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CLIFFORD G RICE

*Wildlife Program, Washington Department of Fish and Wildlife, 600 Capitol Way N, Olympia,
WA 98501 USA*

DON GAY

*Mt. Baker Ranger District, Mt. Baker-Snoqualmie National Forest, 810 State Route 20, Sedro Woolley,
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ABSTRACT—Understanding population dynamics and historical declines for Mountain Goats (*Oreamnos americanus*) is challenging due to sparse data. Speculations regarding the cause of population declines have included habitat change, predation, disease, parasites, recreation impacts, and excessive harvest. Managing for recovery requires an understanding of the relative importance of the factors causing population declines. Using records of Mountain Goat harvest in selected areas of Washington State (USA), we modeled population trajectories for 7 areas with a stage-structured matrix model and compared these trajectories to recent population estimates. Our results supported the hypothesis that observed declines can be attributed primarily to the effects of harvest. We also assessed the level of harvest likely to be sustainable for Mountain Goat populations of varying sizes. Our results were sensitive to vital rates used in the model and were also influenced by population size and the proportion of harvest that is male. Generally, populations of <50 individuals should not be harvested, but larger populations (such as >100) or those where the proportion of males in the harvest is high (90 to 100%) may sustain $\leq 4\%$ harvest. However, due to expected variation of vital rates among populations and years, declines may still occur with harvest at these levels and continued population monitoring is essential for hunted populations.

Key words: Cascade Range, harvest, Leslie matrices, management, Mountain Goats, *Oreamnos americanus*, population dynamics, population models, Washington

Understanding the dynamics of wild populations has been a central pursuit in wildlife management. Given intensive human use of many wild populations, detailed knowledge of population and ecological processes is crucial for management and conservation of these populations (Gordon and others 2004). The ecology of Mountain Goats (*Oreamnos americanus*) is poorly understood compared with that of other ungulates in North America (Côté and Festa-Bianchet 2003). Because of the high public profile of the species and strong interest in hunting Mountain Goats among sportsmen and by Indian tribes, a better understanding of the factors determining population levels and particularly harvest is essential.

In Washington State, Mountain Goats are native throughout the Cascade Range and were introduced in the Olympic Mountains during the 1920s (Houston and others 1991). Evident de-

clines over the past 50 y have raised concerns about the management of this species. In 1961, the Mountain Goat population in the Cascade Range was thought to be about 8500 (excluding Mount Rainier National Park and Yakama Indian Nation lands). More recent estimates are around 3700 (4000 statewide minus 300 for the Olympics; Côté and Festa-Bianchet 2003; Happe and others 2004). However, these declines (and harvest) have been far from uniform. Whereas some areas retain substantial populations and populations are recovering in others, many areas have only remnant populations with indications of declines of $\geq 90\%$ over the last 50 y.

Mountain Goat populations can be sensitive to overharvest (Côté and Festa-Bianchet 2003; Hamel and others 2006), and the acceptable harvest from native populations may be as low as 1% (Hamel and others 2006). Washington State's guidelines currently advocate permitting

harvest of 4% of a population with a minimum population size of 50 animals (Washington Department of Fish and Wildlife 2003).

Although overharvest certainly may have played a role in apparent declines, other factors also may have been responsible. Many possible contributing factors have been reviewed by Côté and Festa-Bianchet (2003) and include disease and parasitism, disturbance caused by recreational activities, winter habitat degradation through timber harvest, predation, and loss of habitat due to conifer intrusion into alpine meadows as a result of fire suppression. Understanding the importance of these factors in population declines is a prerequisite for effective management with the goal of recovery of Mountain Goat populations.

Factors affecting Mountain Goat populations undoubtedly vary temporally and geographically, consistent with variable population trends throughout their range in Washington. However, evidence for most factors is anecdotal and not subject to retrospective analysis. Harvest effects, however, can be readily examined through modeling. The use of matrix models (Caswell 2001) is a common means of integrating information on vital rates (fecundity and survival) in analyzing population dynamics, and has application for both retrospective and prospective analysis. Following the approach that Hamel and others (2006) used for Mountain Goat populations in Alberta, we developed a generalized stage-structured matrix model to examine the hypothesis that past harvest has effected Mountain Goat populations in Washington, and to identify sustainable harvest levels.

METHODS

Study Area

Mountain Goats in the Cascade Range of Washington range in elevation from about 1150 to 2100 m in summer to about 800 to 1750 m in winter (C Rice, unpubl. data). These areas are characterized by Montane Mixed Conifer Forest, Eastside Mixed Conifer Forest, Lodgepole Pine Forest and Woodlands, Subalpine Parkland, and Alpine Grasslands and Scrublands (Johnson and O'Neil 2001). Suitable habitat for Mountain Goats is patchily distributed from the Washington-British Columbia border southward to the slopes of Mt. Adams in south-central Washington.

Harvest Records

Permit only hunting for Mountain Goats (1 Mountain Goat/permit) was established in Washington in 1948, and in 1957 permits were allocated according to 10 management units (Johnson 1983). These units were increasingly subdivided to more equally allocate hunting through 1981 when there were 40 units. Closure of units and reduced permits in open units continued from 1981 to the present.

Based on mandatory hunter reports, harvest records for Mountain Goats in Washington were obtained from 4 sources in 4 formats. From 1948–1970, reports on file with the Washington Department of Fish and Wildlife (WDFW) listed each Mountain Goat harvested by place name and drainage (along with Mountain Goat hunting unit). We used place names to determine harvest localities because unit boundaries for this period are not known. To assign coordinates to each harvest, the place names were matched against a geographic place name list (US Board on Geographic Names, undated). Where duplicates of place names occurred, the appropriate name was selected based on the watershed of the harvest report. If the place name was a creek or river, the coordinates of the headwaters were used. Based on these locations, each harvest was assigned to the appropriate hunting unit.

Mountain Goat harvest from 1971–1981 was obtained from Johnson (1983), who summarized harvest by hunting unit. For 1982–2004, harvest was recorded by unit in WDFW databases.

Population Models

Recently, Hamel and others (2006) presented a model of Mountain Goat populations based on data collected at Caw Ridge, Alberta, Canada. This was a stage-structured matrix model with 12 stages, 6 for each sex (ages 0, 1, 2, 3–4, 5–8, and ≥ 9 y). Hamel and others (2006) estimated vital rates (fecundity and survival) and their variability within and among years by tracking observations of marked individuals from 1993 to 2003. The model was implemented in RAMAS Metapop (Akçakaya 2002).

We followed the structure of the Hamel and others (2006) model because it was the only published assessment incorporating annual variation in vital rates for Mountain Goats. Because of the great geographic separation as

well as climatic and ecological differences between Caw Ridge and the Cascade Range of Washington, we modified both the vital rates and their variability for our basic model by averaging rates reported in other studies. There has been no research on vital rates of Mountain Goats in the Washington Cascade Range, but data are available for an introduced population of Mountain Goats on the Olympic Peninsula of Washington (Stevens 1983; Houston and Stevens 1988).

The population dynamics of introduced Mountain Goat populations often differ from native populations (Côté and Festa-Bianchet 2003), although how long this difference persists is unclear. We found no other reports of Mountain Goat fecundity apart from that of Bailey (1991) for an introduced population in Colorado. Due to the milder climate, it is quite possible that Mountain Goats in the Cascade Range have higher vital rates than those at the interior and higher latitude Caw Ridge study area, so we averaged the rates from Caw Ridge (Hamel and others 2006), Colorado (Bailey 1991), and the Olympics (Houston and Stevens 1988); but we did not include the "off-Klahane" estimates from the Olympic Mountains (Stevens 1983:85) because they likely reflected early post-colonization demographics. We did not attempt to adjust for slightly different age groupings used by Bailey (1991), but directly applied his rates for 3, 4-9, and 10+ y to our basic model stages of 3-4, 5-8, and ≥ 9 y. Because Bailey (1991) did not specify sex of offspring, we partitioned rates according to the ratio observed at Caw Ridge for each female age class.

Cascade Range Mountain Goat populations are likely intermediate between interior and coastal ecotypes (Gilbert and Raedeke 1992). Consequently, we averaged survival rates from the Caw Ridge model (Hamel and others 2006) with those from an earlier study (1988-1992) on Caw Ridge (Smith and others 1992, for kids), Colorado (Adams and Bailey 1982, kids; Kohlmann and Bailey 1991, kids and adults), southeast Alaska (Nichols 1980, kids and yearlings; Smith 1986, yearlings and adults, harvest excluded), and the British Columbia Coast Range (Dane 2002, kids and yearlings). Except for Hamel and others (2006), these authors provided survival estimates pooled across sexes. To partition the reported rates between

sexes, we allocated the pooled estimate to each sex so that the male:female ratio remained constant and equal to that of the Caw Ridge model population (Appendix A). For comparisons among models with different vital rates, we used the finite rate of population change (λ) calculated by RAMAS.

For each stage, we added the variance among vital rate estimates given above to the inter-annual variance (environmental stochasticity) reported by Hamel and others (2006) so that the variation in our basic model approximated pooled process and sampling variation. Thus, this variance represented the total uncertainty about vital rates for simulated populations.

Our models included initial population, vital rates, variation in vital rates (environmental stochasticity), uncertainty of vital rate estimation, demographic stochasticity, and harvest. Like Hamel and others (2006), we did not include density dependence (Côté and Festa-Bianchet 2001; Côté and others 2001), nor did we attempt to evaluate small population impacts such as inbreeding depression (O'Grady and others 2006), Allee effects (Courchamp and others 1999), or metapopulation dynamics. Although immigration and emigration of males has been reported (Stevens 1983; Côté and Festa-Bianchet 2001) and was observed in our collared Mountain Goats in Washington ($n = 2$, CG Rice, unpubl. data), these movements of males would have little impact on population models. Immigration and emigration by females is rare: 3 incidents in about 81 Mountain Goat years of monitoring in Alberta (Festa-Bianchet and Côté 2008); none in the Olympics (Stevens 1983); and none among our collared Mountain Goats in Washington ($n = 31$). Thus demographic impacts of movements beyond modeled population boundaries can be considered insignificant.

Each population was simulated with 1000 random replicates from vital rates by RAMAS Metapop with environmental variation drawn from a lognormal distribution. Each model run was initialized to a stable age distribution and demographic stochasticity was included. Several of the models had small ending populations (<50 individuals), producing model results that were not normally distributed and with average population sizes consistently much higher than the median and often above the 75th percentile.

TABLE 1. Alternate Mountain Goat population model scenarios showing the area modeled (Model), parameter that was changed (Parameter), values that were used in the scenarios (Parameter values), and the reason for considering the alternate scenario (Rationale). Proportional vital rates were applied to both fecundity and survival.

Model	Parameter	Parameter values		Rationale
		Low	High	
Mt. Baker	Initial population	420	650	Low likelihood of initial population having supported reported harvest
Mt. Baker	Proportional vital rates	1.000	1.023	Low likelihood of initial vital rates having supported reported harvest
Penders Canyon	Harvest	78	125	Uncertainty about fall distribution of population estimated in winter
Falls Creek	Harvest	105	172	Uncertainty about fall distribution of population estimated in winter
Falls Creek	Proportional vital rates	1.000	1.045	Low likelihood of initial population having supported reported harvest
East Stevens Pass	Initial population	250	300	Low likelihood of initial population having supported reported harvest
East Stevens Pass	Proportional vital rates	1.000	1.014	Low likelihood of initial vital rates having supported reported harvest
Snoqualmie	Initial population	450	900	Low likelihood of initial population having supported reported harvest
Goat Rocks	Initial population	600	900	Low likelihood of initial population having supported reported harvest
Goat Rocks	Proportional vital rates	1.000	1.015	Low likelihood of initial vital rates having supported reported harvest

Consequently, we used the median of the model replicates as our measure of central tendency. Because RAMAS reports these percentiles only for the final year of the simulation, we ran each simulation multiple times, ending it at 5-y increments over the model period.

In addition to our basic models for each area, we examined a number of scenarios varying the initial population, estimated harvest, or vital rates depending on the uncertainties applying in each case (Table 1). In several of our simulations, population trajectories were considerably lower than corresponding population estimates, and in several models most replicates reached zero while considerable harvest occurred in subsequent years. Because of the potential for inaccuracies in initial population estimates and geographic variation in vital rates, we estimated, through iteration, both the increase in initial population and the proportional increase (Akçakaya 2002) in vital rates (factor applied to both fecundity and survival) for which the median of replicates approximated recent population estimates.

Harvest recorded or estimated (see below) for each area was assigned in the model according to the historic statewide harvest age distribu-

tions, 1959–1962 (Johnson 1983:23, kids: 0%; yearlings: 10%; age 2: 11%; age 3–4: 34%; age 4–8: 38%; and age ≥9 y: 7%; *n* = 289). Because the historic harvest distribution by sex was close to 1:1 (1948–1981, 49% males, Johnson 1983:63), harvest was allocated equally between sexes for each stage.

We selected populations for modeling (Fig. 1, Table 2) based on 3 factors: 1) the existence of historic and recent population estimates for that area; 2) ability to ascribe harvest to that area over the model period; and 3) large or moderate difference between current and historic population status.

For initial population sizes, we used approximations made by WDFW in 1961 (Wadkins 1962; reproduced by Johnson 1983) for most models. These were extrapolations from ground counts and may be considered rough estimates. Consequently, in some cases we modeled scenarios with higher initial populations when it appeared that the respective populations could not have supported the reported harvest. In some cases (for instance Mt. Baker, Goat Rocks), the 1961 areas were larger than that covered by the model. For these we reduced the 1961 estimate by an amount commensurate with our

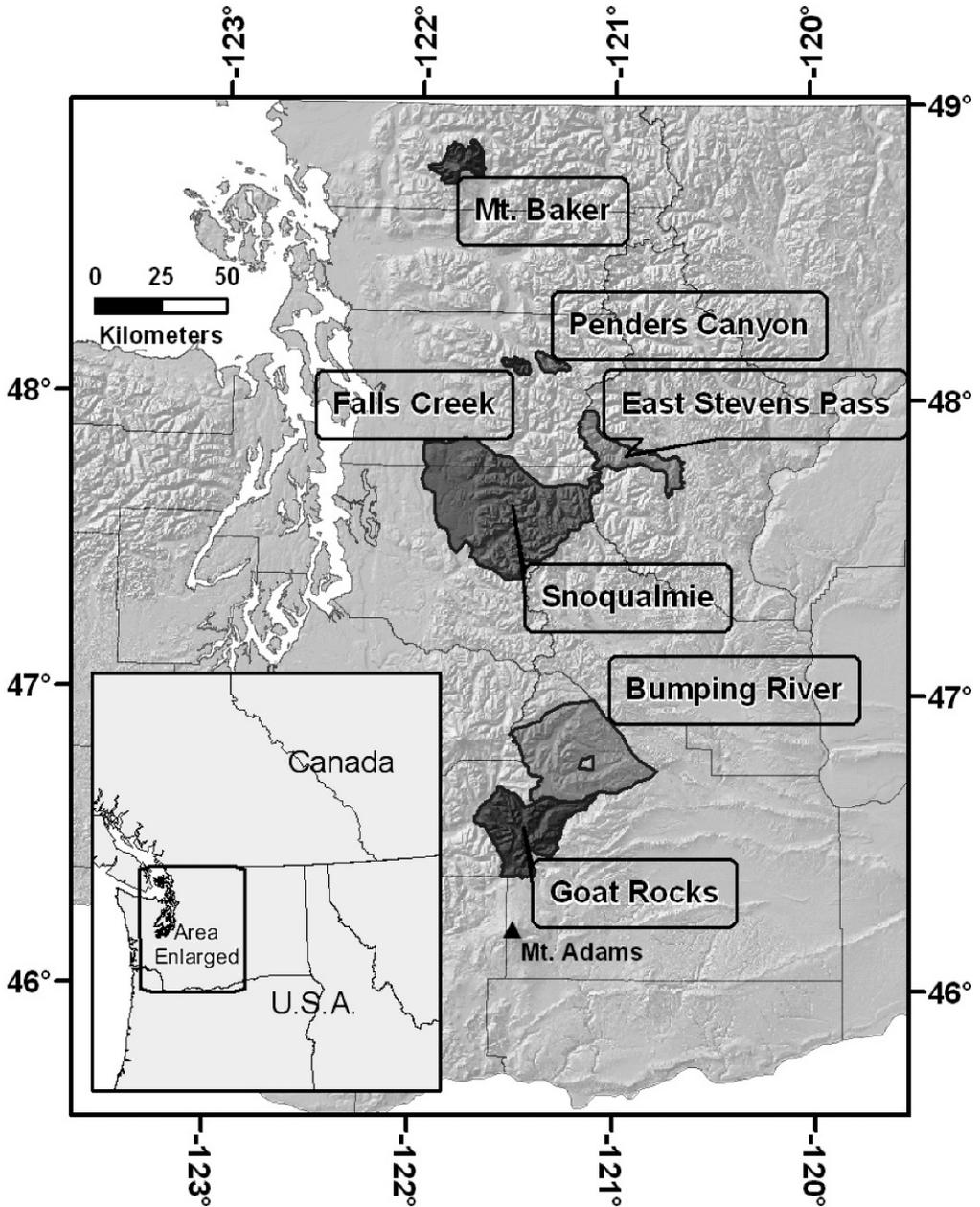


FIGURE 1. Mountain Goat population model locations in Washington State.

knowledge about current and past abundances of Mountain Goats in the respective areas. Historic population estimates for the Penders Canyon and Falls Creek models were based upon notes on Mountain Goats observed by Art Ryals during winter visits (1946–1983). These were compiled into minimum population esti-

mates by Reed (1983, and also reported by Johnson 1983). With the exception of the Snoqualmie model, recent population estimates for all models were based on helicopter surveys (CG Rice, unpubl. data) for which we applied a preliminary sightability correction based on group size (Steinhorst and Samuel 1989):

TABLE 2. Description of areas in Washington selected for Mountain Goat population models.

Model	Area ¹ Above 1500 m	Estimated Population			Harvest reported	Total harvest	Removals	Factors in selection
		1946	1961	2005				
Mt. Baker	105	385–420		420	1964–1995	329		Recovered from substantial decline
Penders Canyon	18	154	72	8	1949–1991	78–125		Large decline, good historic popula- tion records
Falls Creek	3	73	31	5	1949–1994	105–172		Large decline, good historic popula- tion records
East Stevens Pass	62		250	34	1962–1990	173	27	Large decline, good harvest records
Snoqualmie	144		475	≈50	1961–1998	757		Large decline, good harvest records
Bumping River	398		475	100	1957–2005	347		Moderate decline
Goat Rocks	257		600	340	1951–2005	661		Moderate decline

¹ km².

$$\text{Adjusted Estimate} = \frac{1}{1 + e^{0.9207 - 0.3885 \text{ Group Size}}} \text{Group Size}$$

For Snoqualmie, we have no recent population estimates, but judging from incidental observations by other resource agency personnel, a total of 50 animals was judged to be a reasonable rough estimate for this large area.

For 1948–1970, estimated Mountain Goat harvest consisted of all kills with place names in each model area (Fig. 1). Estimating harvest for 1971–2004 was more difficult for models whose area boundaries did not correspond to those of 1 or more hunting units because unit boundaries changed or because population estimates were for only a portion of the unit they were in. In such cases, we assumed that the proportion of harvest in the modeled section of the unit was the same during 1971–2004 as it was during 1948–1970 and prorated the harvest from the unit(s) overlapping the model area according to the proportion of harvest in 1948–1970 that occurred in the area being modeled. For example, for 1971–1979, the Goat Rocks Unit (then called the Packwood Unit) included the Smith Creek Unit. In 1948–1970, of the 300 Mountain Goats harvested with place names in the Packwood Unit, 287 (95.7%) had place names within the Goat Rocks Unit and 13 (4.3%) with place names in the Smith Creek Unit. So, for 1971–1979,

the Goat Rocks harvest estimate was set equal to the 0.957 × the Packwood Unit estimate. There was additional uncertainty about the harvest for the Penders Canyon and Falls Creek models because the population estimates were based on winter counts, and distribution of these animals during the fall hunting season was not precisely known. Based on the movements observed by 2 GPS-collared Mountain Goats in or nearby to these areas and a subjective assessment based on terrain and the movement patterns of 44 other GPS-collared Mountain Goats elsewhere (CG Rice, unpubl. data), we developed conservative and liberal scenarios consisting of nearby and slightly more distant locations to estimate harvest according to the above procedures.

To assess levels of harvest that may be considered sustainable, we developed general models where we considered harvest of 0 to 4% of a Mountain Goat population with the proportion of that harvest being male as 0.50, 0.75, or 0.90. We did this because although historic harvest was about 50% male, recent harvest has strongly favored males (of the 72 Mountain Goats harvested 2002–2006, 89% were males), apparently in response to WDFW efforts to encourage Mountain Goat hunters to kill males. Because vital rates evidently vary geographically (Table 3) and between native and introduced populations, we considered 4 scenarios for vital rates: 1) average vital rates (as above); 2) minimum vital rates for each stage; 3) maximum vital rates for each stage from studies

TABLE 3. Fecundity (a) and survival (b) values used to calculate mean values used in the model. Standard errors are given in parentheses for mean values and for Hamel and others (2006). In the 2nd column, N = native Mountain Goat population, I = introduced population. In the survival table, Y1 = yearling. For all studies except Hamel and others (2006), survival was pooled across sexes within stages; here it has been partitioned by the male:female ratio for each stage from the Caw Ridge model population.

Study		Fecundity (kids per female in stage)											
		Female kids					Male kids						
		2	3-4	5-8	9+	2	3-4	5-8	9+				
Hamel and others 2006 (S.E.)	Caw Ridge, AB (N)	0.021 (0.050)	0.265 (0.166)	0.402 (0.114)	0.257 (0.076)	0.019 (0.065)	0.194 (0.165)	0.345 (0.101)	0.398 (0.068)				
Bailey 1991	Colorado (I)	0.000	0.300	0.382	0.208	0.000	0.220	0.328	0.322				
Houston & Stevens 1988	Olympics, WA (I)	0.000	0.333	0.416	0.548	0.000	0.333	0.286	0.110				
Mean (S.E.)		0.007 (0.051)	0.300 (0.169)	0.400 (0.115)	0.338 (0.199)	0.006 (0.066)	0.249 (0.181)	0.320 (0.106)	0.277 (0.164)				

Study		Survival to next stage										
		Females in stage					Males in stage					
		Y1	2	3-4	5-8	9+	Kid	Y1	2	3-4	5-8	9+
Smith 1986	SE Alaska (N)	0.778	0.992	0.993	0.994	0.714	0.600	0.648	0.988	0.986	0.984	0.580
Kohlmann & Bailey 1991	Colorado (I)	0.600	0.916	0.931	0.942	0.911	0.600	0.600	0.884	0.862	0.844	0.869
Hamel and others 2006 (S.E.)	Caw Ridge, AB (N)	0.619 (0.129)	0.852 (0.137)	0.805 (0.062)	0.944 (0.048)	0.866 (0.084)	0.619 (0.129)	0.765 (0.201)	0.729 (0.185)	0.847 (0.104)	0.849 (0.093)	0.803 (0.284)
Dane 2002	BC Coast Range (I)	0.680	0.778	0.580	0.577	0.570	0.680	0.648	0.677			
Nichols 1980	SE Alaska (N)	0.580	0.797	0.580	0.577	0.570	0.580	0.677				
Smith and others 1992	Caw Ridge, AB (N)	0.577	0.570	0.570	0.570	0.570	0.577	0.577				
Adams & Bailey 1982	Colorado (I)	0.604	0.801	0.904	0.960	0.830	0.604	0.684	0.867	0.899	0.892	0.751
Mean (S.E.)		0.604 (0.135)	0.801 (0.157)	0.904 (0.166)	0.960 (0.073)	0.830 (0.133)	0.604 (0.135)	0.684 (0.209)	0.867 (0.226)	0.899 (0.129)	0.892 (0.123)	0.751 (0.322)

a.

b.

of native populations; and 4) maximum vital rates for each stage from all studies.

We modeled this harvest by first calculating the probability of harvest from each increment of 50 animals in a population as $50 \times \text{percent harvest}/100 \times \text{proportion of harvest male (or female)}$. So, for each 50 animals in a population exposed to 3% harvest, of which 0.9 were male, the initial estimated harvest would be 1.35 males and 0.15 females. This estimated harvest was rounded to the nearest integer to obtain the assigned harvest, with the difference between the estimated harvest and assigned harvest accumulated in successive years. So, with 1.35 males harvested/year, assigned harvest in year 1 would be 1. The estimated male harvest for year 2 would be $1.35 + 1.35 - 1 = 1.70$, yielding an assigned harvest of 2. The estimated harvest for year 3 would be $1.35 + 1.70 - 2 = 1.05$, yielding an assigned harvest of 1. For each sex, the assigned harvest was randomly selected from stages with ages ≥ 2 y. Initial populations were set at 50, 100, 200, 300, and 500, representing the range of population sizes over which harvest would likely be applied, and simulations were run for 10 y.

Sex-biased harvest was expected to affect males and female stages differently. To assess these effects, as well as those for the whole population, we saved the RAMAS final stage abundances for each replicate and evaluated the probability that the population was stable or increasing, whether the female stages were stable or increasing, and changes in the sex ratio of adults from these results.

When developing some of the population models and interpreting the results, we inspected the movements of 46 Mountain Goats throughout the Cascade Range which were fitted with GPS collars and had fix records longer than 10 mo between September 2002 and October 2007. The mean duration of tracking was 678 d (range 249 to 1535 d). The total of 138,846 fixes had intervals of 3 h (85.7%), 5 h (10.0%), or 12 h (4.3%).

RESULTS

Harvest

Of the 4719 harvest reports from 1948–1970, 2.5% did not report a location, 3.4% of the place names could not be matched meaningfully with a place name in the geographic name database, and

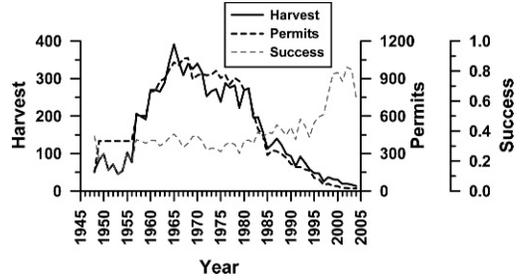


FIGURE 2. History of Mountain Goat harvest permits and success rate (harvest/permits) in Washington, 1948–2004.

0.8% matched with locations outside Mountain Goat range or in Mount Rainier or Olympic National Parks. This yielded a total of 4373 harvest reports that could be assigned to a meaningful location (93% of all reported harvest).

Annual permits issued and total reported harvest of Mountain Goats in Washington was low (<100) before 1955, then harvest increased to between 250 and 400 animals in the 1960s and 1970s (Fig. 2). There was a substantial reduction in permits and harvest in the early 1980s, after which both steadily declined.

Models

General.—The average vital rates were often quite similar to those in the Caw Ridge model (Hamel and others 2006) with a few exceptions (Table 3, Appendix B). These exceptions were for age ≥ 9 y females (production of female kids was higher and production of male kids was lower than at Caw Ridge), and for age 3–4 y females (production of kids of both sexes was slightly higher). Survival of 2-y-olds of both sexes was lower in our basic model, while that of 3–4-y-olds was higher (Table 3). For our basic model, λ was 1.041 compared with 1.024 for the Caw Ridge model. Our basic model had higher standard deviations around the estimates than the Caw Ridge model (Table 3) due to the added component of sampling error, and this difference varied considerably among stages. Overall, variation (expressed as the square root of the sum of all variances) was 29% higher than for Caw Ridge in our basic model for reproduction, and 12% higher for survival.

Individual models.—The median trajectories for models with harvest indicated declining popu-

lations, whereas those without harvest indicated increasing populations with 1 exception; the Falls Creek model with average vital rates which declined from 70 to 20 animals over the modeled period. Larger populations (250 to 900 animals) without harvest approximately doubled with average vital rates, whereas the Penders Canyon population increased only slightly from 150 to 164 animals.

With an initial population of 420 animals and average vital rates, the Mt. Baker model with harvest declined to about 20 animals by 1995 and remained low thereafter (Fig. 3). With an initial population of 650 animals, the median was near recent estimates (Fig. 3). Alternatively, proportional vital rates of 1.023 also produced the median near recent estimates.

For Penders Canyon, populations under both conservative and liberal scenarios showed steady decline over the model period, although the modeled populations tended to remain higher than population estimates (Fig. 3). Notably, the population estimates declined from 1946–1956, whereas modeled populations tended to remain near constant until the onset of regular harvest in 1964.

Modeled Falls Creek populations under both conservative and liberal scenarios generally corresponded to population estimates prior to 1970, after which they declined much more than population estimates shown in Fig. 3. Increasing vital rates by 1.045 yielded median population levels corresponding to recent surveys, but the levels remained well above all earlier counts.

Given an initial population of 250 animals, the East Stevens Pass models yielded median population levels consistently below later population estimates shown in Fig. 3. With a supposed initial population of 300 animals, modeled populations were nearly centered on later estimates, as was true with proportional vital rates of 1.014.

With an initial population of 450 animals, the Snoqualmie unit showed a precipitous decline, with the median trajectory reaching zero in 1981, well before harvest ended (Fig. 3). An initial population of 900 animals appeared to be more realistic, yielding a median final population of 51 animals. No reasonable proportional vital rates adjustment (that did not bring survival up to 1.0 for several stages) produced a median final population near 50 animals.

The median of population trajectory in the Bumping River Unit declined steadily. The median at the end of the modeled period corresponded roughly to recent population estimates from helicopter surveys as shown in Fig. 3.

The Goat Rocks modeled populations tended to decline with the median well below recent population estimates (Fig. 3). Increasing the initial population to 900 animals brought the median up to recent estimates as did a proportional vital rate of 1.015.

General models.—Without harvest, λ for the 4 scenarios were 0.958 for minimum vital rates, 1.041 for average vital rates, 1.084 for maximum vital rates for native populations, and 1.137 for maximum vital rates for all estimates. With minimum vital rates, populations had low probabilities of being stable or increasing regardless of population size or harvest rates (Fig. 4). For average vital rates, the probability of being stable or increasing increased in a nonlinear fashion with population size and percent of harvest that was male, and decreased with percent harvest (Fig. 4). For populations of 50 animals, the probabilities of being stable or increasing were below 0.50 for all average vital rate scenarios, but for larger populations this threshold was achieved for greater levels of percent harvest as the percent of harvest that was male increased (Fig. 4). For maximum vital rates from native populations, similar trends in the probability of being stable or increasing occurred, but the probabilities were higher. Given maximum vital rates, populations of all sizes and harvest scenarios had a high probability of being stable or increasing (Fig. 4). When considering only female stages, the probability of being stable or increasing was slightly higher than that of the whole population when harvest was 50% male. When harvest was 90% male, there was virtually no effect of harvest level on the probability of female stages being stable or increasing at 0.50, but there was some evidence for an effect at higher probabilities of being stable or increasing (Fig. 4).

Unlike population trajectories, the adult sex ratio was not strongly affected by population size, especially for populations ≥ 100 animals (Fig. 5), and the proportional change in sex ratio was similar among vital rate scenarios. In this

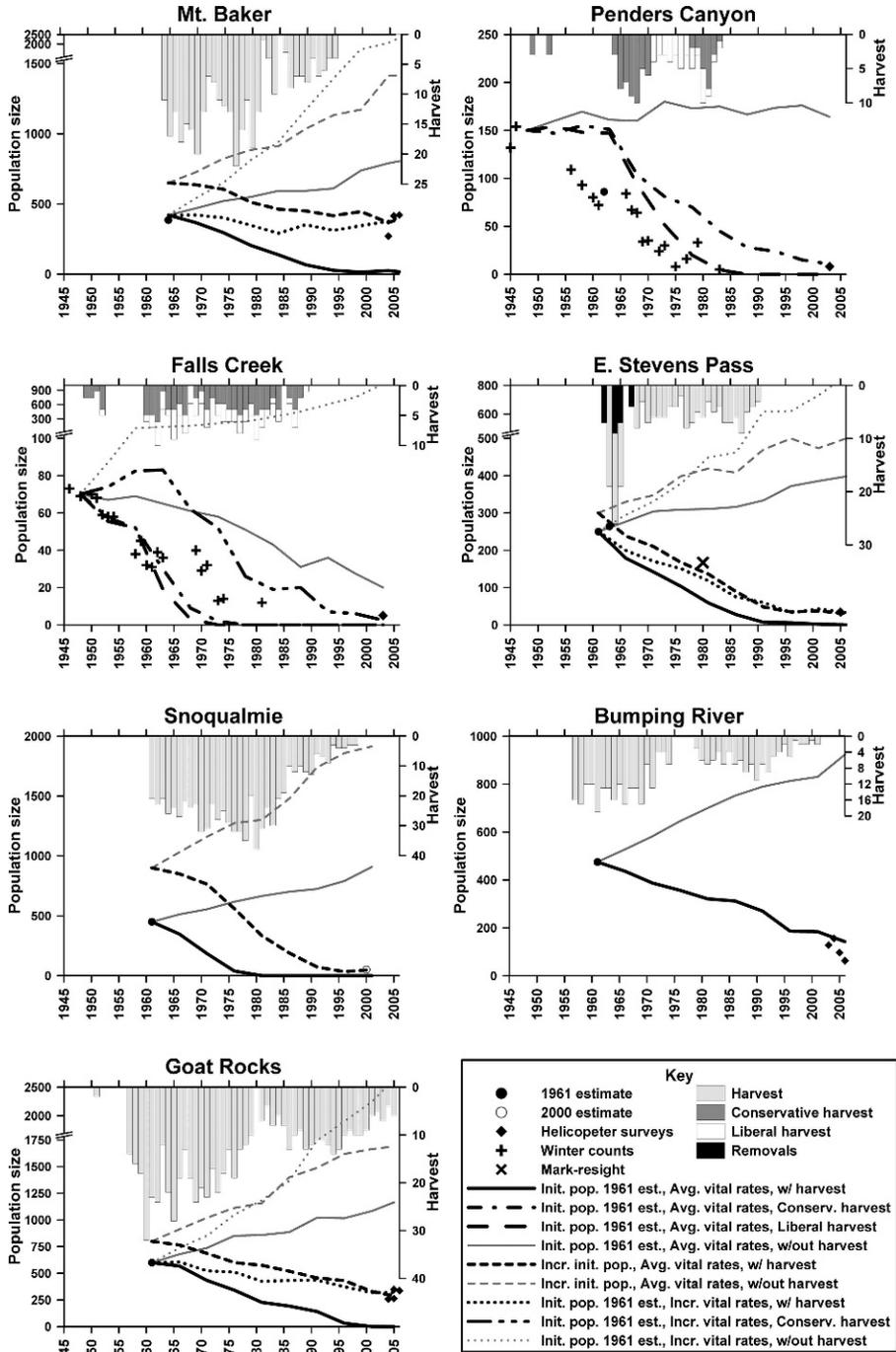


FIGURE 3. Mountain Goat median population model trajectories for 7 areas in Washington with and without harvest referenced against population estimates from 1961 Washington Department of Fish and Wildlife Estimates (all areas), 2000 estimate (Snoqualmie), helicopter surveys (all areas but Snoqualmie), Winter counts (Penders Canyon and Falls Creek), and mark-resight estimate (East Stevens Pass). Abbreviations: Init. = Initial; pop. = population; est. = estimate; Avg. = Average; w/ = With; Conserv. = Conservative; w/out = Without; Incr. = Increased. Values for increased initial populations and vital rates are in Table 1.

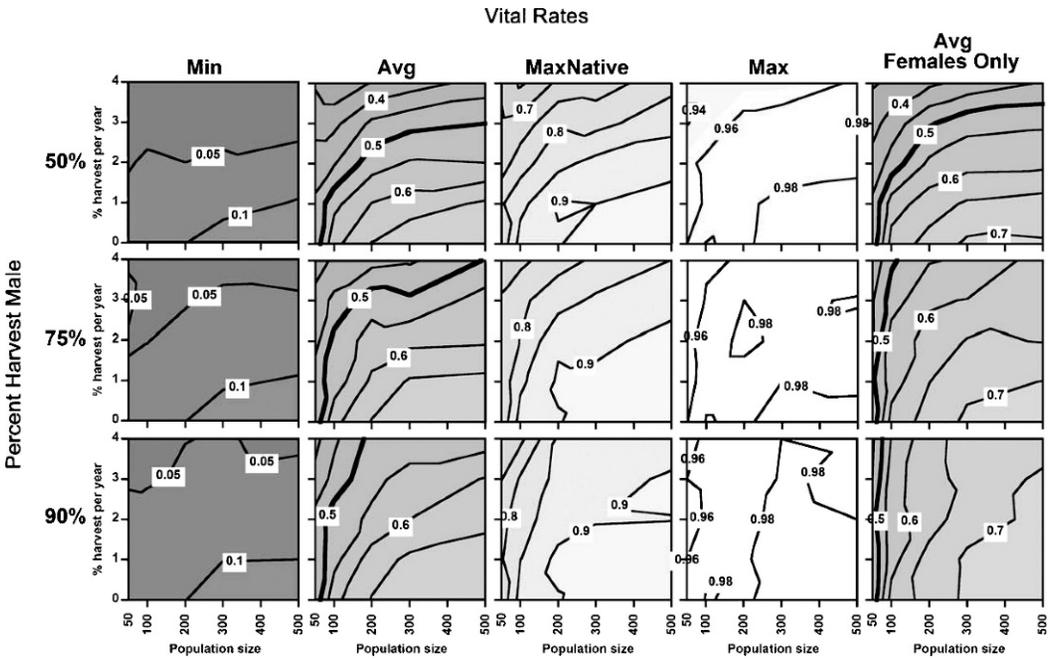


FIGURE 4. Contour graph of the probability of a Mountain Goat population remaining stable or increasing for all stages and female stages only (Avg Females Only) given: 1) the proportion of the harvest that is male, 2) population size, and 3) percent harvest for vital rates that were minimum (Min), average (Avg), the maximum for native populations (MaxNative), and maximum for all populations (Max).

context, compared with no harvest, at 4% harvest the ratio of males:females was about 20% less when the harvest was made up of 50% males, 45% less when the harvest was 75% male, and 60% less when the harvest was 90% male. Likewise, the proportion of males in each adult male stage was similar among vital rate scenarios and population sizes, but changed with percent harvest and percent of harvest that was male (Fig. 6). For example, for average vital rates with 50% of the harvest male (M), declines in the older stages (5–8 y-M and 9+ y-M) with increasing percent harvest were moderate as were increases in the younger stages (2 y-M and 3–4 y-M). These differences were much greater with 90% of the harvest male. With 4% harvest, the proportion of males in the oldest male stage (9+ y-M) declined to about 50% of that with no harvest, while males 5–8-y-old declined by about 30%. Males 3–4-y-old increased by about 16% of that with no harvest, and the proportion of youngest adult males (stage 2 y-M) approximately doubled when compared with 0% harvest (Fig. 6).

DISCUSSION

General Comments

Given the limited information on vital rates for Mountain Goats, we included estimates from introduced populations when computing our average vital rates. Notably, for survival of 2 out of 3 of the adult female stages, the highest values were from native populations (Smith 1986). Adult female survival had the highest elasticities in the Hamel and others (2006) model, so it is not surprising that the λ for our basic model was only slightly higher. Because we did not have vital rate estimates from Washington, our basic model reflects all available estimates. As such, it has general applicability and is suitable for modeling Mountain Goat populations wherever local estimates are not available.

Although density dependence has been described in several large herbivores as delayed primiparity and increased juvenile mortality (Festa-Bianchet and others 2003), this has not been described in Mountain Goats. In fact, no

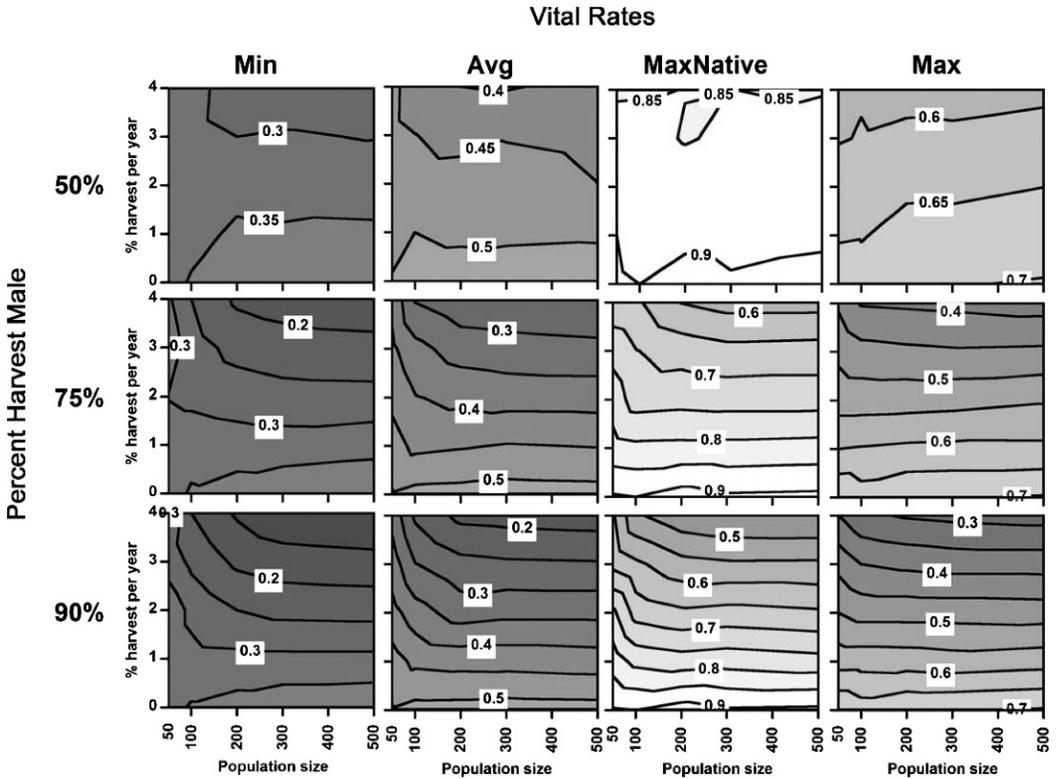


FIGURE 5. Contour graph of adult (age ≥ 2 y) sex ratios (males:female) of Mountain Goat populations given: 1) the proportion of the harvest that is male, 2) population size, and 3) percent harvest for vital rates that were minimum (Min), average (Avg), the maximum for native populations (MaxNative), and maximum for all populations (Max).

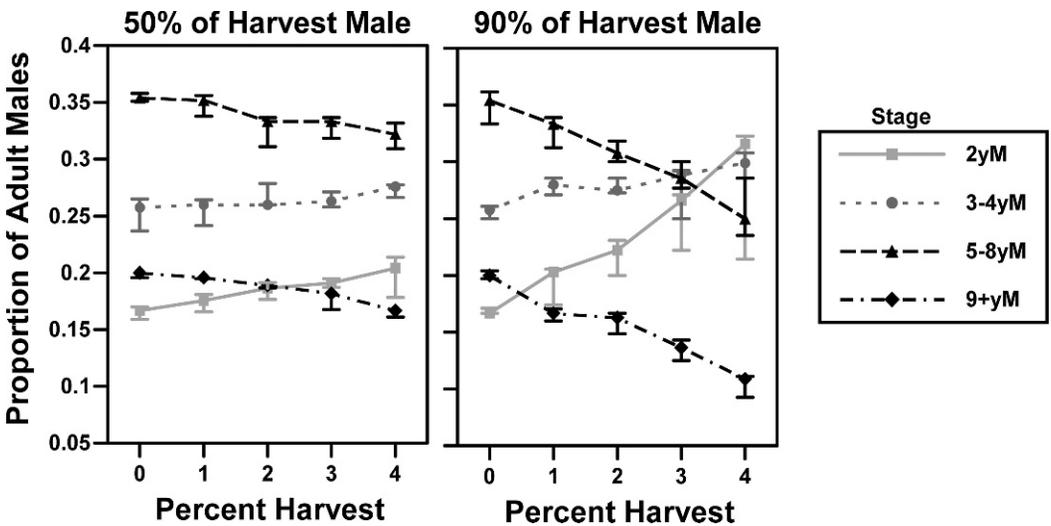


FIGURE 6. The proportion of adult male Mountain Goats in each stage of simulations using average vital rates when harvest is 50% male or 90% male. Error bars show the 90% nonparametric confidence interval of the medians across population sizes (50 to 500 animals).

density dependent effects were detected in the Caw Ridge population despite a doubling of the population over the period of study (Côté and Festa-Bianchet 2001; Côté and others 2001; Festa-Bianchet and others 2003; Hamel and others 2006). Conversely, Kuck (1977) presented some evidence for weak inverse density dependence in a Mountain Goat population in Idaho. Forage resources are limiting for Mountain Goats primarily in winter (Hebert and Turnbull 1977), and Kuck (1977) described a system in which Mountain Goats selected winter habitats on the basis of escape terrain with dominant animals occupying the most favorable sites. After a population decline, prime escape terrain sites continued to be used while less favorable sites were not, despite the likelihood of more favorable forage conditions at the sites with poor escape terrain characteristics (Kuck 1977). Consequently, negative impacts on vegetation at favored locations remain high and may be long lasting (Wadkins 1967). Although it is probable that if Mountain Goat populations continue to decline and at some point forage resources at these sites recover, it is not known what magnitude of decline would produce this recovery, and it is likely that there would be a time lag of uncertain duration before vegetation responded at the favored sites. Given the lack of compelling evidence of density dependence in Mountain Goats and uncertainty about its magnitude and lag effects, we felt justified in excluding it from our models. While including density dependence may have prevented unrealistic increases in some model replicates, our use of the median as the measure of central tendency limited the impact of unrealistic increases in some model replicates on our interpretation.

Individual Models

When modeled over several decades, there was large variation in modeled population trajectories due to the high temporal variation in vital rates (Côté and others 2003). This precluded precise evaluation of model fit, but the differences of model trajectories between models with and without harvest were without exception substantial; and including harvest in the model usually changed realized λ from >1 to <1 . Large populations modeled with 1961 population estimates and averaged vital rates

tended to be comparable to (Bumping River) or below later population estimates (Mt. Baker, East Stevens Pass, Snoqualmie, and Goat Rocks). This was despite the exclusion from the models of 7.3% of harvest for 1948–1970, wounding losses, tribal harvest, kid mortality associated with female harvest mortality, uneven spatial distribution of harvest, Allee effects, or inbreeding depression; all of which would be expected to increase the impact of harvest on population levels.

Harvest may have had a greater impact in models than population estimates suggest for a variety of reasons, but we evaluated 2 potential parameters: initial population size and vital rates. Either increases (1.2–2.0 times) in initial population or increases (1.010–1.023 times) in vital rates accounted for these discrepancies. Hamel and others (2006) noted that vital rates probably differ among populations even within a confined geographic area, and therefore an increase in vital rates may be the more likely of these scenarios. However, it is unlikely that variations in vital rates are constant between fecundity and survival and among age classes as were the proportional vital rates we used for some models; but given the lack of detailed information available to construct more detailed scenarios, proportional vital rates can provide an approximate assessment of these differences. A field assessment of vital rates in Washington (and for other Mountain Goat populations) would be of great value in confirming this finding and contribute substantially to our ability to manage this species. Some of the increases in initial populations or proportional vital rates used in our models seem unrealistic. For instance, the 2-fold increase in initial population for the Snoqualmie model may be excessive. Similarly the projected 14-fold increase in the modeled population for Falls Creek with increased vital rates and no harvest would be unlikely for a Mountain Goat population. In reality, it is more likely that a combination of underestimation of initial populations and higher vital rates resulted in the final population sizes after harvest.

The Penders Canyon and Falls Creek models had the most frequent population estimates, but assigning harvest for these populations was problematic. For the Penders Canyon model, both the conservative and liberal harvest sce-

narios resulted in declining populations for most replicates. The median of these corresponded more closely to the earlier population estimates of Ryals (Johnson 1983; Reed 1983) for the liberal scenario, while the conservative scenario yielded a median closer to recent helicopter survey results. In both scenarios, replicated runs tended to be above Ryals' counts and this was particularly evident in the decline in the counts before regular harvest commenced in 1964. It is possible that this was due to illegal harvest thought to have taken place in this area. Ryals reported finding 7 Mountain Goat carcasses in this area in 1968 (Johnson 1983:74) with the implication that this may not have been exceptional. In the Falls Creek area, both model scenarios initially tracked declines, but then declined more precipitously for nearly all replicates than did the population estimates. Increased vital rates that yielded median population levels corresponding to recent surveys were unrealistic and fit earlier population estimates very poorly. For unknown reasons, declines in both the Penders Canyon and Falls Creek populations apparently paused in the 1960s despite continuing harvest. When modeled from 1967 and 1969 respectively (not shown), these populations behaved as did other models in that they declined below recent estimates (even with conservative harvest estimates) unless vital rates were increased. In these 2 populations which declined >90%, density dependence may have been a factor.

Had many of our models tended to decline less than the actual populations, other causes of decline might have been considered to explain such a discrepancy. Because this was not the case, we think that while other factors (disease, predation, illegal harvest, winter habitat modification, conifer intrusion-fire suppression) may have played a minor role in particular areas (for instance illegal harvest of the Penders Canyon populations), their impacts were probably minor on a statewide level. For mortality from these other sources to have a comparable effect on populations as did harvest, initial populations and vital rates would need to be increased by a comparable magnitude over and above the increases already invoked, passing plausible levels with even greater frequency. While such scenarios cannot be categorically rejected, the consistent finding of declining

populations exposed to historic harvest which is known to have occurred even with augmented initial populations or vital rates makes large additional increases in these parameters unlikely. We therefore conclude that past harvest was the predominant factor in population declines in these areas, and by extension, for Washington in general.

General models

The method we used to assess the impacts of harvest on hypothetical populations differed from that of Hamel and others (2006) in that simulated harvest increased when each simulation replicate increased (according to percent harvest specified), and decreased when each replicate decreased rather than remaining a constant number harvested over all replicates regardless of their changing size. This more closely matches the management scenario where harvest is increased with increasing population and decreased during population declines. Consequently, the impacts of the stated level of harvest on replicates with low population sizes would be less, resulting in a higher level of allowable harvest. However, the importance of this effect was probably less than the difference in vital rates between our models and those of Hamel and others (2006).

Our simulations indicate that the effect of harvest on populations is most pronounced for small populations, especially if a substantial proportion of the harvest is female. We evaluated the effects of percent harvest on populations by selecting a $\geq 50\%$ probability of stability or increase, which equates to a $< 50\%$ probability of decline. While a higher probability of stability or increase would be desirable, due to the considerable variability in population projections such a goal would be difficult to achieve. Considering that some simulated declines were small, and that continued monitoring would be expected to detect substantial declines that did occur in real populations, we judged $\geq 50\%$ probability of stability or increase to be a suitable threshold. Basically, this means we decided that we could tolerate moderate declines and correct for larger declines, but would not want to manage under a scenario that favored declines over stability or increases.

It is not surprising that the probability of a population being stable or increasing is highly

TABLE 4. Maximum percent harvest (0–4%) resulting in $\geq 50\%$ probability of stable or increasing Mountain Goat population given initial population size, proportion of harvest male, and average (Avg), maximum for native populations (MaxNative), and maximum (Max) vital rates and for all stages, and female stages only (Female Stages). (Maximum percent harvest was always zero for minimum vital rates and the same for all stages and female stages for MaxNative and Max vital rates).

Population	% harvest male	All stages			Avg female stages only
		Avg	MaxNative	Max	
50	50	0	4	4	0
50	75	0	4	4	0
50	90	0	4	4	0
100	50	1	4	4	1
100	75	2	4	4	3
100	90	2	4	4	4
200	50	2	4	4	2
200	75	3	4	4	4
200	90	4	4	4	4
300	50	2	4	4	3
300	75	3	4	4	4
300	90	4	4	4	4
500	50	3	4	4	3
500	75	4	4	4	4
500	90	4	4	4	4

dependent on its vital rates. However, interpretation of the results using the maximum and minimum rates warrants some caution. Apart from the Caw Ridge rates, most of those we included were based on a few years of study (5 to 10 y) and <200 animals. Hence, sampling and inter-annual variation may have resulted in more extreme values than would have been obtained from studies of longer duration and of more animals. That the average rates we used were fairly similar to those from Caw Ridge supports the possibility that this was the case and that most Mountain Goat populations are, over the long term, closer to the average than the maximum and minimum rates would seem to indicate. Nevertheless, given the limited amount of information available on Mountain Goat vital rates these minimum and maximum rates bracket the potential variation among populations.

For average vital rates, a population of 50 animals would not be expected to sustain any harvest regardless of the percent of the harvest that is male. Despite a theoretic λ of 1.041, populations of 50 animals had a median realized λ of 0.994 due to stochastic effects. With higher than average vital rates, a population of 50 animals could sustain harvest, but a population with high vital rates would be expected to increase, in which case it would seem prudent to allow it to do so rather than subject it to harvest.

Also for average vital rates, harvest of 4% has a probability of the population being stable or increasing ≥ 0.5 only for large populations, and only then if it is largely male. However, the probability of the female stages achieving a probability ≥ 0.5 of being stable or increasing is true for populations ≥ 200 animals if the harvest is 70% male, and for populations ≥ 100 animals if the harvest is 90% male. In many of these cases, the total population would be expected to decline, but the female stages would not.

Although harvest that is biased toward males increases the probability of a population being stable or increasing, whether one considers the total population or only the female stages, it can have substantial effects on population structure. This was true for both the sex ratio of adults and the age structure of males. Milner and others (2007) recently reviewed impacts of such changes for a variety of ungulates which can lead to lower fecundity, delayed conception and hence lower body weight and survival of offspring, and reduced condition of males. The extent to which these factors may impact Mountain Goat populations is unknown, but they warrant consideration when harvest management favors males.

Conclusions

An important implication of the finding that past harvest accounts for population declines is

that the prospects for recovery are good if populations are sufficiently protected. The exception to this is small populations, where we agree with Hamel and others (2006) that populations <50 animals are prone to decline. Where only remnants of former populations exist, or where Mountain Goats have been locally extirpated, supplementation or reintroduction may be a necessary part of recovery. In cases where recovery to former population levels is desired, harvest at any given level reduces the probability of the population increasing and should be zero or at least lower than indicated by our results.

Our simulations indicated a complex interaction between acceptable harvest, vital rates, population size, and proportion of harvest that is male. Given assessments of these elements, managers may use Table 4 to guide decisions about the harvest of Mountain Goats. Because these thresholds are based on a 50% probability of the population remaining stable or increasing, and due to expected variability of vital rates among populations, there is a reasonable possibility that populations may decline under such management. Hence, we concur with Hamel and others (2006) and Côté and Festa-Bianchet (2003) that continual monitoring is an essential feature of Mountain Goat population management where harvest is allowed.

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APPENDIX A

Partitioning survival estimates pooled across sexes. For each age class, survival was partitioned so as to maintain a constant male:female ratio equal to that of the Caw Ridge model (Hamel and others 2006). This calculation is for female survival.

$$m_r = \frac{m_F}{m_M}$$

$$m_M = \frac{m_F}{m_r}$$

$$m_F p_F + m_M p_M = m_{FM}$$

$$m_F p_F + \frac{m_F}{m_r} p_M = m_{FM}$$

$$m_F = \frac{m_{FM}}{p_F + \frac{p_M}{m_r}}$$

$$s_F = 1 - m_F$$

$$s_F = 1 - \frac{1 - s_{FM}}{p_F + \frac{p_M}{\left(\frac{1 - s_{FHamel}}{1 - s_{MHamel}}\right)}}$$

where :

m = mortality, s = survival

m_r = mortality ratio

s_F = female survival, m_{FM} = mortality of males and females (pooled)

p_F = proportion of females in population (for each stage)

s_{MHamel} = survival of males in Hamel et al. 2006

APPENDIX B

Matrix population model parameters for Mountain Goats: minimum vital rates (Min), average (Avg), maximum of native population (MaxNative), and maximum for all populations (Max). The constant standard deviation (StdDev) is from Hamel and others (2006).

Stages		Vital Rate				StdDev
From	To	Min	Avg	MaxNative	Max	
Reproduction						
2 y-F	Kids F	0.000	0.007	0.021	0.021	0.050
2 y-F	Kids M	0.000	0.006	0.019	0.019	0.065
3-4 y-F	Kids F	0.265	0.300	0.265	0.333	0.166
3-4 y-F	Kids M	0.194	0.249	0.194	0.333	0.165
5-8 y-F	Kids F	0.382	0.400	0.402	0.416	0.114
5-8 y-F	Kids M	0.286	0.320	0.345	0.345	0.101
9+ y-F	Kids F	0.208	0.338	0.257	0.548	0.076
9+ y-F	Kids M	0.110	0.277	0.398	0.398	0.068
Survival						
Kids F	1 y-F	0.570	0.604	0.680	0.680	0.129
Kids M	1 y-M	0.570	0.604	0.680	0.680	0.129
1 y-F	2 y-F	0.778	0.801	0.852	0.852	0.153
1 y-M	2 y-M	0.648	0.684	0.765	0.765	0.201
2 y-F	3-4 y-F	0.805	0.904	0.992	0.992	0.137
2 y-M	3-4 y-M	0.729	0.867	0.988	0.988	0.185
3-4 y-F	3-4 y-F	0.480	0.493	0.516	0.516	0.045
3-4 y-F	5-8 y-F	0.443	0.455	0.477	0.477	0.042
3-4 y-M	3-4 y-M	0.431	0.457	0.502	0.502	0.075
3-4 y-M	5-8 y-M	0.416	0.441	0.484	0.484	0.072
5-8 y-F	5-8 y-F	0.707	0.720	0.746	0.746	0.046
5-8 y-F	9+ y-F	0.156	0.240	0.249	0.249	0.015
5-8 y-M	5-8 y-M	0.693	0.733	0.808	0.808	0.091
5-8 y-M	9+ y-M	0.151	0.160	0.176	0.176	0.020
9+ y-F	9+ y-F	0.714	0.830	0.866	0.911	0.084
9+ y-M	9+ y-M	0.580	0.751	0.803	0.869	0.284