats also was reported by Stevens (1983).

Sex Ratio. The sex ratio of kids is 1:1, but with age it becomes progressively skewed in favor of females because of the higher mortality rate of males. In the unhunted population of Caw Ridge, 50.2% of 245 kids of known sex were males (Côté and Festa-Bianchet 2001d, and unpublished data), but in most years there were $\leq 1/3$ as many males as females 3 years and older (Fig. 49.9). At Caw Ridge, kid sex ratio is affected by maternal age. Females produce an increasing proportion of sons as they become older, from about 70% daughters for mothers 3–6 years of age to about 80% sons for mothers 11 years of age and older (Côté and Festa-Bianchet 2001d). Because these results have major implications for management of mountain goats, it would be useful to know whether this pattern is repeated in other populations.

Heavily female-biased adult sex ratios have been reported for other populations. Foster and Rahs (1985) observed 30 adult males:100 females in the Stikine River population in British Columbia, Rideout (1974) reported 32 adult males:100 females in the Sapphire Mountains of Montana, and Chadwick (1983) counted 37 adult males:100 females in the Swan Range, Montana. Hayden (1984) reported 32 and 51 adult males:100 females over 2 consecutive years in an introduced population in Idaho. Before the removal experiment, Houston and Stevens (1988) reported 29–51 males:100 females (2 years and older) over 5 years in Olympic National Park.

Longevity. The oldest known individual is often reported as a measure of longevity, but that is a misleading statistic of little practical use because in most cases only a very small proportion of adults will survive to that age. The oldest reported male and female mountain goats were 15.5 (B. L. Smith 1986) and 18 years old (Cowan and McCrory 1970), respectively. Very few goats, however, survive >12 years. At Caw Ridge, age-specific survival data suggest that only 25% of yearling females and 6% of yearling males would survive to age 13 years (assuming that all goats that disappeared died). Because mountain goat females can only produce one (rarely two) young a year, longevity likely has an important effect on their lifetime reproductive success.

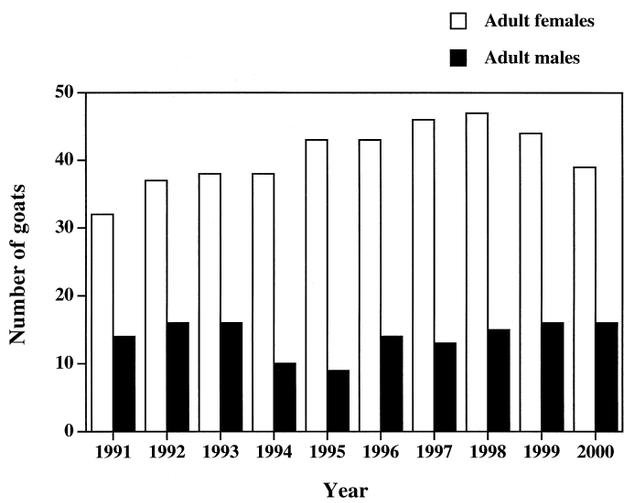

FIGURE 49.9. Adult (≥3 years old) sex ratio in the Caw Ridge mountain goat population, Alberta, in mid-September, 1991–2000.

MANAGEMENT

Capture and Marking. Several capture and marking techniques have been used for mountain goats, including drop nets, foot snares, traps, net guns, and darting with immobilizing drugs either from a helicopter or from the ground. This species, however, is much more sensitive to handling than most other ungulates. Therefore, we recommend that great care should be used in capturing mountain goats, and that the number of captures should be minimized.

A drop net was used to capture goats during 1981–1984 in Washington (Houston et al. 1989) and in 1986–1988 at Caw Ridge (Côté et al. 1998b), without injuring any goats. Drop nets are difficult to operate in strong winds, usually result in only one capture /day, and require several people in place, because as soon as the net is dropped, there should be at least 1 person restraining and blindfolding each goat. During the snow-free season, remotely controlled wooden box traps and self-tripping nylon mesh Clover traps baited with salt have been used successfully (Clover 1956; Côté et al. 1998b). Because goats normally visit salt licks in the early morning, the traps can be left open overnight, but should be checked every 45 min starting at first light (Côté and Festa-Bianchet 2001c). Goats in box traps cannot see outside and remain very calm, but those in Clover traps can become frightened, especially after the rest of the group leaves the area. A total of 465 goats has been captured and handled using these traps at Caw Ridge (Côté et al. 1998b). Goats older than about 14 months should be chemically immobilized before handling. Kids can be handled without drugs, and so can most yearlings until sometime in August when their aggressive behavior and larger body and horn size make them dangerous to handlers. We recommend a long-pole syringe to immobilize trapped adult goats via intramuscular injection of xylazine hydrochloride (5 mg/kg), the effect of which can be reversed by intramuscular injection of 0.7–1.2 mg of idazoxan (Haviernick et al. 1998). A mixture of ketamine hydrochloride and xylazine hydrochloride was used to immobilize 11 goats captured in Clover traps in Glacier National Park, Montana (Singer and Doherty 1985). Immobilized goats should be blindfolded and hobbled, and manipulated for a maximum of 40 min (Côté et al. 1998b; Haviernick et al. 1998; Côté and Festa-Bianchet 2001c). Xylazine is an effective and safe drug for immobilization of mountain goats captured in traps (Haviernick et al. 1998). Goats take 3–9 min to recover after injection of the antagonist idazoxan (Haviernick et al. 1998). Chemical immobilization, however, decreases the probability of kid production the following year by 3- and 4-year-old females, and increases the risk of kid abandonment by females of all ages (Côté et al. 1998b). Not surprisingly, abandonment decreases kid survival (Côté and Beaudoin 1997; Côté et al. 1998b). Although goats in box traps are more calm than those caught in Clover traps, trap type does not affect the efficiency of the drug or the risk of injury (Haviernick et al. 1998). We recommend use of traps to capture mountain goats, but strongly suggest not drugging or manipulating young (3- and 4-year-olds) or lactating females (Côté et al. 1998b).

Free-ranging goats have been caught by darting, but this technique is risky because during the 5–15 min induction, a goat could reach precipitous terrain where handling could be very difficult and, more important, where the drugged goat could fall. Net guns fired from helicopters have also been used to capture mountain goats, notably for transplants (Jorgenson and Quinlan 1996). That technique, however, is costly and involves considerable risk for the animals and the aircraft crew because of the precipitous and rugged habitat of mountain goats. In addition, mountain goats are very sensitive to helicopter disturbance compared to other alpine ungulates (see Censusing) (Foster and Rahs 1983; Côté 1996). We strongly suspect that kid abandonment is likely when lactating females are caught by darting or net-gunning.

Goats can be marked with radio-collars (about 0.8% of body weight) (Côté et al. 1998b), canvas collars, and plastic ear tags. Because uncollared kids may be more likely to survive to 1 year of age

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than kids with radio-collars (Côté et al. 1998b), radio-collaring kids should be avoided or conducted with caution.

Censusing. Because most mountain goats are in rugged mountainous terrain, most management and research agencies use helicopters or fixed-wing aircraft to survey populations, usually in summer when goats are easy to see (Johnson 1977; Thompson and Baker 1981). Aerial counts of mountain goats, however, have limited precision (Ballard 1977; Hebert and Langin 1982; Houston and Stevens 1988; Williams 1999; Gonzalez-Voyer et al. 2001). In Alberta, the percentage of kids observed during helicopter surveys in July, for example, varied from 41% to 121% of the number in the population, and the total number of goats seen varied from 55% to 83% (average = 70%) of the number present (Gonzalez-Voyer et al. 2001). Cichowski et al. (1994) observed only 19 of 28 marked goats (68%) during aerial surveys in British Columbia. Because they are solitary or form small groups and use forested areas, adult males likely are less observable than other age–sex classes (Risenhoover and Bailey 1982). Adults can be recognized during aerial surveys, but yearlings and kids are difficult to classify; even experienced observers can confuse these two age classes (Gonzalez-Voyer et al. 2001). Summer age ratios, in addition, are very poor predictors of recruitment or of population changes (McCullough 1994), partly because overwinter juvenile survival is highly variable (Gaillard et al. 2000). Nevertheless, Gonzalez-Voyer et al. (2001) concluded that helicopter surveys could detect long-term trends in total population size and number of adults for mountain goats.

Mountain goats appear to be more sensitive to helicopter disturbance than other open-terrain ungulates such as bighorn sheep or caribou (*Rangifer tarandus*) (Miller and Gunn 1979; Foster and Rahs 1983; Stockwell et al. 1991; Côté 1996). Goats showed overt responses to 58% of helicopter flights within 2 km (Côté 1996). When helicopters flew within 500 m, 85% of flights caused the goats to move >100 m or to be alert for >10 min (Côté 1996). Based on these observations, Côté (1996) recommended avoiding helicopter flights within 2 km of mountain goat habitat. Clearly, wildlife managers must take the strong sensitivity of mountain goats to helicopters into account when planning the frequency of aerial censuses.

Ground counts are more precise than aerial surveys, but are time-consuming and difficult to perform in remote areas (Ballard 1977; B. L. Smith 1988). From the ground, mountain goats can be classified as kids, yearlings, 2-year-old females, 2-year-old males, adult females, and adult males (B. L. Smith 1988). Only very experienced observers can reliably distinguish yearling males and females. Where possible, we strongly recommend ground counts over aerial surveys.

Hunting and Harvest. Native Americans hunted mountain goats for their pelts and meat, and used the hide as breast armor and the sharp horn sheaths as weapons (Ballard 1977; Wigal and Coggins 1982). Because of the remoteness and harshness of goat habitat, however, it is unlikely that Native people had a strong impact on most mountain goat populations. Nowadays, mountain goats are primarily hunted in most of their range for their trophy horns. Mountain goat meat is reputed to have an unpleasant and strong taste (Rideout and Hoffmann 1975).

Mountain goats are normally hunted in a limited-entry season, but open seasons exist in some management units in British Columbia. Most hunting seasons are from September to November, but may start as early as August and extend until February in parts of British Columbia. Most sport hunting of mountain goats occurs in British Columbia, with an average of 902 goats harvested each year (range = 706–1029 in 1995–1999), or 1.4–2.5% of the estimated population (Table 49.1) (I. Hatter, Wildlife Branch, British Columbia Environment, pers. commun., 2001). Recent goat harvests in British Columbia are slightly lower than in 1972–1976, when an average of 1079 were harvested annually (Johnson 1977). Elsewhere, hunting intensity can be much higher. In Montana, 211 goats were harvested each year from 1995 to 1999, corresponding to 7 – 9% of the total estimated population (Table 49.1) (J. McCarthy, Montana Fish, Wildlife, and Parks, pers. commun., 2001). Hunter success during 1995–1999 in Montana averaged 77%.

Native populations of mountain goats are very sensitive to overharvest. During the twentieth century, some populations were severely reduced or extirpated through sport hunting, often combined with increased motorized access (Hebert and Turnbull 1977; Hoefs et al. 1977; Johnson 1977; Kuck 1977; K. G. Smith 1988). In Alberta, harvest rates based on minimum population estimates were 4.5–9% during 1973–1987. Hunted populations declined in 1980–1987 despite a >50% reduction in harvest (K. G. Smith 1988). The goat hunting season was closed in Alberta in 1988 (K. G. Smith 1988), but population recovery has been very slow. In 2001, following the recovery of some populations and because of the important interest shown by hunters in this species, wildlife managers reopened the mountain goats hunting season to a few restricted areas. A total of 3.921 applications for 3 tags were received across Alberta.

Management of mountain goats for sport hunting is challenging because different populations appear to have radically different reactions to harvests. Historical population declines likely occurred because mountain goats were managed by applying knowledge obtained from other ungulates, such as bighorn sheep, that are not as susceptible to harvest (K. G. Smith 1988). Introduced mountain goat herds, however, are generally much more productive than native herds and can tolerate much higher harvest levels (Swenson 1985; Houston and Stevens 1988; Williams 1999; but see Côté et al. 2001). Many introduced herds show several years of rapid growth, which can sometimes be sustained through much higher levels of harvest than those possible in native herds. Hayden (1984) reported 20% yearly increases over 12 years in Idaho. In the Absaroka Mountains, Montana, 23 goats introduced in 1956–1958 resulted in a population of at least 86 individuals by 1969, despite 6–9% annual harvests beginning in 1964 (Swenson 1985). Consequently, harvest plans for mountain goats must consider the history of individual populations. Harvest rates <10% were unsustainable in Alberta (K. G. Smith 1988). Recruitment and productivity declined as harvest rates increased in native mountain goat populations in Idaho and British Columbia (Kuck 1977, Hebert 1978).

Native goat populations may be unable to sustain a yearly harvest greater than 2–3%, possibly because kid production is low and age at first reproduction is late (Côté and Festa-Bianchet 2001c). Adams and Bailey (1982) concluded that a yearly 7% harvest was sustainable in an introduced population in Colorado, but their simulation suggested that harvests of 7.5% or more would lead to a population decline. Hebert and Turnbull (1977) suggested that harvest of coastal herds in British Columbia should not exceed 4% of the total population. It is likely that sustainable harvest rates are substantially greater in introduced mountain goat populations with good range conditions and without predators, but the harvest rate of 15–20% recommended by Williams (1999) is unlikely to be sustainable (see also Wigal and Coggins 1982; Swenson 1985; Côté et al. 2001). Although Swenson (1985) and Houston and Stevens (1988) suggested that introduced mountain goat population show evidence of density dependence in reproduction, most studies report no effect of population size on reproductive success or evidence of compensatory reproduction in native populations (Hebert and Turnbull 1977; Kuck 1977; K. G. Smith 1988; Côté and Festa-Bianchet 2001a). Hunting appears to lead to additive mortality in native populations (Hebert and Turnbull 1977; Kuck 1977; C. A. Smith 1986).

Because mountain goats are sensitive to overharvest, we caution wildlife managers to set conservative harvest goals (Côté et al. 2001). We suggest a strategy of tracking harvest (C. A. Smith 1986): Population size should be monitored almost annually and hunting effort adjusted accordingly. Hunting programs that encourage harvest of males may have a lower impact on Population dynamics that those that allow either-sex harvest. A male-only hunting program, however, would be difficult because most hunters cannot reliably identify the sex of mountain goats and because adult males are scarce in mountain goat populations. The best management strategy for native populations of mountain goats would combine a 2–3% yearly harvest with a strong encouragement to harvest adult males. Education should be provided to teach hunters how to distinguish males and females. Managers must be prepared to

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close hunting seasons or drastically reduce the number of permits issued following years when an excessive number of females is harvested.

Hunting programs and quotas must be set on a herd-specific base. The dynamics of neighboring herds can be very different (K. G. Smith 1988) and managers can only control hunter distribution by setting very precise geographic boundaries to hunt areas. For example, in 1986–1987, managers in southwestern Alberta assigned seven permits to a "population" of about 150 goats, but hunters shot seven goats from a readily accessible small herd that could be seen from a major road (J. T. Jorgenson, Alberta Natural Resources Service, pers. commun., 2001).

Artificial Introductions and Reintroductions. Mountain goats have been reintroduced to parts of their historical distribution in Alaska, Idaho, Montana, Washington, and southern Alberta. The success rate of mountain goat transplants has been relatively high, although reintroduced mountain goat populations tend to show a low rate of increase compared to other reintroduced ungulates (Komers and Curman 2000).

Mountain goats have also been introduced in many states outside their original range including Colorado, Oregon, Nevada, South Dakota, Utah, and Wyoming since about 1950 (Johnson 1977). Mountain goats have done well in many introductions because of the absence of predators, good range conditions, and relatively mild climates. In Colorado, for example, goats dispersed and colonized extensive mountain ranges considerable distances from release sites (Hopkins et al. 1992). In some areas, such as in Olympic National Park in Washington, introduced populations of mountain goats expanded and had a negative effect on alpine vegetation, raising important concerns and a debate about the legitimate presence of introduced populations, especially in national parks (Pfitsch and Bliss 1985; Lyman 1994, 1995; Houston 1995; Hutchins 1995). Grazing by mountain goats can alter the fragile alpine plant community. Much of the current debate about introduced mountain goats is due to uncertainties about their historical and fossil distribution (Nagorsen and Keddie 2000). Introduced populations outside the historical range are exotics and incompatible with the mission of national parks to preserve natural biodiversity.

RESEARCH, MANAGEMENT, AND CONSERVATION NEEDS

Despite much progress in the 1990s, the mountain goat remains among the least-understood ungulates in North America. Future research should focus on factors determining mountain goat population dynamics and attempt to develop precise and noninvasive census methods. The causes of changes in population size of mountain goats are poorly understood. In particular, we know little about why native populations are highly susceptible to harvest, whereas some introduced populations are not. Management concerns include late age of primiparity, poor recruitment, and high susceptibility to harvest (Kuck 1977; Adams and Bailey 1982; Swenson 1985; Houston and Stevens 1988; K. G. Smith 1988; Bailey 1991; Festa-Bianchet et al. 1994). Within a population, annual differences in kid survival and reproductive success are substantial but much of that variation is unexplained (Côté 1999; Côté and Festa-Bianchet 2001c). Research is needed to understand why recruitment is often low in mountain goat populations that do not appear to show evidence of density dependence and why goats are unable to sustain lower harvest rates than those commonly applied to other species of similar-sized ungulates. Productivity estimates for mountain goat herds inhabiting areas with contrasting predation risk and climate would provide information on factors determining population dynamics. Information on the lifetime reproductive strategies of females would help us understand the effects of maternal characteristics on recruitment and population growth rates. Because of the harsh environmental conditions of their habitat, mountain goat population dynamics may be more susceptible than other ungulates to density-independent factors such as weather (Rideout 1974; Adams and Bailey 1982; Hopkins et al. 1992). Predation may play an important yet unpredictable role because it appears to be density independent. Local information on movements, migration patterns, and dispersal would be useful for managing mountain goats for hunting. We know very little about dispersal patterns, yet emigration of young goats may have an important effect on population dynamics, particularly in leading to the strongly female-biased adult sex ratio.

Population structure may have a profound effect on the success of different management regimes. In particular, the skewed adult sex ratio that seems typical of unhunted populations (Fig. 49.9) can invalidate harvest regulations based on unrealistic sex ratio assumptions. For example, the Caw Ridge population of about 102 goats (August counts) recruited on average only two 4-year-old males/year, suggesting a sustainable adult male harvest of perhaps 1/year, or 1% of the population.

Mountain goats are sensitive not only to harvesting, but also to disturbance (Pendergast and Bindernagel 1977; Foster and Rahs 1983, 1985; Joslin 1986; Pedevillano and Wright 1987; Côté 1996; Côté and Beaudoin 1997). Industrial and recreational activities in mountain goats range are common, yet information on the effects of these activities on goat behavior and ecology is very scarce. The rapidly increasing frequency of helicopter flights for industrial and recreational activities in mountainous areas necessitates more research on the potential effects of these activities. For example, mining exploration relies on heavy and noisy equipment, flown in by helicopter and used in goat range during the lactation period. The effects of these activities on goats are virtually unknown (Côté 1996). Similarly, the effects of industrial activities that increase accessibility and destroy habitat on or near goat ranges, such as mining, logging, and recreational facilities, are almost unknown and could potentially be important (Pendergast and Bindernagel 1977; Foster and Rahs 1985; Joslin 1986). Critical areas such as winter range, parturition areas, and salt licks must be identified and protected from industrial or recreational activities. Impact of intense wildlife-viewing activities in some areas such as national parks should also be monitored. At the same time, more research is needed about whether mountain goats can habituate to some types of human activities. In some national parks (e.g., Glacier in Montana and Jasper in Alberta), goats are very tolerant of road traffic and of tourists in certain specific locations, but in general goats appear less able than bighorn sheep to habituate to human activities. Penner (1988) reported some habituation to persistent and predictable noise stimuli, but not to stimuli that were unpredictable. Goats appear unable to habituate to helicopter flights; Côté's study (1996) was done on goats that had been exposed to helicopters for at least 25 years.

ACKNOWLEDGMENTS

We thank the wildlife managers who provided us with recent population estimates of mountain goats in their jurisdictions. The Caw Ridge mountain goat project has been funded by the Alberta Conservation Association; the Alberta Natural Resources Service; the Alberta Sports, Recreation, Parks, and Wildlife Foundation; the Alberta Wildlife Enhancement Fund; the Fonds pour la Formation de Chercheurs et Aide à la Recherche (Québec); the Natural Sciences and Engineering Research Council of Canada; the Rocky Mountain Goat Foundation, the Mammal Conservation Trust (U.K.); and the Université de Sherbrooke. We thank C. Beaudoin, F. Fournier, Y. Gendreau, A. Gonzalez-Voyer, S. Hamel, M. Haviernick, K. Smith, and M. Urquhart for their contributions to the Caw Ridge study. This chapter was written while SDC was at the Centre for Ecology and Hydrology in Banchory, Scotland.

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