Research Article

Population Dynamics and Harvest Potential of Mountain Goat Herds in Alberta

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Abstract

The understanding of population dynamics is a central issue for managing large mammals. Modeling has allowed population ecologists to increase their knowledge about complex systems and better predict population responses to diverse perturbations. Mountain goats (Oreamnos americanus) appear sensitive to harvest, but the relative influence of survival and reproductive rates on their population dynamics are not well understood. Using longitudinal data on age- and sex-specific survival and reproduction from a marked mountain goat population in Alberta, Canada, we built a stage-class matrix model to predict short-term numerical changes for 11 other goat populations in Alberta for which the only data available were from annual aerial surveys. Overall, the model provided an acceptable fit to changes in population size for 8 of 12 populations. Temporal trends in population size were underestimated in 2 populations and overestimated in another 2, suggesting that these populations had different vital rates than those of the intensively studied population. Sensitivity analyses revealed that the survival of mature females (aged 5 yr and older) had the greatest elasticity for population growth. Modeled management scenarios indicated that nonselective yearly harvest rates above 1% of goats aged 2 years and older were not sustainable over the short-term for some populations. The simulations also revealed that small (n = 25) and medium-size (n = 50) populations, which correspond to most goat populations in Alberta, had high extinction risk (18 to 82% over 40 years), even in the absence of harvest. Our results confirm that mountain goat populations are very sensitive to harvest, indicate that wildlife managers should prevent female harvest, and suggest that although a high demand for goat hunting exists in Alberta, most populations in this province—and probably small populations elsewhere—cannot withstand exploitation. (JOURNAL OF WILDLIFE MANAGEMENT 70(4):1044–1053; 2006)

Key words

A complex but central goal in population ecology and wildlife management is to understand and predict the dynamics of populations. Population age–sex structure and variations in vital rates, such as age-specific survival and reproductive rates, are major determinants of population dynamics (Coulson et al. 2001, Lande et al. 2002, Olsson and van der Jeugd 2002). Environmental stochasticity and density dependence also influence the dynamics of populations (Escos et al. 1994, Sæther 1997, Albon et al. 2000).

Modeling can be used to predict population responses to various management actions (Hutchings 1996, Nichols 2001, Trenkel 2001, Lalas and Bradshaw 2003). The study of population dynamics in age- or stage-structured populations, for example, is often performed with matrix population models (Eberhardt 1985, Caswell 2001, Oli 2003). To complement modeling, sensitivity analyses are a prospective tool that can identify which vital rates have the greatest potential influence (or elasticity) on the rate of population change (Crouse et al. 1987, Escos et al. 1994, Caswell 2001). Although adult survival typically is the vital rate with the greatest elasticity in large herbivores (Gaillard et al. 1998, 2000), recruitment could be the main determinant of population changes in some instances because it is more variable than adult survival (Gaillard et al. 2000).

Demographic data based on longitudinal studies of marked individuals of known age can build accurate models of population dynamics. For most long-lived species, however, such information is rarely available (Oli 2003). Instead, studies usually use censuses of unmarked individuals to estimate population numbers. For numerous ungulate species, researchers perform aircraft surveys, which can only reliably identify and count some age–sex classes of individuals. Aerial surveys allow the estimation of population numbers for species distributed over vast areas and in remote habitats. Their accuracy, however, has been questioned (Seber 1992, Reilly and Hensbergen 2002, Bender et al. 2003) because they commonly underestimate population sizes, and sightability varies greatly among years and among age and sex classes (Wolfe and Kimball 1989, Woolley and Lindzey 1997, Gonzalez-Voyer et al. 2001).

Population dynamics of mountain goats are poorly understood (Festa-Bianchet et al. 1994, Côté and Festa-Bianchet 2003) and appear to vary widely among herds. Some introduced populations appear to show compensatory reproduction following artificial reductions (Adams and Bailey 1982, Swenson 1985, Houston and Stevens 1988), while most native populations seem highly sensitive to harvesting (Smith 1988b, Festa-Bianchet et al. 1994, Côté et al. 2001). Since hunting appears almost totally additive to natural mortality, the sensitivity of native populations to harvest could be partly explained by the late primiparity of females (i.e., 4.7 years) and low recruitment (Adams and Bailey 1982, Swenson 1985, Smith 1986, 1988b, Festa-Bianchet et al. 1994, Côté and Festa-Bianchet 2001a).

In Alberta, Canada, goat numbers declined substantially in the 1980s, and hunting was closed in 1987 (Smith 1988b). Some populations have since recovered, while others remained stable or continued to decline (Gonzalez-Voyer et al. 2003). Since 1973, annual or biennial helicopter surveys were carried out to count

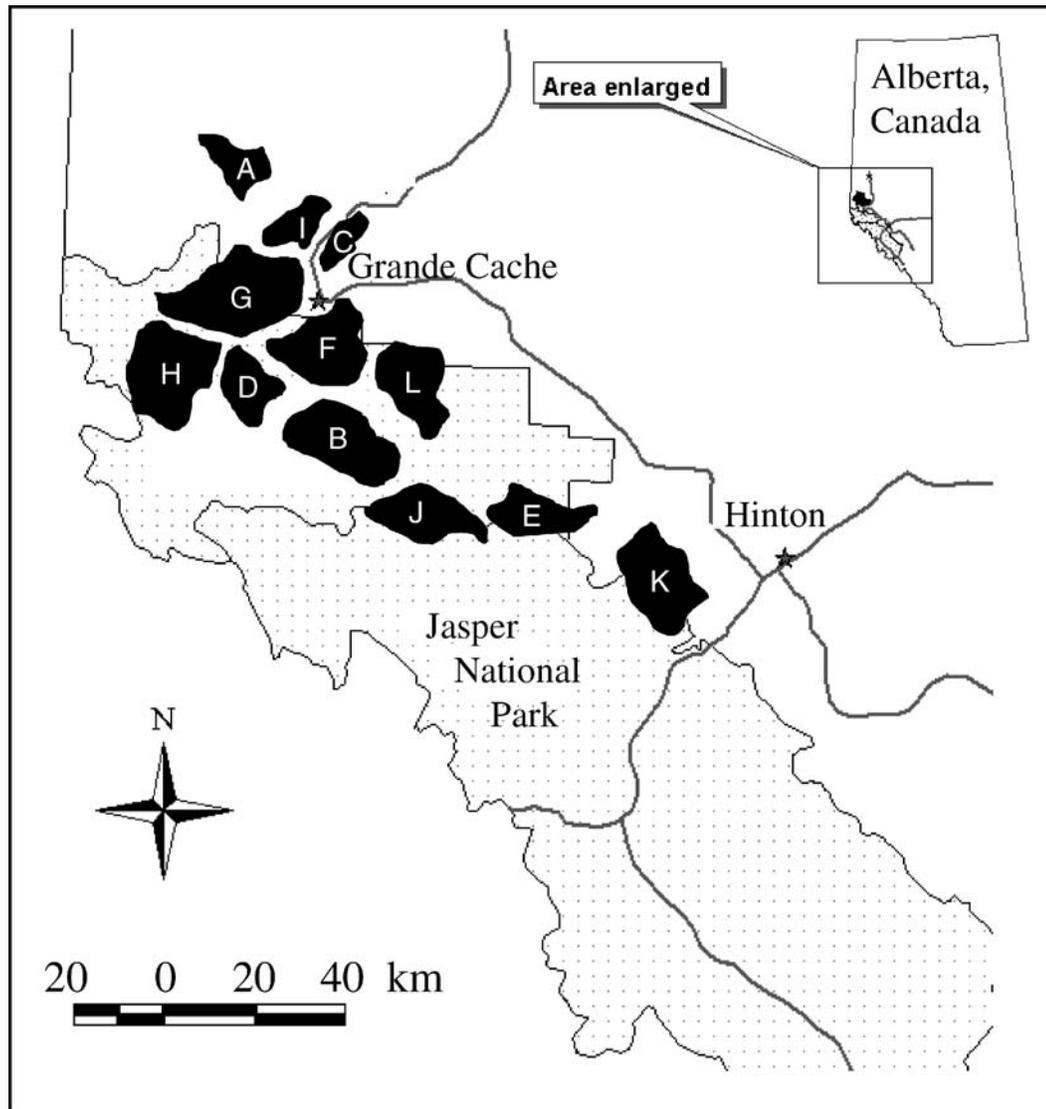[1] E-mail: Sandra.hamel@bio.ulaval.ca

Figure 1. Mountain goat populations studied between 1973 and 2003 in west-central Alberta, Canada: Caw Ridge (A), Monoghan Creek (B), Goat Cliffs/Grande Mountain (C), Kvass (D), Daybreak Peak (E), Triangle (F), Llama-Turret (G), Mount Deveber (H), Mount Hamell (I), Sunset Peak (J), Moosehorn (K), and Persimmon North (L). The northern part of the stippled area is Willmore Wilderness Park, and the southern part is Jasper National Park.

mountain goats in 12 populations in and near the Willmore Wilderness Area in west-central Alberta. During helicopter surveys, observers counted the number of adults, yearlings, and kids. Gonzalez-Voyer et al. (2001) suggested that aerial surveys over several years could detect population trends.

Since 1988, we monitored survival and reproduction of individually marked mountain goats at Caw Ridge, Alberta. Our objectives were to model the dynamics of the Caw Ridge population based on precise demographic data and to assess the reliability of this model population to predict short-term changes in population sizes for other herds for which the only data available were from annual or biennial aerial surveys. We also aimed at evaluating the sensitivity of survival and fecundity estimates and determining which age and sex classes had the greatest potential influence on population change. Finally, our last objective was to model various management practices to determine which harvest rate would be sustainable over the long-term for populations of different sizes.

Study Area

We studied mountain goat populations in the front range of the Rocky Mountains, north and west of Jasper National Park in west-central Alberta, Canada (Fig. 1). Elevation ranges from 975 to 3,100 m above sea level, and habitat is alpine tundra and subalpine open forest of Engelmann spruce (*Picea engelmanii*). Potential goat predators include wolves (*Canis lupus*), grizzly bears (*Ursus arctos*), black bears (*U. americanus*), cougars (*Puma concolor*), coyotes (*C. latrans*), wolverines (*Gulo luscus*), and golden eagles (*Aquila chrysaetos*; Festa-Bianchet et al. 1994, Côté and Beaudoin 1997, Côté et al. 1997).

Methods

Population Estimates from Aerial Surveys

Between 1973 and 2003, in early July, we surveyed 12 populations annually or biennially by helicopter. We counted the number of adults, yearlings, and kids (Gonzalez-Voyer et al. 2001). We pooled both sexes. Populations existed on distinct mountain

complexes delimited by wide forested valleys that goats generally avoided. Five populations were not hunted (including the intensively studied Caw Ridge population), and 7 were hunted until 1988. Of the 5 populations that were not hunted, 2 had goats removed for transplants (21 from Caw Ridge before 1988, and 12 from Mount Hamell between 1992 and 1995).

Population Data from Caw Ridge
Starting in 1989, the Caw Ridge population ranged between 76 and 152 goats. Since 1993, we marked an average of 98% of goats aged 1 year and older. We marked and released 316 goats during the study. From mid-May until late September, we conducted counts almost daily from at least 15 vantage points. Because nearly all animals were marked and thus individually recognizable, we assumed the counts to be a census (i.e., a complete enumeration of all animals). With the exception of 2 males, no goat missed during censuses one year was ever seen again on Caw Ridge. Most animals were seen >50 times every summer. Survival estimates are therefore very precise. Because most kids were born between 20 May and 1 June (Côté and Festa-Bianchet 2001b), we calculated kid survival from birth to 1 June the following year. We determined the reproductive status of each female from observations of nursing kids. Females produced singletons in all but 2 occasions ($n = 421$ births). Kids were sexed by their urination posture and by direct observations of the vulvar patch in females (Côté and Festa-Bianchet 2003). Further descriptions of capture techniques, age determination, and censuses and population estimates are presented in Côté and Festa-Bianchet (2001a,b).

Demographic Parameters and Population Modeling
Goat survival patterns at Caw Ridge were similar to those of other ungulates (Gaillard et al. 2000). Adult survival was higher than yearling survival, which was higher than kid survival (Côté and Festa-Bianchet 2003). Adult male survival was lower than adult female survival (Côté and Festa-Bianchet 2003), but kid survival was independent of sex (Côté and Festa-Bianchet 2001b). Primiparity occurred at 4 or 5 years of age for most females, and only 3.5% of 3-year-old females reproduced (Festa-Bianchet et al. 1994, Côté and Festa-Bianchet 2001a). Productivity increased slightly from ages 6 to 9, and reproductive senescence began at 10 years of age (Côté and Festa-Bianchet 2001a). Females produced an increasing proportion of sons as they aged (Côté and Festa-Bianchet 2001c).

Based on these variations in survival and reproduction among age-sex classes, we built a 12 life-stages population matrix (Table 1A) including 6 age classes (kid, yearling, 2-year-old, 3- and 4-year-old, 5- to 8-year-old, and 9 years and older) for each sex. We used 3 adult (≥3-yr-old) age classes to make inferences on 3 fundamental life-history stages: primiparous (3- and 4-yr-old), prime-aged (5- to 8-yr-old), and senescent (9 yr and older) females (see above and Côté and Festa-Bianchet 2001a for more details on these stages). In addition, this grouping provided more accurate estimations of vital rates because the number of individuals in some cohorts and in the older age classes was very small. Age here refers to age during the rut, in November of each year. We used year as the time step in the models. For each stage, we calculated the fecundity, survival, and probability of remaining in the same stage or moving to another stage the following year, as described in Caswell (2001).

Population Projections
We used RAMAS Metapop software to project changes in population size over time (Akçakaya 2002a). This software simulates the growth of a population using an age- or stage-structured matrix (Table 1). We multiplied the matrix by a vector that represents the number of individuals in each life stage at a specific time step to predict the number of individuals in each life stage at the next time step. We used corrected standard deviations of vital rates as a surrogate for environmental stochasticity (Akçakaya 2002b). We modeled environmental stochasticity using a lognormal distribution, and since we had 2 survival values per column in some stages (survival within the age class and survival when switching to the following age class), we used the option "pooled variance for survivals" to avoid truncations (Akçakaya 2002b). We included demographic stochasticity in the models because it may be important for small populations (Akçakaya 1991, Caswell 2001, Lande et al. 2003). We did not include density dependence in the models because it did not affect reproduction (Côté et al. 2001) or survival (Côté and Festa-Bianchet 2001b, Festa-Bianchet et al. 2003) in the Caw Ridge population, even though the population doubled during our study (see Discussion). We performed 1,000 replicates for each simulation and present the average ±1 SD interval of model predictions.

To assess model fit, we first simulated changes in population size for Caw Ridge from 1993 to 2003 and then calculated the correlation between predicted values and ground counts. We used Chi-square tests to determine the fit of predicted changes for each life stage. A significant effect indicated a difference between the observed and predicted values of a specific life stage. Second, we reduced the initial model to 2 life stages (Table 1B), including only adult and juvenile stages, so that this model could be used with data from helicopter surveys, where only 2 age classes are available. The juvenile stage included both kids and yearlings. Even though these 2 age-classes have different survival rates (Table 1A), Gonzalez-Voyer et al. (2001) found that kids and yearlings could not be reliably distinguished during aerial surveys. We therefore followed their recommendation and pooled these 2 age-classes to avoid potential bias.

We then ran simulations with the reduced model to predict short-term changes in population sizes for all populations counted during aerial surveys. We first ran one set of 1,000 simulations for each population based on estimates from annual aerial surveys. Goat sightability during helicopter surveys of Caw Ridge averaged 70% and ranged from 55 to 84%. To minimize the effects of annual variations in sightability, we ran other simulations using the average number of adults and juveniles counted during the first 3 and 5 consecutive surveys as initial population numbers rather than using the first survey only. We modeled harvest and translocation events by removing exact numbers of individuals at specific time steps, since this information was available for each population each year. We considered that models had an acceptable fit when intervals of ±1 SD of model predictions included 70% of the yearly population counts from aerial surveys. We repeated this analysis using raw data from aerial surveys and

Table 1. Matrix population model of (A) 12 life stages and (B) 2 life stages (juvenile and adult) based on demographic data gathered between 1993 and 2003 for marked mountain goats at Caw Ridge, Alberta, Canada.[a]

A[b]

F_{F0}	0	F_{F1}	0	F_{F2}	0	F_{F3-4}	0	F_{F5-8}	0	F_{F9+}	0
0.000	0	0.000	0	0.021	0	0.265	0	0.402	0	0.257	0
±0.000	0	±0.000	0	±0.050	0	±0.166	0	±0.114	0	±0.076	0
F_{M0}	0	F_{M1}	0	F_{M2}	0	F_{M3-4}	0	F_{M5-8}	0	F_{M9+}	0
0.000	0	0.000	0	0.019	0	0.194	0	0.345	0	0.398	0
±0.000	0	±0.000	0	±0.065	0	±0.165	0	±0.101	0	±0.068	0
S_{F0}	0	0	0	0	0	0	0	0	0	0	0
0.619	0	0	0	0	0	0	0	0	0	0	0
±0.129	0	0	0	0	0	0	0	0	0	0	0
0	S_{M0}	0	0	0	0	0	0	0	0	0	0
0	0.619	0	0	0	0	0	0	0	0	0	0
0	±0.129	0	0	0	0	0	0	0	0	0	0
0	0	S_{F1}	0	0	0	0	0	0	0	0	0
0	0	0.852	0	0	0	0	0	0	0	0	0
0	0	±0.153	0	0	0	0	0	0	0	0	0
0	0	0	S_{M1}	0	0	0	0	0	0	0	0
0	0	0	0.765	0	0	0	0	0	0	0	0
0	0	0	±0.201	0	0	0	0	0	0	0	0
0	0	0	0	S_{F2}	0	S_{F3}	0	0	0	0	0
0	0	0	0	0.805	0	0.480	0	0	0	0	0
0	0	0	0	±0.137	0	±0.045	0	0	0	0	0
0	0	0	0	0	S_{M2}	0	S_{M3}	0	0	0	0
0	0	0	0	0	0.729	0	0.431	0	0	0	0
0	0	0	0	0	±0.185	0	±0.075	0	0	0	0
0	0	0	0	0	0	S_{F4}	0	S_{F5-7}	0	0	0
0	0	0	0	0	0	0.443	0	0.708	0	0	0
0	0	0	0	0	0	±0.042	0	±0.046	0	0	0
0	0	0	0	0	0	0	S_{M4}	0	S_{M5-7}	0	0
0	0	0	0	0	0	0	0.416	0	0.697	0	0
0	0	0	0	0	0	0	±0.072	0	±0.091	0	0
0	0	0	0	0	0	0	0	S_{F8}	0	S_{F9+}	0
0	0	0	0	0	0	0	0	0.236	0	0.866	0
0	0	0	0	0	0	0	0	±0.015	0	±0.084	0
0	0	0	0	0	0	0	0	0	S_{M8}	0	S_{M9+}
0	0	0	0	0	0	0	0	0	0.152	0	0.803
0	0	0	0	0	0	0	0	0	±0.020	0	±0.284

B[c]

S_0	F_A
0.395	0.394
±0.057	±0.088
S_1	S_A
0.288	0.858
±0.041	±0.054

[a] The rows are organized in triplets, where the first row of each triplet describes the vital rate, the second shows the observed value, and the third shows the estimated standard deviation.

[b] The table is a sequence of female–male stages, starting with a female stage. The first triplet represents the production (i.e., fecundity, which is assumed to be equal to birth rate) of female kids (F_F) and the second the production of male kids (F_M) for each female stage. The diagonals represent survival rates (S_F: survival of females, S_M: survival of males): the shorter diagonal is the probability of remaining in a stage at the next time step, and the longer diagonal is the probability of moving to the following stage at the next time step.

[c] F_A is adult fecundity. S_A is the probability that adults will remain in the adult stage at the next time step, and hence represents adult survival. S_0 is the probability that kids and yearlings will remain in the juvenile stage at the next time step. Therefore, it represents the proportion of juveniles that are kids and that survive to the next time step. S_1 is the probability that juveniles will move to the adult stage at the next time step. It represents the proportion of juveniles that are yearlings and survive to the next time step.

data corrected for the sightability bias (i.e., we increased raw data from aerial surveys by 30%; Gonzalez-Voyer et al. 2001). Results were very similar for both data sets. For simplicity, we only present results using raw data.

Sensitivity Analyses

To assess the relative effects of changes in survival or recruitment on the population growth rate, we compared their elasticities. Elasticities are the relative changes in population growth rate (λ) for a given proportional change in the parameter (Caswell 2001). We computed the elasticities by simulating successively the same proportional change for each vital rate and assessing its effects on

λ. For ungulates, adult survival typically has the greatest elasticity (Gaillard et al. 2000). However, adult survival does not necessarily have a greater influence on λ than recruitment, since the latter is often more variable than adult survival and hence might be as likely to affect λ (Gaillard et al. 1998, Mills et al. 1999). Elasticities only measure the potential effect of a parameter on λ, but one needs empirical data on the parameter's temporal variability to determine its actual effect on population growth. To consider empirical variability and produce more realistic estimates, we calculated the coefficient of variation (CV) of adult survival and recruitment. Then, rather than using the same proportional change for both parameters, we used a variation that

was proportional to the CV of each parameter. Because recruitment had a CV 2.3 times greater than that of adult survival, we forced a variation 2.3 times greater for recruitment than for survival in the analyses, and then successively assessed the effects of these variations on λ.

Management Scenarios

We ran simulations to assess the effects of different harvest rates on short- and long-term changes in population size. We used the 12 life-stages model for these simulations because it was more precise. We modeled the effects of specific harvest rates and initial population sizes on the growth rate (λ) of the population over 20 years and the probability of extinction over 40 years. We used 4 categories of initial population sizes (25, 50, 75, 100) to represent the range of population sizes in the study area. For all simulations, harvested goats were chosen randomly among males and females aged 2 years and older because most inexperienced hunters cannot age and sex adult goats accurately (Smith 1988*a*, Côté and Festa-Bianchet 2003) and 43% of goats harvested in Alberta between 1974 and 1985 were females, when hunters were not discouraged from taking females (Smith 1988*b*).

Results

Population Projections

The 12 life-stages population model (Table 1A) provided a good fit to the true population size data from Caw Ridge (*r* = 0.9, *P* < 0.001; Fig. 2A). The good fit of this model, however, may occur because the data used to build it are the same as those used to test it. Therefore, we built a similar model using only the data from 1993 to 1996 to predict population changes for 1997 to 2003. The results were very similar, and the fit to the model was as good as for the previous one (*r* = 0.9, *P* = 0.01). Most specific life stages presented a good fit to the model (Table 2). However, predictions differed significantly from real population numbers for yearlings of both sexes, 2-year-old males, and ≥9-year-old males (Table 2). Reducing the complete model to 2 life stages (Table 1B) still presented a good fit to observed data (*r* = 0.9, *P* < 0.001; Fig. 2B). Both models had similar λ values (complete model: 1.024; reduced model: 1.035), but the reduced model was less variable (complete model: absolute values of the SD of the model predictions varied from 15 goats at the first time step to 56 at the last time step; reduced model: SD varied from 11 to 41).

The reduced model provided an acceptable fit to changes in the size of 4 of 12 populations when based on the population size from the first aerial survey available (Fig. 3; accurate: A to D, inaccurate: E to L). However, when using the average of the first 3 and 5 consecutive surveys as the basis for initial population size, the model was representative of changes in 6 and 8 populations, respectively (Fig. 3I′–L′). The model underestimated temporal trends in population size for 2 populations (Fig. 3G,H) and predicted a stronger impact of harvest than what was observed. For 2 other populations (Fig. 3E,F), the model overestimated population trends. One of these populations was not hunted but was small (Fig. 3E), while the other had a high harvest rate (9.8%) that may have had a stronger impact than what the model predicted (Fig. 3F). Hunted populations showed important declines under high harvest rates (>8%; Fig. 3D,F,K).
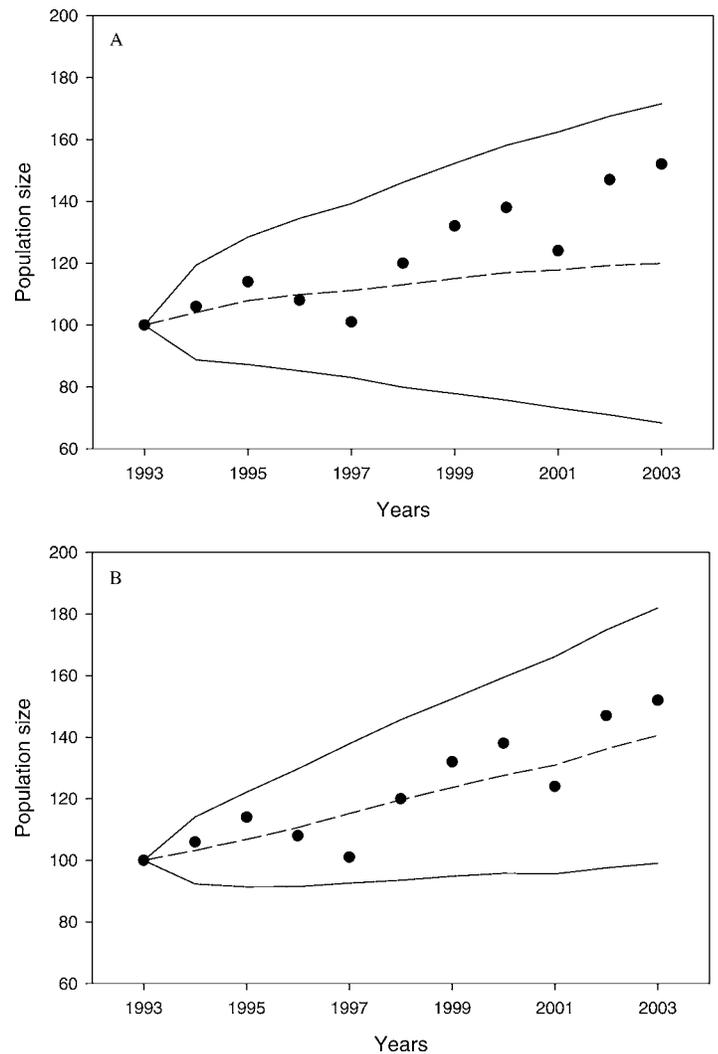

Figure 2. Predicted population sizes from a Leslie matrix model of (A) 12 life stages and (B) 2 life stages, for the Caw Ridge mountain goat population, Alberta, Canada, 1993–2003. Dots are real population sizes from ground counts. Dashed and solid lines represent, respectively, the average and ±1 SD interval of model predictions based on 1,000 replications.

The harvest rates shown in Fig. 3 included 51% of females (*n* = 117).

Sensitivity Analyses

Adult survival had the greatest elasticity (Fig. 4A). Recruitment, however, was 2.3 times more variable than adult survival (CV: recruitment = 0.152, adult survival = 0.065). Therefore, we simulated a variation 2.3 times greater for recruitment than for adult survival in the model and found that the proportional change in λ for adult survival was still 1.45 times greater than that for recruitment. Elasticity increased with female age and was highest for females >5 years old (Fig. 4B). Elasticities for males were too small to appear on Fig. 4B, illustrating the small potential influence of male survival on λ.

Management Scenarios

Using the 12 life-stages model and projecting population changes over 20 years, we found that a population of 25 individuals would always have a negative growth rate, even without hunting (Table

Table 2. Goodness-of-fit of model predictions for each life stage compared with true population data from mountain goats at Caw Ridge, Alberta, Canada, 1993–2003.[a]

Life stage	χ^2 value	P value
Kid female	8.02	0.5
Kid male	10.77	0.3
Yearling female	18.07	0.03*
Yearling male	19.98	0.02*
2-yr-old female	10.43	0.3
2-yr-old male	17.75	0.04*
3- to 4-yr-old female	11.49	0.2
3- to 4-yr-old male	9.87	0.4
5- to 8-yr-old female	4.72	0.9
5- to 8-yr-old male	7.69	0.6
≥9-yr-old female	7.46	0.6
≥9-yr-old male	18.00	0.04*

[a] Significant differences are shown by an * and indicate a difference between the number of individuals observed and predicted by the model for a specific life stage; $n = 10$ years for all stages.

3). When we permitted hunting, the risk of extinction in 40 years was very high and increased rapidly with higher harvest rate (Table 3). Even without hunting, simulations suggested that about half of small populations would go extinct in 40 years. For a population of 50 individuals, which is about the average size of mountain goat populations in Alberta (Smith 1988b), we found that harvest of 1 goat every 20 years would be sustainable (Table 3). Without hunting, however, the population would have a positive growth rate and a lower probability of extinction. In populations of 75 individuals, the harvest of 1 goat every 2 years should be sustainable. For populations of 100 individuals, harvest of 1 goat every year would be sustainable, but higher harvest rates would lead to negative growth rates (Table 3). When allowing harvest only on 2-year-old goats, similar population trends were found, but not surprisingly, the probabilities of extinction averaged 35% lower than those presented in Table 3.

Discussion

Our research objective was to model the population dynamics of mountain goats to determine key elements that we should consider to maintain sustainable populations. Our results produced 4 major findings. First, the model we used was representative of many populations we studied, suggesting that these populations exhibited similar vital rates as the model population. However, the model did not represent some populations well, even though they live in similar environments. This suggests that variation in vital rates or dispersal rates may differ in those populations. Second, the survival of females aged 5 years and older had the greatest potential to influence population changes. Third, goat populations are very sensitive to harvest, as yearly harvest rates above 1% did not appear sustainable over the short-term. Finally, we should not harvest small populations because their long-term viability—even in the absence of hunting—is low.

The 12 life-stages model provided a good fit to the dynamics of the Caw Ridge population. As expected, the accuracy of the model decreased as the number of time steps increased (Fig. 2), underlining the need for frequent counts. Predictions were less accurate, however, for younger individuals, particularly males

(Table 2). In most mammals, young males are much more likely to disperse than other age–sex classes (Greenwood 1980, Dobson 1982). At Caw Ridge, males aged 1 to 3 years old were involved in 17 of 23 known dispersal events recorded since 1988 (S. D. Côté, unpublished data). Emigration is difficult to distinguish from mortality. In our models, emigration was indirectly included within mortality rates, but we did not account for immigration. This may explain why predictions for males and younger individuals were less accurate than for other age–sex classes. An alternative explanation is that juvenile survival rates are much more variable than other vital rates in most large mammals (Gaillard et al. 1998, 2000) and, hence, predicting changes in these age–sex classes is more difficult.

The reduced model presented a good fit with population sizes estimated during helicopter surveys for 8 populations out of 12 (Fig. 3A–D, I′–L′). Predictions were accurate for 4 hunted and 4 nonhunted populations, suggesting that the predictive capabilities of the model were not influenced by hunting. These results indicate that these populations had comparable vital rates to the Caw Ridge population. For 4 populations, however, the model was inaccurate (Fig. 3E–H), suggesting that different vital rates determined the changes occurring in these populations. Populations that increased more than predicted by the model may have had an age–sex structure biased toward mature females, whereas the reverse might have occurred for populations that decreased more than predicted. Variations in the age-sex structure of populations can affect recruitment (Holand et al. 2003, Dabin et al. 2004) and survival (Festa-Bianchet et al. 2003), demonstrating the important influence of age-sex structure on the population dynamics of long-lived species (Coulson et al. 2001). Because all goat populations were located in the same general area (Fig. 1), we suspected that they were encountering similar weather conditions. Differences in habitat quality, predation pressure, dispersal, population structure, or a combination of these factors may therefore have caused the discrepancy we observed for some populations and suggests that we should apply distinct harvesting policies to each population.

In mountain goats, sightability during aerial surveys varied widely among years and age-classes (Gonzalez-Voyer et al. 2001). The inclusion of kids and yearlings, as well as males and females, in the same life stages, however, allowed us to control for the differential sightability of age-classes. We apparently reduced the potential bias linked to the annual variation in sightability by averaging the population estimates for 3 to 5 annual surveys. This allowed us to accurately predict the dynamics of 4 populations for which using only one survey did not provide a good fit. We suggest using information from more than one survey when available as it provides better estimates of population size.

We did not include density dependence in the simulations because we had no evidence of its occurrence in the model population, even though the number of individuals doubled in 15 years (Côté et al. 2001, Côté and Festa-Bianchet 2001b, Festa-Bianchet et al. 2003). We also did not expect to find strong density-dependent effects in the other populations we studied since they are smaller and inhabit larger areas than the Caw Ridge population. The inclusion of density dependence in a population model can prevent unrealistic increases in large populations and
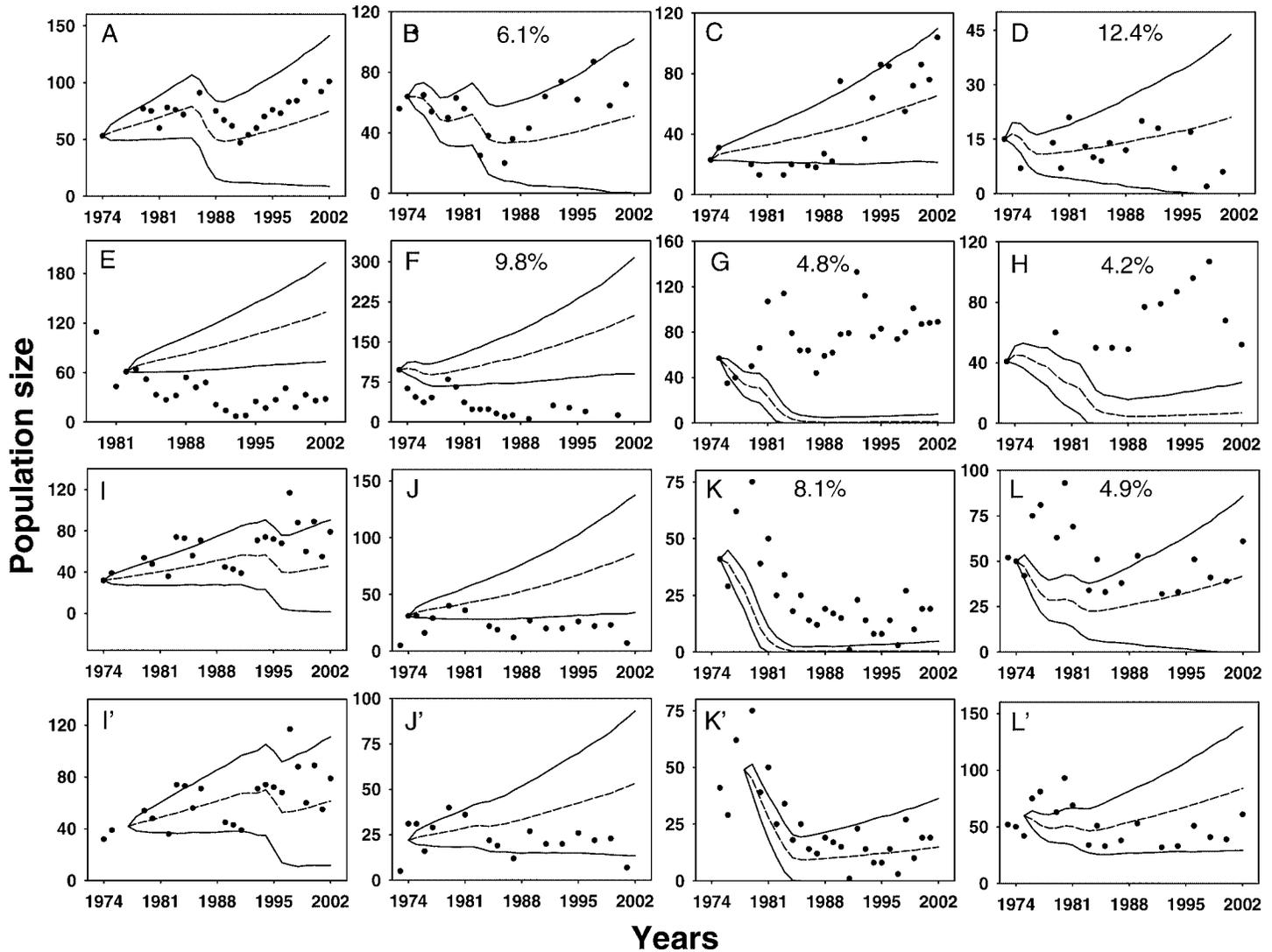
Figure 3. Predictions of population sizes based on a 2 life-stages matrix model for 12 mountain goat populations in Alberta, Canada, between 1973 and 2003. Dots represent population counts from aerial surveys. Dashed and solid lines represent, respectively, the average and ±1 SD interval of model predictions based on 1,000 replications. Populations: Caw Ridge (A), Monoghan Creek (B), Goat Cliffs/Grande Mountain (C), Kvass (D), Daybreak Peak (E), Triangle (F), Llama-Turret (G), Mount Deveber (H), Mount Hamell (I and I′), Sunset Peak (J and J′), Moosehorn (K and K′), Persimmon North (L and L′). Panels A to L represent predictions based on 1 annual aerial survey. Panels I′ and J′ represent predictions based on the average of 3 consecutive annual surveys as initial population size, whereas panels K′ and L′ represent predictions based on the average of 5 consecutive annual surveys. Panels A, I, and I′ are nonhunted populations where removals for transplants occurred. Panels B, D, F, G, H, K, K′, L, and L′ represent populations that were hunted before 1988. Mean harvest per year, excluding years when no harvest occurred, is shown in %.

reduce the chances for small populations to become extinct through demographic stochasticity. While there must be some density dependence at some point in growing populations, it seems that our model population has not reached carrying capacity and that environmental variation in this population might mask density dependence. Furthermore, when we included density dependence in the model, it was very sensitive to the estimation of carrying capacity, which we could not determine for the Caw Ridge population. Therefore, we reasoned that it was more appropriate to exclude density dependence of the models because we had no empirical basis for its inclusion.

Sensitivity analyses revealed that adult survival had the greatest potential to influence population changes of mountain goats over time, even if recruitment was more variable. Relatively constant adult survival and variable recruitment are typical of large

herbivores (Gaillard et al. 2000, Eberhardt 2002, Gaillard and Yoccoz 2003). Despite its lower elasticity than adult survival, recruitment could be the main determinant of changes in population growth rate in some instances because it is more variable than adult survival. Therefore, it is difficult to disentangle the different contributions of these vital rates on changes in population size (Gaillard et al. 1998, Mills et al. 1999). In our study, even after considering the CV of each parameter, adult survival had a greater effect on population growth rate than recruitment. Gaillard and Yoccoz (2003) suggested that environmental canalization (i.e., selection against variability induced by environment) may occur in fitness components showing high elasticities, such as adult survival in large mammals. Consequently, adult female mountain goats may have been selected to favor their own survival over investment in current reproduction (Côté and
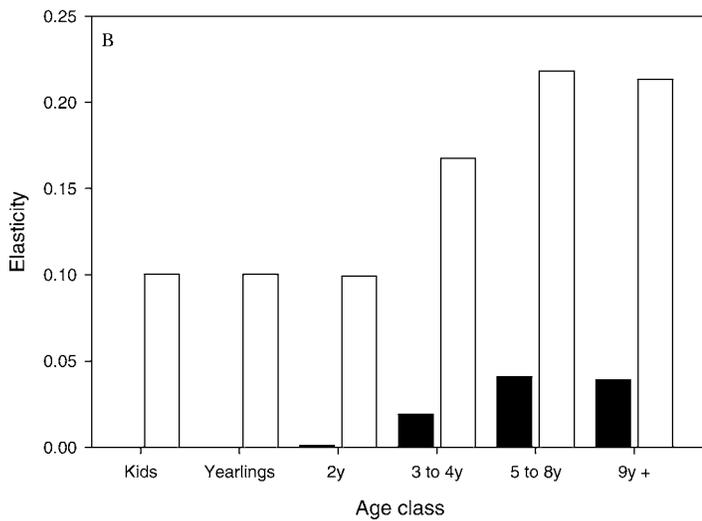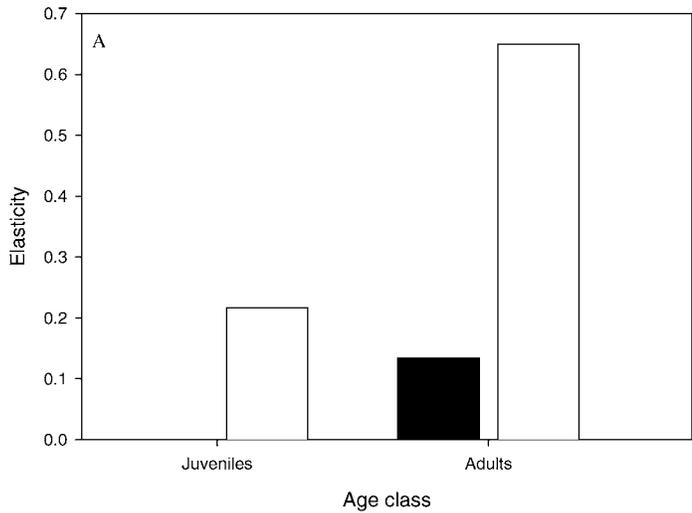
Figure 4. Elasticities of survival (open bars) and fecundity (closed bars) for various age–sex classes of the Caw Ridge mountain goat population between 1993 and 2003, according to (A) a 2-age class model combining both sexes, where juveniles refer to kids and yearlings, and (B) a 12-age-sex class model. Only elasticities for female parameters can be seen in B because elasticities for males were too small for the figure's resolution.

Table 3. Simulated effects of different modeled harvest rates and population sizes on mountain goat population growth (λ) over 20 yr and on probability of extinction (P) over 40 yr.[a]

| | Population sizes | | | | | | | |
| | **25** | | **50** | | **75** | | **100** | |
Harvest rates	λ	P	λ	P	λ	P	λ	P
2 goats harvested per year	<1	100%	<1	98%	<1	81%	<1	60%
1 goat harvested per year	<1	99%	<1	85%	<1	50%	≈1	33%
1 goat harvested per 2 yr	<1	95%	<1	60%	≈1	27%	>1	16%
1 goat harvested per 3 yr	<1	87%	<1	51%	>1	20%	>1	10%
1 goat harvested per 4 yr	<1	82%	<1	42%	>1	19%	>1	9%
1 goat harvested per 5 yr	<1	79%	<1	36%	>1	16%	>1	8%
1 goat harvested per 10 yr	<1	71%	<1	28%	>1	13%	>1	5%
1 goat harvested per 15 yr	<1	64%	<1	26%	>1	10%	>1	4%
1 goat harvested per 20 yr	<1	62%	≈1	23%	>1	10%	>1	4%
No harvest	<1	57%	>1	18%	>1	6%	>1	3%

[a] We based all values and trends on the average of 1,000 simulations for each harvest rate. Using 10,000 simulations provided equivalent results. For all simulations, harvested goats were chosen randomly among males and females aged 2 yr and older.

Festa-Bianchet 2001a,b), as suggested for other ungulates (Clutton-Brock 1991, Festa-Bianchet and Jorgenson 1998).

Wildlife managers often assume that younger females are more productive and have a greater influence on population dynamics than older females (Gaillard et al. 2000). In mountain goats, however, our results suggest that older females have a greater potential to influence population changes compared to younger females (see also Côté and Festa-Bianchet 2001a,b). This finding demonstrates the importance of sensitivity analyses in management and conservation to identify which component of a population has the greatest potential to respond to a perturbation, such as a management or a conservation action (Caswell 2001). In threatened loggerhead sea turtles (*Caretta caretta*), sensitivity analyses revealed that management efforts targeted the least responsive component of the population by concentrating on protecting eggs (Crouse et al. 1987). This life stage seemed to be more tolerant to uncertainties than other parameters of the model such as juvenile survival, and the authors suggested that these

findings may explain why recovery had not occurred despite 20 to 30 years of protecting eggs.

Our results suggest that native mountain goat populations, provided they are sufficiently large, can only tolerate harvest rates around 1% (Table 3). In introduced populations, sustainable harvest rates were estimated at 7 to 15% (Adams and Bailey 1982, Williams 1999, but see Côté et al. 2001). Introduced populations may tolerate greater harvest rates (Swenson 1985, Houston and Stevens 1988) than native populations because they often have access to better range conditions and predator-free environments, possibly leading to earlier primiparity, higher twinning rates, and greater survival of all age classes. In natural populations, however, management agencies have typically applied harvest rates of 4 to 5% (Hebert and Turnbull 1977, Kuck 1977, Smith 1988b). Recently, harvest rates greater than 3% in Alberta were deemed not sustainable (Côté and Festa-Bianchet 2003, Gonzalez-Voyer et al. 2003).

Traditionally, mountain goats were managed based on the ecology of similar-sized ungulates, such as bighorn sheep (*Ovis canadensis*), which are not as susceptible to harvest as goats. For instance, Jorgenson et al. (1993) recommended harvest of about 5% of the total winter population of ≥1-year-old sheep. This recommendation contrasts with our results suggesting a harvest strategy of about 1%. In Alberta, goat harvest rates based on minimum population estimates ranged from 4.5 to 9% between 1973 and 1987, and approximately half of harvested goats were females (Smith 1988b). Many populations experiencing those harvest rates declined (e.g., Fig. 3F,K). Our analyses suggest that these harvest rates were too high and included too many females, which may explain the decline of many mountain goat populations in Alberta during the early 1980s.

The strong effects of population size on viability could explain why some populations in Alberta have not recovered after 14 years without harvest (Fig. 3). Our results suggest that only populations of 75–100 goats can sustain some harvest. Smaller populations appear more susceptible to stochastic events and appear unable to sustain any harvest. Even without harvest, populations of 25

individuals have on average a 50% chance of becoming extinct in 40 years (Table 3). Berger (1990, 1993) found that populations of less than 50 bighorn sheep had higher chances of becoming extinct over 50 years than larger populations. He concluded that 50 individuals was not a minimum viable population size for this species (but see Wehausen 1999). Our results suggest that this situation may also occur for goat populations of less than 25 individuals in Alberta. However, immigration can have a profound influence on the persistence of small populations, and we did not consider this in the models. Indeed, some small goat populations appear to persist over time (Fig. 3), suggesting that some populations may be part of a metapopulation, where immigration could prevent population extinction or decline.

Management Implications

Our study demonstrates that we should consider several elements when managing mountain goats for harvest in order to maintain sustainable populations. First, management decisions should be herd-specific since goat population dynamics vary among populations despite geographical proximity. We should only issue tags for populations that are increasing. Our results also suggest that λ should be calculated over at least 3 years, and preferably 5 when available, as the model provided better fit when population estimates were averaged over 3 and 5 consecutive surveys. Second, we should prevent harvest of adult females, particularly those older than 5 years. We must inform hunters of the importance of selecting a male mountain goat. Managers should also provide

information on how to determine the sex of an adult mountain goat (as illustrated in Smith 1988a). Hunters should demonstrate their ability to distinguish between sexes before they receive a tag. If a female is shot, that population should not be hunted for at least one year. In addition, even though trophy horns are the primary reason why hunters harvest mountain goats, managers should promote harvesting of subadults because this strategy would lower the probabilities of extinction of populations. Third, in populations with vital rates similar to those we documented at Caw Ridge, harvest levels should be near 1% to be sustainable. Finally, hunting should not be allowed on populations of <50 individuals. Since many populations in Alberta include <50 goats, few populations can be sustainably exploitable in this province.

Acknowledgments

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