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Variation in age of primiparity in mountain goats estimated from horn growth increments

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Abstract

Variation in age of primiparity is important for population dynamics and wildlife management because it can affect population growth. Using a novel technique based on the trade-off between annual horn growth and reproduction, we estimated the age of primiparity for 2274 female mountain goats (*Oreamnos americanus*, de Blainville 1816) harvested across British Columbia, Canada, from 1976 to 2019. We then investigated spatio-temporal variation in the probability that harvested females were primiparous when aged three, four or five years and older using Bayesian ordinal regressions. We found that the probability of primiparity at three years decreased over time in nearly all mountain ranges. In the Coastal Mountain range, however, the probability of primiparity at age three significantly increased. These results suggest that the large coastal populations of mountain goats could be more resilient to harvest than other populations in British Columbia, which may be experiencing environmental effects promoting later primiparity. Models predicting age of primiparity from annual growth measures are a valuable tool for wildlife management and could help conservation of many species.

Key words: Mountain goat, *Oreamnos americanus*, primiparity, wildlife management, growth, reproduction, ungulate, increment, trade-offs

Résumé

L'âge à primiparité est une composante importante de la dynamique des populations et de la gestion de la faune, car elle peut affecter la croissance des populations. Utilisant une technique innovatrice qui se base sur les compromis entre la croissance annuelle des cornes et la reproduction, nous avons estimé l'âge à primiparité de 2 274 chèvres de montagne (*Oreamnos americanus*, de Blainville 1816) femelles en Colombie-Britannique, Canada, de 1976 à 2019. Ensuite, en utilisant des régressions ordinales bayésiennes, nous avons examiné les tendances spatio-temporelles dans la probabilité que les femelles soit primipare a trois, quatre ou cinq ans et plus. Nous avons constaté un déclin temporel de la probabilité de récolter une femelle primipare à 3 ans dans la majorité des chaînes de montagne de la province. Cependant, dans la chaîne de montagne côtière, cette probabilité augmente au fil du temps. Ces résultats suggèrent que les grandes populations de la chaîne de montagne côtière seraient plus résilientes aux récoltes annuelles que les autres populations en Colombie-Britannique qui semblent souffrir d'effets environnementaux qui retardent la primiparité. Les modèles qui prédisent l'âge à primiparité à l'aide de mesures annuelles de croissance sont un outil a fort potentiel pour la gestion de la faune et pourraient être utiles pour la conservation de plusieurs espèces.

Mots-clés : Chèvres de montagnes, *Oreamnos americanus*, primiparité, gestion de la faune, croissance, reproduction, ongulé, incrément, compromis

Introduction

Reproduction is energetically costly in female mammals (Archie *et al.*, 2014). At its peak, energy expenditure of lactating females is 2.5 to 5 times greater than non-reproducing females (Gittleman and Thompson, 1988). Despite high energetic costs, females of long-lived mammals usually adopt conservative reproductive tactics that prioritize survival and future reproductive potential over allocation to current reproduction (Festa-Bianchet and Jorgenson, 1998). Hence, in long-lived species, adult female survival is expected to show less inter-annual variation than fecundity of young females and juvenile survival (Gaillard *et al.*, 2000). Therefore, despite its high elasticity, adult survival is often less influential on population growth rate than juvenile recruitment, which generally has lower elasticity but higher variation (Gaillard *et al.*, 2000).

In long-lived mammals, females that are primiparous before reaching asymptotic size face a resource allocation trade-off between growth and reproduction (Gallant *et al.*, 2001). Lactating bighorn sheep (*Ovis canadensis* Shaw, 1804) females gain less mass than non-reproductive females of the same age (Festa-Bianchet *et al.*, 1995; Gallant *et al.*, 2001). Lactation results in a smaller body mass the following year for bison (*Bison bison*, Linnaeus, 1758) (Green and Rothstein, 1991) and possibly lower asymptotic mass in northern elephant seal (*Mirounga angustirostris*, Gill, 1866) (Reiter *et al.*, 1981). Growth versus reproduction trade-offs have also been documented in humans (*Homo sapiens* Linnaeus, 1758) where a one-year delay in age of primiparity in Finnish women was correlated to increased height

(Helle, 2008). On the other hand, studies of mountain goats (*Oreamnos americanus*, de Blainville 1816) and bighorn sheep (Hamel et al. 2009) suggest that early primiparity is typical of females that are in good condition and can reproduce early without compromising their potential lifetime reproductive success. Because of its tight link to population dynamics, for example in northern elephant seals (Reiter and LeBoeuf, 1991), age of primiparity should be considered in harvesting and conservation policies. Changes over time in age of primiparity may also reveal changes in environmental conditions, as reported for bighorn sheep (Martin and Festa-Bianchet 2012).

Multiple techniques exist to estimate when females reproduce, including direct observation, and analyses of progesterone level in blood (FLNR, 2010; Robeck et al., 2016) (mountain goat), blubber (Inoue et al., 2019) (Antarctic minke whales (*Balaenoptera bonaerensis* Burmeister, 1867)), milk (Friggens et al., 2008) (cow (*Bos taurus* Linnaeus, 1758) and feces (multiple species) (Schwarzenberger et al., 1996). These tests, however, must be done repeatedly on the same female to determine complete reproductive history (Duffield et al., 1995) (killer whale, (*Orcinus orca* Linnaeus, 1758)) and provide no information on previous reproduction. If repeatable sampling is not possible, as in most wild species, another method relies on trade-offs between growth and reproduction (Miura et al., 1987) (Japanese serow (*Capricornis crispus* Temminck, 1836)). This trade-off can be measured in traits that form distinct visible marks called annuli at the end of each growing season, for example in bighorn sheep and mountain goats (Larue et

et al., 2021). Growth between consecutive annuli is referred to as annual growth increment. Below-average annual increments could reflect a growth trade-off in reproductive years, as reported in Japanese serow, northern sea otter (*Enhydra lutris kenyoni* Wilson, 1991) and black bear (*Ursus americanus* Pallas, 1780) (Miura *et al.*, 1987; Von Biela *et al.*, 2008; Allen *et al.*, 2017). A technique used for several animals consists of measuring the width between consecutive tooth cementum annuli and comparing it to a threshold under which reproduction is predicted, with examples for black bear and northern sea otter (Coy and Garshelis, 1992; Von Biela *et al.*, 2008; Allen *et al.*, 2017). The threshold is established from individuals with observed reproductive histories. Similarly, yearly horn growth increments can estimate reproductive history in bovids (Miura *et al.*, 1987; Larue *et al.*, 2021). For example, young lactating mountain goats and bighorn sheep had lower horn growth than non-lactating females of the same age (Larue *et al.*, 2021). In many bovids, increments can be easily measured at a much lower cost than tooth cementum annuli. Unlike tooth annuli, horn growth increments can be measured on live animals without causing pain or removing teeth. These measures can also be collected post-mortem and could easily be included in established registration protocols for hunted species.

Variability in age of primiparity can substantially affect individual fitness (Bell, 1980) and population dynamics (Reiter and LeBoeuf, 1991; Descamps *et al.*, 2006). In ungulates, age of primiparity is also one of the vital rates most sensitive to changes in environmental conditions (Gaillard *et al.* 2000). Consequently, long-term

monitoring of changes in age of primiparity could provide information on trends in environmental suitability. In mountain goats, late primiparity and low recruitment could explain high sensitivity to hunting, which is mostly additive to natural mortality (Smith, 1986; Smith, 1988; Festa-Bianchet *et al.*, 1994; Côté and Festa-Bianchet, 2001b). The additive nature of mountain goat hunting mortality contributed to declines in several populations in Alberta (Hamel *et al.*, 2006). A hunting closure in 1987 allowed partial recovery of four declining populations (Gonzalez-Voyer *et al.*, 2003). A greater rate of population growth may allow higher harvest rates, especially considering that hunters cannot always reliably identify the sex of mountain goats from a distance, and up to a third of the harvest is made up of females (Festa-Bianchet and Côté, 2008). Information on age of primiparity could help establish hunting regulations to avoid population declines.

Our main objective was to examine spatial and temporal variation in age of primiparity for mountain goats across British Columbia (BC), Canada. We first validated a model to predict age of primiparity from the length of horn growth increments using data from females of known age of primiparity. We then used this model to predict age of primiparity of females harvested across BC from 1976 to 2019. Finally, we evaluated the effect of spatial and temporal factors on age of primiparity of harvested goats. Given substantial climate change during the study period (IPCC, 2021), we examined possible temporal trends. We expected to find spatial variation because mountain goats near the Pacific coast have been reported to have a younger age of primiparity (Smith, 1984; Houston *et al.*, 1991)

than inland goats (Festa-Bianchet and Côté, 2008; FLNR, 2010). Some coastal populations with a younger reported age of primiparity, however, were introduced outside their native range, and introduced mountain goats typically show greater productivity than native populations (Williams, 1999). All populations included in our study, however, were native.

Material and methods

Study areas and data collection

Growth data

Mountain goat horns grow around the inner bony core, from the base upwards, so that previous increments move further from the skull each year. During their first winter (at 6-11 months of age), mountain goat horns do not completely stop growing (Festa-Bianchet and Côté, 2008). The first clearly visible annulus, a ring around the horn (Figure 1), thus appears at 1.5 years during the second winter (Brandborg, 1955). Then, an additional annulus appears following each winter (Festa-Bianchet and Côté, 2008).

When a mountain goat is harvested during the hunting season, generally from August to November, its age can be determined by adding one to the number of visible horn annuli, although for goats older than 5 years the technique is less reliable (Stevens and Houston, 1989). Here, we will refer to the age at last birthdate. Given the short parturition season in late May and early June (Côté and Festa-Bianchet, 2001a), a goat harvested in September aged 4 years and 4

months will be referred to as a 4-year-old. We only considered horn increments 3 and 4, grown in the summers when the female was aged 3 and 4 years, because the lowest age of primiparity in our validation data is three years and accuracy to age individuals with annuli decreases for older goats (Steven and Houston, 1989). To our knowledge, primiparity at age two in native populations was only reported in one study (Smith, 1984).

Caw Ridge

Caw Ridge (54°N, 119W°), Alberta, Canada, comprises 28 km² of alpine tundra and open subalpine forest. Since 1989, goats have been captured in traps baited with salt and those older than two years old were chemically immobilized (Haviernick *et al.*, 1998). Adult females were marked with a collar with a distinctive pattern and colour. The length of every horn growth increment was measured at each capture (Côté *et al.*, 1998). Female reproduction and age of primiparity were determined in the field by female-kid associations during repeated censuses each year. Of 254 females captured at Caw Ridge, 40 females of known reproductive success and horn growth increment lengths were kept for analyses. Animal-handling procedures at Caw Ridge were approved by the Animal Care Committee of Université Laval, affiliated with the Canadian Council on Animal Care (protocol 2019-242, VRR-18-033). Ear tissue samples are kept at Laval University and are available for further species confirmation.

British Columbia

The British Columbia Ministry of Forest, Lands, Natural Resource, Operations and Rural Development (FLNR) provided us with data from compulsory inspections of harvested mountain goats from 1976 to 2019. Sex, age and distance from horn tip to all annuli were recorded by a government employee or private contractor (FLNR, 2018). The hunter provided GPS coordinates of the harvest location. Before GPS units became widely available, hunters showed locations on a map. Later, these locations were transformed in GPS coordinates. Horn measurements were done with a measuring tape. Annual horn growth increment length was calculated by subtracting the length between horn tip and an annulus from the length between horn tip and the next annulus.

Data analyses

Predicting age of primiparity

All statistical analyses were done using *R* version 4.04 (R Core Team, 2021) and Bayesian regressions used the package *brms* version 2.15.0 (Bürkner, 2018). Code is available in supplementary materials. We compared the mean and standard deviation (sd) for the third and fourth increment between individuals from Caw Ridge and British Columbia. We created three horn growth indexes (HGI) to overcome multicollinearity between previous increment length (increment $x-1$), previous horn length (sum of all increments before increment x), current increment length (increment x) and age (Dormann *et al.*, 2013). These indexes are the residuals from Bayesian gaussian regressions of the log of previous increment length, previous total horn length and current increment length on age as a factor.

Individual identity (ID) was added as a random intercept to account for individual variation and avoid pseudo-replication. These indexes were created with Caw Ridge and British Columbia data merged and represent age-independent previous, previous total and current horn growth, with positive values representing above-average growth for a given age. Previous HGI ranged from -2.26 to 0.96, previous total HGI ranged from -0.10 to 0.08 and current HGI ranged from -2.06 to 1.42.

We included different combinations of HGIs and age of Caw Ridge females with known reproductive history in six competing Bernoulli Bayesian regressions with a logit link function to predict female lactation status (0 = no lactation and 1 = lactation; Table S1). From our candidate set, we selected the model with the lowest leave-one-out cross-validation information criterion (LOOIC) (Bürkner, 2018; Vehtari A *et al.*, 2020) for further analyses (Tables S1 and S2). All models were run for 20 000 iterations with a warmup of 10 000 iterations. Model convergence was assessed using the Gelman-Rubin statistic (Gelman and Rubin, 1992), effective sample size (ESS) and visual inspection of the four Markov chains (Gelman *et al.*, 2013). The selected model was validated using 8-fold block cross-validation (Roberts *et al.*, 2017) in which Caw Ridge females with known age of primiparity were used to establish age-specific binary classification thresholds to predict primiparity. Following Larue *et al.* (2021), the threshold for 3-years-olds was set by maximizing the sum of true positives and true negatives using the *roc* function of the *pROC* package version 1.17.01.1 (Robin *et al.*, 2011). If a female was predicted to have reproduced at three years, we considered this her age of

primiparity. Females predicted to be primiparous at three cannot be primiparous at a later age. Because this condition could not be implemented in the *pROC* package, we used a *for* loop to create a confusion matrix (Kuhn, 2020) for every threshold between 0 and 1 at 0.005 intervals for four-year-old goats. The mean of the thresholds with the highest cumulative true positives and true negatives was chosen as the 4-year-old threshold. Females not predicted to have reproduced before five years were classified as primiparous at five years or older (5+). Finally, we used the *predict* function and the previously selected model to predict age of primiparity of harvested female goats across British Columbia using the horn growth data from compulsory inspections and the established thresholds.

Factors affecting age of primiparity

We divided the province according to mountain ranges that represent large-scale spatial variation in precipitation, temperature, genetics, geological formations and topography (Shafer *et al.*, 2010; Demarchi, 2011; Hasler *et al.*, 2015; Coxson *et al.*, 2019). Therefore, mountain goats from different ranges could be primiparous at different ages. GPS coordinates were projected in ArcGis 10.5 (ESRI, 2016) to classify harvested individuals in their respective mountains range. The few individuals reportedly harvested in the interior plateau and interior plains were assigned to the nearest mountain range since there are no censused goat populations in these regions (Figure 2). Year of harvest was also included to evaluate potential temporal variation in age of primiparity. Five models including different combinations of the fixed effects of mountain range, year of harvest and

their interaction were parametrized and compared using LOOIC (Bürkner, 2018; Vehtari A *et al.*, 2020) (Table S4). We present estimates from the model with the lowest LOOIC (Table 1). All models were run for 20 000 iterations with a warmup of 10 000 iterations.

Finally, to evaluate potential impacts of changes in age of primiparity on population growth, we used simulations with female-only Leslie population matrices (Caswell, 2001; Hamel *et al.*, 2006). The 13x13 population matrix M of age-specific survival and reproduction was:

$$M = \begin{pmatrix} 0 & 0 & F_2 & F_3 & F_4 & F_5 & F_6 & F_7 & F_8 & F_9 & F_{10} & F_{11} & F_{12+} \\ S_0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & S_1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & S_2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & S_3 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & S_4 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & S_5 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & S_6 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_7 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_8 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_9 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_{10} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_{11} & S_{12+} \end{pmatrix}$$

Note that reproduction refers only to the probability of producing a female offspring. We used data from the Caw Ridge population to establish a baseline matrix (Festa-Bianchet and Côté 2008; Figure S1). We first moderately increased primiparity at three years by increasing fecundity of 3-year-olds (F_2) to that measured for 4-year-olds (F_3) (from 0.018 to 0.235, Figure S1). All other vital rates remained unchanged. For the second simulation, we highly increased primiparity at three

years to 0.3948, the fecundity of females aged 6-10 years (Figure S1) which have the highest fecundity at Caw Ridge (Festa-Bianchet and Côté, 2008). To simulate no primiparity at age three, we set fecundity F_2 at zero in a third simulation. Finally, to simulate a population where primiparity was delayed to five years (F_4) or older, we set F_2 and F_3 to zero in a fourth simulation. The function *eigenanalysis* from the package *demogR* (Jones, 2018) was used to extract values of lambda.

Results

Comparison of horn growth increments

The average length of the third horn growth increment of mountain goat females was 19.9 mm (sd = 5.3) at Caw Ridge and 16.6 mm (sd = 7.94) for those harvested in British Columbia. For the fourth increment, average length was 7.5 mm (sd = 3.25) at Caw Ridge and 8.1 mm (sd = 4.30) for females harvested in British Columbia (Figure S2 and S3).

Predicting age of primiparity

Model one, which included fixed effects of current horn growth index and age was selected to predict reproductive status since it had the lowest LOOIC amongst our candidate set (Table S1). Based on this model, a four-year-old female with an HGI of -0.25 has a 0.40 [95% CI: 0.10, 0.78] probability to have reproduced (Figure 3). A three-year-old female with the same HGI had a 0.74 [95% CI: 0.51, 0.90] probability to have reproduced (Figure 3). Using model 1 in an 8-fold cross validation, we set the binary classification thresholds to predict primiparity at 0.11

on the response scale at age 3 and 0.38 at age 4. Therefore three-year-old females with predictions over 0.11 on the response scale were predicted to have been primiparous at three. Our cross-validated predictions had high balanced accuracy for Caw Ridge females at 95.95%, 90.54% and 87.50% for primiparity at ages of three, four and five plus, respectively (Table S3). Model sensitivity, which is the percentage of Caw Ridge females whose age of primiparity was correctly assessed, was 100%, 94% and 75% at the ages of three, four and five plus, respectively (Table S3). Age of primiparity of harvested females in BC was predicted using model 1 and the stated classification thresholds. The model predicted that 1043 females were primiparous at three, 629 at four and 602 at five or more years.

Factors affecting age of primiparity

Model one, which included fixed effects of mountain range, year and the interaction between mountain range and year, had the lowest LOOIC (Tables 1 and S4). Based on this model, we found an overall trend for later primiparity over time. The probability of being primiparous at 3 years increased over time for coastal females from 0.44 [95% CI: 0.38, 0.50] in 1976 to 0.54 [95% CI: 0.45, 0.63] in 2019. The temporal trend, however, was opposite in all other mountain ranges (Table 1). The smallest decrease was in the Columbia Mountains from 0.49 [95% CI: 0.37, 0.61] in 1976 to 0.46 [95% CI: 0.28, 0.65] in 2019 (Figure 4). The largest decrease was in the Rocky Mountains from 0.57 [95% CI: 0.51, 0.64] in 1976 to 0.38 [95% CI: 0.29, 0.49] in 2019 (Figure 4). The probability of being primiparous at 4 years was

similar across mountain ranges and showed little variation over time (Figure 4). The probability of being primiparous at 5 years decreased over time for coastal mountain goats from 0.28 [95% CI: 0.22, 0.35] in 1976 to 0.18 [95% CI: 0.11, 0.27] in 2019. Goats in all other mountain ranges had increasing probabilities of late primiparity over time (Table 1). The smallest increase was in the Columbia Mountains from 0.24 [95% CI: 0.13, 0.37] in 1976 to 0.26 [95% CI: 0.11, 0.48] in 2019, the largest in the Rocky Mountains from 0.16 [95% CI: 0.11, 0.21] in 1976 to 0.35 [95% CI: 0.23, 0.47] in 2019 (Figure 4). An interactive map of spatio-temporal variation in age of primiparity in harvested mountain goats across BC is available at https://bcmountaingoat.shinyapps.io/Probabilite_BC/ (code for map creation was based on Verkroost (2019)).

Impacts of age of primiparity on population growth

When used to populate our baseline Leslie population Matrix, survival and fecundity estimates from Caw Ridge in Festa-Bianchet and Côté (2008) suggested a growth rate of 4.5% a year. In Simulation 1, when the probability of conception and subsequent fecundity of 2-year-olds was set to that of 3-years olds, population growth rate increased to 6.7%. In simulation 2, which increased fecundity of 3-years-old to the highest age-specific fecundity in the baseline matrix, population growth rate increased to 7.0%. In Simulation 3, with no female primiparous at three years, population growth rate slightly decreased to 4.4%. In Simulation 4, with no female primiparous before age 5, population growth rate decreased to 3.2%.

Discussion

We parameterized a model based on the trade-off between horn growth and reproduction to predict age of primiparity in female mountain goats across British Columbia, Canada. We first validated our model by showing it accurately predicted age of primiparity in females with known reproductive history at Caw Ridge, Alberta. We assumed that annual horn growth of lactating and non-lactating females at Caw Ridge was representative of species-wide patterns. This assumption appears reasonable given similarities in horn growth. The longer third increment at Caw Ridge compared to populations in British Columbia is likely due to the rarity of primiparity at age three in the Caw Ridge population (Festa-Bianchet and Côté, 2008). Using the validated model, we then estimated out of sample predictions of age of primiparity of harvested females across British Columbia. Finally, our Bayesian ordinal model highlighted potential spatio-temporal trends in the probability that harvested female goats were primiparous at different ages. The main difference between mountain goats monitored at Caw Ridge and harvested in British Columbia was the prevalence of lactation among 3-year-olds. To further validate if horn growth reliably measures age of primiparity, it would be useful to inspect reproductive organs of 3-year-olds harvested in British Columbia.

Long-term data collected from harvested animals have several advantages such as large sample sizes, ample geographical coverage, and the possibility of comparing populations subjected to different climates and hunting regulations (Mysterud *et al.*, 2000; Yoccoz *et al.*, 2002; Mysterud *et al.*, 2005b; Mysterud *et*

al., 2005a). These data, however, also have disadvantages such as one-time sampling and possible biases induced from hunter selectivity (Martinez *et al.*, 2005; Mysterud *et al.*, 2006). By examining growth over multiple years in a trait that preserves clear yearly annuli, our approach overcomes the typical limitations of one-time sampling. Hunter selectivity bias should also be negligible because analyses were limited to females shot when at least four years old. After this age, female horn length shows little variation in residual growth, as more than 86% of horn growth is completed (Festa-Bianchet and Côté, 2008). Despite potential limitations, harvest data from compulsory inspections enabled us to infer general trends of spatial and temporal variation in age of primiparity at the species level, because British Columbia holds more than half the global mountain goat population (FLNR, 2010).

Our results underline temporal trends in the probability that harvested female goats were primiparous at different ages in mountain ranges across BC. In support of previous studies, we found notable variation between females from coastal and interior mountains (Hebert and Turnbull, 1977; Smith, 1984; Houston *et al.*, 1991; Festa-Bianchet and Côté, 2008). Although Hebert and Turnbull (1977) reported that recruitment and productivity of coastal females was lower than interior females in Southeast BC, later studies found that coastal goats had earlier ages of primiparity than their inland counterparts (Smith, 1984; Houston *et al.*, 1991; Festa-Bianchet and Côté, 2008; FLNR, 2010). Our analyses suggest that both Hebert and Turnbull (1977) and later studies are likely correct, because primiparity was

earlier among inland goats in 1976 but was significantly earlier among coastal goats by 2019 based on our model. Our result for coastal goats could also apply to southeastern Alaska which holds most of the coastal land between the Pacific Ocean and northern British Columbia. Because annuli are not measured for harvested goats in Alaska, trends in age of primiparity remain unknown.

Variation in temporal trends in age of primiparity among mountain ranges has important implications for mountain goat conservation. The increase in age of primiparity in most of British Columbia suggests a reduced rate of population growth, and implies that these populations have become more sensitive to harvest in recent decades (Gaillard *et al.*, 2000; Festa-Bianchet and Côté, 2008). Our simulations suggest that changes in age of primiparity within the range we observed could lead to a 2-2.5% change in annual population growth. Under the light harvests typical for mountain goats (Hamel *et al.* 2006), a 2% change could make the difference between a sustainable harvest and a population decline, assuming all other vital rates remain unchanged. Previous research on mountain goats has shown short-term costs of early primiparity (Hamel *et al.*, 2010) but over the lifetime, early primiparity is generally correlated with greater reproductive success (Hamel *et al.*, 2009; Martin and Festa-Bianchet, 2012). We suggest that early primiparity is a sign that environmental conditions are favorable and females can develop more rapidly. Early primiparity could therefore be positively correlated with other population-level vital rates such as juvenile survival.

Our analyses suggests that goat populations in the Rocky Mountains and Stikine Plateau are currently the most sensitive to sport harvest, based on late primiparity of harvested females. On the other hand, coastal populations appear less susceptible. Overall, a conservative management policy should be prioritised because of current negative repercussions of anthropogenic climate change on mountain goat demographic rates (White *et al.*, 2018). It is possible that the overall temporal trend for later primiparity that we report may partly reflect the consequences of climate change. Warmer temperatures have been associated with decreasing growth and recruitment in chamois (*Rupicapra rupicapra* Linnaeus, 1758) in the Alps (Ruggetti and Festa-Bianchet, 2012; Chirichella *et al.*, 2021), but increased horn growth of ibex (*Capra ibex* Linnaeus, 1758) in Switzerland (Büntgen *et al.*, 2014).

Predicting the reproductive history of females based on simple measures of yearly growth holds much potential to assist the management and conservation of multiple species from many ecosystems. Here, by applying the method to growth measures collected from compulsory inspections of harvested individuals, we underlined its ease of use and practicality (Allen *et al.* 2017; Larue *et al.* 2021). Like mountain goats, female Japanese serow (Miura *et al.*, 1987), chamois (Ruggetti and Festa-Bianchet, 2011) and ibex (Büntgen *et al.*, 2018) have growth annuli on their horns that could be easily measured on harvested individuals. Extensive datasets including horn growth increment lengths of females harvested across large geographical areas are already available for some species (Ruggetti

and Festa-Bianchet, 2011; Reiner *et al.*, 2020). Similarly, the width between tooth cementum annuli could be measured and used in other species (Tochigi *et al.*, 2018). The greatest challenge to wide use of models that predict the reproductive status of females based on their growth remains the difficulty of obtaining validation data from females with known reproductive success. Data from semi-captive individuals could potentially help alleviate the sample size issue at low cost. Promisingly, our study shows that precise models can be parametrized with a relatively low sample of validation data (Larue *et al.* 2021). We therefore encourage new and continued efforts to collect high quality growth and validation data. For instance, our sample size could have benefited from 5 721 additional harvested female mountain goats in BC that were removed from our data because of incomplete or absent measures of horn growth increments.

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Authors' contribution

CR and MFB collected data. CR conceived the project, analyzed data and wrote the first draft of the manuscript. BL and MFB contributed to conceiving the project and BL oversaw analyses. All authors contributed to writing and revising the manuscript.

Data availability statement

The British Columbia hunting data are the property of the FLNR and were leased to us via a confidentiality agreement.

Competing interests statement

The authors declare there are no competing interests.

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Figure 1: Horns of a mountain goat (*Oreamnos americanus*, de Blainville 1816) female aged 3 years. The white bar represents the second horn growth increment (grown in the third year of life) situated between the first annulus on top and the second annulus on the bottom. The first increment (grown in the first 2 years of life) is from the tip of the horn to the first annulus. Picture by Emmanuelle Marchand.

Figure 2: Mountain ranges in British Columbia, Canada (DataBC, 2021). Dots show the harvest location of 2274 female mountain goats (*Oreamnos americanus*, de Blainville 1816) between 1976-2019 considered in this study. Individuals from the Interior Plateau and Interior plains were assigned to the nearest mountain range. Create with ArcMap 10.5 and projected with NAD 1983 BC Environment Albers coordinate system.

Figure 3: Lactation probability as a function of horn growth increment index (HGI) for mountain goat females (*Oreamnos americanus*, de Blainville 1816) aged 3 and 4 years at Caw Ridge, Alberta, Canada, 1989-2020.

Figure 4: Variation in the probability of harvesting mountain goat females (*Oreamnos americanus*, de Blainville 1816) that were primiparous at different ages between 1976 and 2019 in the different mountain ranges of British Columbia.

Table 1: Coefficients (β – on the logit scale) of fixed effects with corresponding 95% credible intervals (95% CI) of variables included in the selected model assessing the determinants of age of primiparity in mountain goats (*Oreamnos americanus*, de Blainville 1816) harvested in British Columbia, 1976-2019. The coastal mountain range is the reference represented by intercepts 1 and 2.

Variable	β	95% CI
Intercept 1	-18.1	[-42.6; 6.2]
Intercept 2	-17.9	[-42.4; 6.5]
Columbia Mountains	-23.3	[-81.0; 34.4]
Rocky Mountains	-54.2	[-91.3; -17.5]
Skeena Mountains	-24.8	[-54.8; 5.0]
Stikine Plateau	-34.9	[-74.0; 4.27]
Years	-0.0091	[-0.0214; 0.0032]
Columbia Mountains : Years	0.012	[-0.017; 0.041]
Rocky Mountains : Years	0.027	[0.009; 0.046]
Skeena Mountains : Years	0.013	[-0.002; 0.028]
Stikine Plateau : Years	0.018	[-0.002; 0.037]

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