

Dynamics of hunted and unhunted mountain goat Oreamnos americanus populations

Authors: Voyer, Alejandro Gonzalez, Smith, Kirby G., and Festa-

Bianchet, Marco

Source: Wildlife Biology, 9(3): 213-218

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.2003.053

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Dynamics of hunted and unhunted mountain goat *Oreamnos* americanus populations

Alejandro Gonzalez Voyer, Kirby G. Smith & Marco Festa-Bianchet

Gonzalez Voyer, A., Smith, K.G. & Festa-Bianchet, M. 2003: Dynamics of hunted and unhunted mountain goat *Oreamnos americanus* populations. - Wildl. Biol. 9: 213-218.

Native populations of mountain goats *Oreamnos americanus* are sensitive to harvest. To assess the potential effects of limited hunting on population dynamics, we analysed long-term data obtained from aerial counts of 12 native mountain goat herds in Alberta, Canada, during 1973-2001. Seven herds were hunted until 1987 and five were not hunted. Despite a decrease in the number of permits issued, mountain goat numbers declined in most hunted herds between 1980 and 1983. Hunting was closed in 1987. Only three of seven herds increased after hunting was closed. Unhunted herds also showed substantial among-herd differences in population trends. Our results suggest that factors other than sport hunting contributed to the population decline. Future harvests should target adult males, but the adult sex ratio of one intensively studied population was heavily biased in favour of females. A herd of 100 goats may only sustain the harvest of 1-2 adult males per year.

Key words: aerial surveys, Alberta, censusing, hunting, mountain goat, population dynamics, sex ratio

Alejandro Gonzalez Voyer* & Marco Festa-Bianchet, Groupe de Recherche en écologie, nutrition et énergétique, Département de biologie, Université de Sherbrooke, Sherbrooke, PQ J1K 2R1, Canada - e-mail addresses: aglez@miran da.ecologia.unam.mx (Alejandro Gonzalez Voyer); marco.festa-bianchet@usherbrooke.ca (Marco Festa-Bianchet)

Kirby G. Smith, Fish and Wildlife Division, 111-54 Street, Edson, AB T7E 1T2, Canada - e-mail: kirby.smith@gov.ab.ca

*Present address: Laboratorio de Conducta Animal, Instituto de Ecología, Universidad Nacional Autónoma de Mexico, A.P. 70-275, 04510, Mexico D.F.

Corresponding author: Alejandro Gonzalez Voyer

Received 25 January 2001, accepted 30 September 2002

Associate Editor: Harry V. Reynolds

The population dynamics of mountain goats *Oreamnos americanus* are poorly understood (Bailey 1986). Density-dependent responses to harvest or to natural declines have been reported for introduced populations (Swenson 1985, Houston & Stevens 1988, Williams 1999), but not for native populations (Hebert & Turnbull 1977, Kuck 1977, Smith 1988b). In native populations, mountain goats appear to be more sensitive to harvest than other

ungulates, likely because of poor recruitment, either-sex harvest, and high susceptibility to harvest in accessible areas (Adams & Bailey 1982, Smith 1988b, Festa-Bianchet, Urquhart & Smith 1994). In introduced populations, estimates of sustainable harvest vary from 7% to as much as 20% (Adams & Bailey 1982, Swenson 1985, Williams 1999, but see Côté, Festa-Bianchet & Smith 2001), but in native populations hunting mortality

© WILDLIFE BIOLOGY · 9:3 (2003)

appears to be additive (Hebert & Turnbull 1977, Kuck 1977), and most management agencies use more conservative harvest goals for native herds. An average harvest of 4% was allowed in Idaho, USA (Kuck 1977). During 1973-1985, some herds in Alberta were managed by harvesting up to 5% of the number seen during aerial surveys (Hall 1977, Hall & Bibaud 1978, Smith 1988b). Like other ungulates, mountain goat populations are extremely sensitive to adult female mortality (Gaillard, Festa-Bianchet & Yoccoz 1998), but because the sexes are difficult to distinguish (Smith 1988a), most jurisdictions allow either-sex harvesting (Johnson 1977, Bailey 1986). Colorado, Idaho, Montana and Washington currently have limited-entry goat seasons open for both sexes. In British Columbia, both open and limited-entry goat hunting seasons exist, depending on the vulnerability of each population (I. Hatter, pers. comm.). In Alaska, an unlimited number of permits is issued, but kills must be registered (K. Whitten, pers. comm.). Smith (1986) suggested that a 'tracking harvest strategy' was essential for management of mountain goats.

We examined data from aerial surveys of 12 native mountain goat populations in west-central Alberta to determine the impacts of harvest. Most hunted herds showed stable or increasing trends during 1973-1982, but after 1983 numbers began to decline. Harvests were substantially reduced in 1984, and hunting was closed following the 1987 season (Smith 1988b). An intensive study of mountain goat ecology was initiated in the Caw Ridge herd in 1989 (Festa-Bianchet et al. 1994), and we used data from that study to assess potential mountain goat harvest under a male-only hunting regime.

Study area

The mountain goat survey units were mountain complexes at elevations of 975-3,098 m a.s.l., north and west of Jasper National Park in west-central Alberta. This area is characterised by long cold winters and cool, wet summers. Mountain goats spent most of their time at or above the treeline (~1,700 m a.s.l.). Most populations were not accessible by motorised vehicles. Predators included wolves *Canis lupus*, cougars *Puma concolor* and grizzly bears *Ursus arctos* (Festa-Bianchet et al. 1994, Côté & Beaudoin 1997, Côté, Peracino & Simard 1997).

Methods

Annual helicopter surveys were conducted from 1973 to 2001 by flying counter clockwise around mountain

complexes above the timberline. A number of geographically distinct 'herds', separated by wide forested valleys, were censused. These 'herds' were considered discrete populations, although dispersal likely took place among them, and some may consist of two or more subpopulations. Most surveys were conducted in the first week of July after the snow had melted and nursery herds had congregated. Goats were classified as kids, yearlings and adults, both sexes pooled. After 1982, five of the 12 herds were inventoried only in alternate years. Hunting was allowed until 1987 in nine 'herds', but we classified two of these herds as non-hunted, because only one goat was ever shot in one (Sunset Peak), and none were ever taken from the other (Daybreak). Therefore seven herds were classified as hunted and five as unhunted.

Helicopter surveys detect broad long-term trends, but the proportion of goats seen during surveys shows considerable year-to-year variation (Gonzalez Voyer, Smith & Festa-Bianchet 2001). Aerial survey counts were divided into two periods for all populations: 1973-1987 (when all hunting was stopped) and 1988-2001. Linear regression analysis of total goat count over survey year was used to determine trends for each population during each of the two periods. To determine whether hunted and unhunted herds showed similar trends during the hunting period (1973-1987), we compared the slopes of the regression analyses of hunted and unhunted herds using a t-test. To determine whether harvested populations increased after the hunting closure, we compared their regression slopes before and after hunting was stopped using a one-tailed paired t-test. The use of a one-tailed test was justified since we expected harvested populations to increase following the hunting closure.

Weather can affect survival of juvenile mountain goats (Adams & Bailey 1982). Analysis of aerial surveys of a population of known composition, however, suggested that classified counts of kids and yearlings had very low accuracy (Gonzalez Voyer et al. 2001). We do not report analyses of the effects of weather or harvest regime on age ratios (Gonzalez Voyer 2000) based on the low accuracy of age classification combined with poor reliability of age ratios to assess recruitment (McCullough 1994).

A study of mountain goats was initiated at Caw Ridge in 1989, based on monitoring of marked individuals. The population had been counted during aerial surveys since 1973, but had not been hunted since 1969. The proportion of marked goats (excluding kids) on Caw Ridge increased from 72.7% in 1991 to 78.2% in 1999; therefore classified ground counts for the population were very accurate.

© WILDLIFE BIOLOGY • 9:3 (2003)

Table 1. Total number of observed goats in 12 censused herds in Alberta during 1973-2001. Herds that were harvested before 1988 are marked with an asterisk (*), and the herds were: 1) Caw Ridge, 2) Daybreak, 3) Deveber*, 4) Goat Clifs, 5) Hamell, 6) Kvass*, 7) Llama-Turret*, 8) Monoghan*, 9) Moosehorn*, 10) North Persimon*, 11) Sunset Peak and 12) Triangle*. Columns 13 and 14 give the total number for harvested and unharvested populations, respectively.

Herd														
Year	1	2	3*	4	5	6*	7*	8*	9*	10*	11	12*	13	14
1973			41			15		56		52	5	98	262	5
1974	53			23	32			64		50	31	63	177	139
1975				31	39	7	57	107	41	42	31	47	301	101
1976							35	65	29	75	16	37	241	16
1977							40	54	62	81	29	46	283	29
1978														
1979	77	109	60	20	54	14	50	50	75	63	40	80	392	300
1980	75			13	48	7	66	63	39	93		66	334	136
1981	60	43				21	107	56	50	69	36	37	340	139
1982	78	61			36				25			24	49	175
1983	76	64		13	74	13	114	25	34	34		24	244	227
1984	72	52	50	20	73	10	79	38	18	51	22	24	270	239
1985		33			56	9	64		25	33	19	16	147	108
1986	91	27	50	19	71	14	64	20	14			10	172	208
1987		32		18	98		44	36	12	38	12	13	143	160
1988	75	54	49	27		12	59		19				139	156
1989	67	42		22	45		62	43	17	53	27	6	181	203
1990	62	48	77	75	43	20	78		15				190	228
1991	47	21		48	39		79	64	1		20		144	175
1992	54	14	79			18	133		23	32		31	316	68
1993	60	7		37	71		112	74	14		20		200	195
1994	70	8	87	64	74	7	76		8	33		27	238	216
1995	76	25		86	72		83	62	8		28		153	287
1996	73	17	96	85	68	17	110		14	51		20	308	243
1997	83	27		38	80		74	87	3		22		164	250
1998	84	41	107	55	88	2	80		27	21			237	268
1999	101	18		72	60		101	58	10		23		169	274
2000		33	68	86	89	6	87		19	39		13	232	208
2001	92	26		76	55		88	72	19		7		179	256

Results

An average of 47 goats per herd per year were observed during the 29 years of surveys, ranging from two in the smallest herd to 133 in the largest (Table 1). During 1973-1987, a total of 173 goats were harvested (range: 4-42 goats/hunted herd; Table 2). When we analysed temporal trends for individual herds, 15 of 24 regressions were significant, despite the relatively short duration and missing data for herds that were not counted every year.

We found no difference in trends between hunted and unhunted herds during the harvest period (t = -0.422, df = 10, P = 0.682). When we examined the reaction of harvested populations to the hunting closure, we found a significant difference in trends suggesting that after hunting was stopped, herds generally increased (one-tailed paired t = -2.166, df = 6, P < 0.05). The overall trend for all harvested populations, calculated using the total number of goats present in the seven harvest-

Table 2. Number of goats harvested per year for seven herds during 1973-1987, and total number harvested.

				Herd			
Year	Deveber	Kvass	Llama-Turret	Monoghan	Moosehorn	NorthPersimon	Triangle
1973	3	1	0	2	0	0	8
1974	0	0	4	3	4	1	0
1975	2	2	4	3	3	5	6
1976	2	1	2	7	4	3	3
1977	1	0	5	1	3	3	0
1978	2	0	2	0	2	0	0
1979	4	0	0	0	6	0	0
1980	0	0	1	0	3	0	0
1981	2	0	7	9	4	2	0
1982	1	0	4	0	2	2	0
1983	8	0	7	1	4	0	0
1984	2	0	3	0	0	0	0
1985	0	0	0	0	0	0	0
1986	1	0	2	1	0	0	1
1987	2	0	1	0	0	0	0
Total	30	4	42	27	35	16	18

© WILDLIFE BIOLOGY · 9:3 (2003)

Table 3. Population trends expressed as the slope of a linear regression of total census size over year of count for 12 mountain goat herds in Alberta before (1973-1987) and after (1988-2001) hunting was closed. Harvested populations are marked with an asterisk (*).

Population	1973-1987	1988-2001		
Caw Ridge	2.458	2.778		
Daybreak	-8.298	-1.057		
Deveber*	0.520	3.464		
Goat Clifs	-0.677	3.159		
Hamell	3.728	2.636		
Kvass*	0.011	-0.982		
Llama-Turret*	1.929	1.257		
Monoghan*	-3.527	1.571		
Moosehorn*	-3.164	0.130		
North Persimon*	-1.431	-1.235		
Sunset Peak	-0.215	-0.929		
Triangle*	-4.587	0.096		

ed populations (see Table 1), was negative during harvest (1973-1987; b = -6.01) and positive following the hunting closure (during 1988-2001; b = 3.34).

Temporal trends varied substantially among hunted herds before and after the hunting closure (Table 3). One herd continued to decrease, another was stable while hunted and decreased after hunting was closed, two herds continued to increase and three herds increased, changing from a negative to a positive slope following the hunting closure. Unhunted herds also showed no consistent pattern: two increased both before and after 1987, one changed from a negative to a positive slope after 1987 and two continued to decrease following 1987 (see Table 3).

The negative impact of hunting on mountain goats may be lessened by male-only harvests. Data on adult sex ratios are needed to evaluate the potential for male-only harvests; however, little information is available in the literature. Adult male to female ratios in western Montana during 1971-1973 ranged within 23:100-56:100 as reported by Rideout (1974, in Rideout 1978) and Chadwick (1973, in Rideout 1978). During that period, the lowest male to female ratios followed winters with excessive snowfalls, indicating that mortality of males exceeded that of females during severe winters (Rideout 1978). Over nine years of monitoring of the Caw Ridge population, the number of males ≥ 3 years of age was consistently much lower than the number of adult females (Fig. 1). During this period, 92% of goats ≥3 years of age were marked. The few unmarked adults were seen repeatedly by experienced observers and were known individually. Their sex was confirmed by observation of testicles or presence of a nursing kid. The number of 4-year-old males recruited yearly into the population varied from one to four and averaged two. Since 1991, four goats have immigrated to Caw Ridge, all males ≥2 years old. We excluded from this calculation

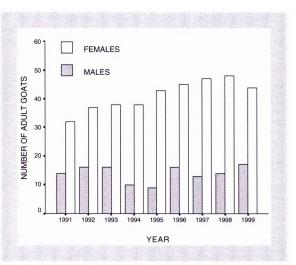


Figure 1. Number of adult (≥3 years old) male and female mountain goats in September in the Caw Ridge herd during 1991-1999.

the first two years of study because the proportion of marked adults was lower and therefore counts by sex and age class may not have been as accurate.

Discussion

Mountain goat herds reacted differently both to changes in management regimes, and there was little temporal consistency in changes in size of different herds (see Table 1). Hunting appeared to have a negative impact on some herds, but not on others. It is unlikely that hunting was the only cause of the population decline in the 1980s, because not all herds increased after hunting was stopped. These results strongly suggest that management of mountain goats must be herd-specific, as recommended by Hebert & Smith (1986).

Herd-specific factors other than hunting appeared to affect population dynamics of mountain goats. The wide variation in population trends among herds in the same geographical area suggests that factors other than weather were responsible for changes in population size, because all herds experienced the same yearly changes in weather. Other extrinsic factors that could have affected individual herds include disease, accidents, poaching and predation. We have no evidence of disease, and we recorded no mortalities due to falls or other accidents in the intensively studied Caw Ridge herd. The inaccessibility of most herds suggests that poaching was unlikely to be a problem. We know of no cases of mountain goats being shot illegally during our study. Our study area, however, has a full complement of large predators. A single predator specialising on mountain goats could have a strong impact on a herd, similar to what has been reported for bighorn sheep *Ovis canadensis* (Wehausen 1996, Ross, Jalkotzy & Festa-Bianchet 1997, Ernest, Rubin & Boyce 2002). At Caw Ridge, attacks by wolves and grizzly bears have been witnessed (Côté et al. 1997, Côté & Beaudoin 1997) and most kid mortality appears to be due to predation by wolves, grizzly bears and cougars (Festa-Bianchet et al. 1994). Predation by individual specialist predators may be density independent and may not depend on changes in predator populations, possibly explaining the unpredictable, herd-specific changes in numbers that we recorded. Because we have no data on predation for any herd other than Caw Ridge, however, our interpretation is speculative.

Females in the Caw Ridge population do not reproduce until four or five years old, and only about 50% of yearling females survive to four years (Festa-Bianchet et al. 1994). These characteristics make mountain goat populations very sensitive to harvest of adult females. Females made up at least 43% of the harvest in Alberta during 1974-1985, and the mean annual age of shot females ranged from 4.6 to 8.5 years (Smith 1988b). Most hunters probably search for a billy, but we found that adult males make up a small proportion of goat populations. Therefore, some hunters may approach a nursery herd and likely shoot the longest-horned female, thereby removing dominant females of the most productive age group (Côté & Festa-Bianchet 2001). This harvest could have strong effects on herds of 50-90 goats, that may include only 10-20 females aged ≥7 years, the age group that accounts for most recruitment (Festa-Bianchet et al. 1994, Côté & Festa-Bianchet 2001).

Our analysis suggests that hunting had a negative effect on some mountain goat herds, but also that other factors prevented or retarded population recovery after harvests ended. Closing the hunting season in 1987 was an appropriate management action, and future management of mountain goats should continue to be on a herd-specific basis. If the hunting season was to reopen, harvest should be directed to adult males. Because of the difficult field identification of goat sex, maleonly seasons have not been implemented, but hunter education could increase the proportion of males in the harvest. In British Columbia, 34-37% of goats harvested in 1980-1984 were females (Hebert & Smith 1986), and in Washington 50% of goats shot in 1970-1985 were females (Johnson 1986). In the Yukon, however, females make up less than 15% of the harvest (J. Carey, pers. comm.), suggesting that increased identification efforts can decrease female harvest.

Hunting programs that target adult males, however, must take into account the very skewed sex ratio that we observed at Caw Ridge. The population of about 100 goats only recruited two 4-year-old males a year, on average (M. Festa-Bianchet & S.D. Côté, unpubl. data). Based on those observations, a management strategy that encouraged hunters to harvest adult males should confine itself to a harvest goal of about 1% of the estimated population, assuming that removal of 50% of the yearly recruitment of adult billies would not have negative consequences over the long term. Small herds may only be able to sustain a harvest in alternate years. It would be problematic to enforce a male-only hunting season because of the difficulty of correctly identifying both sexes. Thus, a more practical management strategy would be to establish 'total' and 'female' quotas for each population. If female harvest one year exceeded the 'female' quota, hunting could be closed for the following season(s). A similar 'double-quota' system is used in Alberta to manage cougar harvests (Ross, Jalkotzy & Gunson 1996) and has recently been implemented for mountain goat seasons in Alberta.

Acknowledgements - we thank Steeve Côté, Martin Urquhart and Yanick Gendreau for their pivotal contributions to the Caw Ridge goat study. Our research received financial support from the Alberta Fish and Wildlife Division, the Natural Sciences and Engineering Research Council of Canada, the International Order of Rocky Mountain Goats, the Alberta Conservation Association, the Alberta Sport, Recreation, Parks and Wildlife Foundation, the Alberta Wildlife Enhancement Fund, the Fonds pour la formation de Chercheurs et l'Aide à la Recherche (Québec), and the Université de Sherbrooke. Many pilots and biologists assisted with aerial surveys, and we are grateful to all of them. Constructive comments by H. Reynolds, K. Whitten and S. Arthur improved an earlier version of the manuscript.

References

Adams, L.G. & Bailey, J.A. 1982: Population dynamics of mountain goats in the Sawatch Range, Colorado. - Journal of Wildlife Management 46: 1003-1009.

Bailey, J.A. 1986: Harvesting mountain goats: strategies, assumptions, and needs for management and research. - Proceedings of the Northern Wild Sheep and Goat Council. 5: 37-47.

Côté, S.C. & Beaudoin, C. 1997: Grizzly bear (Ursus arctos) attacks and nanny-kid separation on mountain goats (Oreamnos americanus). - Mammalia 61: 614-617.

Côté, S.C. & Festa-Bianchet, M. 2001: Reproductive success in female mountain goats: the influence of maternal age and social rank. - Animal Behaviour 62: 173-181.

Côté, S.C., Festa-Bianchet, M. & Smith, K.G. 2001: Com-

- pensatory reproduction in harvested mountain goat populations: a word of caution. Wildlife Society Bulletin 29: 726-730.
- Côté, S.C., Peracino, A. & Simard, G. 1997: Wolf, Canis lupus, predation and maternal defensive behaviour in mountain goats, Oreamnos americanus. Canadian Field-Naturalist 111: 389-392.
- Ernest, H.B., Rubin, E.S. & Boyce, W.M. 2002: Fecal DNA analysis and risk assessment of mountain lion predation of bighorn sheep. Journal of Wildlife Management 66: 75-85.
- Festa-Bianchet, M., Urquhart, M. & Smith, K.G. 1994: Mountain goat recruitment: kid production and survival to breeding age. - Canadian Journal of Zoology 72: 22-27.
- Gaillard, J-M., Festa-Bianchet, M. & Yoccoz, N.G. 1998: Population dynamics of large herbivores - variable recruitment with constant adult survival. - Trends in Ecology and Evolution 13: 58-63.
- Gonzalez Voyer, A. 2000: Gestion des populations de chèvres de montagne: recensements et dynamique des populations.
 M.Sc. thesis, Université de Sherbrooke, Sherbrooke, Canada, 62 pp. (In French).
- Gonzalez Voyer, A., Smith, K.G. & Festa-Bianchet, M. 2001: Efficiency of aerial censuses of mountain goats. - Wildlife Society Bulletin 29: 140-144.
- Hall, W.K. 1977: Status and management of the Rocky Mountain goat, Oreamnos americanus, in the province of Alberta. - Proceedings of the First International Mountain Goat Symposium, pp. 8-14.
- Hall, W.K. & Bibaud, J.A. 1978: Goats and their management in Alberta. - Proceedings of the Northern Wild Sheep and Goat Council 1: 142-164.
- D.M. & Smith, T. 1986: Mountain goat management in British Columbia. - Proceedings of the Northern Wild Sheep and Goat Council 5: 48-59.
- Hebert, D.M. & Turnbull, W.G. 1977: A description of southern interior and coastal mountain goat ecotypes in British Columbia. Proceedings of the First International Mountain Goat Symposium, pp. 126-146.
- Houston, D.B. & Stevens, V. 1988: Resource limitation in mountain goats: a test by experimental cropping. Canadian Journal of Zoology 66: 228-238.

- Johnson, R.L. 1977: Distribution, abundance and management status of Mountain Goats in North America. - Proceedings of the First International Mountain Goat Symposium, pp. 1-7
- Johnson, R.L. 1986: Mountain goat management in Washington.
 Proceedings of the Northern Wild Sheep and Goat Council 5: 60-62.
- Kuck, L. 1977: The impact of hunting on Idaho's Pahsimeroi mountain goat herd. - Proceedings of the First International Mountain Goat Symposium, pp. 114-125.
- McCullough, D.R. 1994: What do herd composition counts tell us? Wildlife Society Bulletin 22: 295-300.
- Rideout, C.B. 1978: Mountain goat. In: Big Game of North America: Ecology and Management. Stackpole Books, Harrisburg, pp. 149-159.
- Ross, P.I., Jalkotzy, M.G. & Festa-Bianchet, M. 1997: Cougar predation on bighorn sheep in southwestern Alberta during winter. - Canadian Journal of Zoology 74: 771-775.
- Ross, P.I., Jalkotzy, M.G. & Gunson, J.R. 1996: The quota system of cougar harvest management in Alberta. Wildlife Society Bulletin 24: 490-494.
- Smith, B.L. 1988a: Criteria for determining age and sex of American mountain goats in the field. - Journal of Mammalogy 69: 395-402.
- Smith, C.A. 1986: Rates and causes of mortality in mountain goats in southeast Alaska. - Journal of Wildlife Management 50: 743-746.
- Smith, K.G. 1988b: Factors affecting the population dynamics of mountain goats in west-central Alberta. Proceedings of the Northern Wild Sheep and Goat Council 6: 308-329.
- Swenson, J.E. 1985: Compensatory reproduction in an introduced mountain goat population in the Absaroka mountains, Montana. Journal of Wildlife Management 49: 837-843.
- Wehausen, J. 1996: Effects of mountain lion predation on bighorn sheep in the Sierra Nevada and Granite Mountains of California. - Wildlife Society Bulletin 24: 471-479.
- Williams, J.S. 1999: Compensatory reproduction and dispersal in an introduced mountain goat population in central Montana. - Wildlife Society Bulletin 27: 1019-1024.