RESEARCH ARTICLE

Growth and reproduction trade-offs can estimate previous reproductive history in alpine ungulates

Benjamin Larue[1] [iD] | Fanie Pelletier[1] | Steeve D. Côté[2] | Sandra Hamel[2] |
Marco Festa-Bianchet[1]

[1]Département de biologie, Université de Sherbrooke, Sherbrooke, QC, Canada

[2]Département de biologie and Centre d'études Nordiques, Université Laval, Québec, QC, Canada

Correspondence
Benjamin Larue
Email: benjamin.larue@usherbrooke.ca

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Abstract

1. Life-history theory predicts energy allocation trade-offs between traits when resources are limited. If females reduce allocation to growth when they reproduce, annual growth could reveal past reproductive effort, which would be useful to assess population dynamics and harvest sustainability. The potential and accuracy of growth measures for predicting reproductive success have rarely been evaluated with individuals with known reproductive history.

2. We used long-term monitoring of annual growth and reproduction of marked female bighorn sheep and mountain goats, two species in which primiparity normally occurs well before growth completion, to evaluate growth versus reproduction trade-offs and their potential for predicting reproductive history of young females using mixed models and 10-fold block cross-validation.

3. We documented a significant reduction in mass gain and horn growth in young reproducing females of both species. This trade-off was affected by individual differences in energy acquisition and allocation because population density and previous allocation to growth affected the trade-off. We then parameterized models to predict individual reproductive history of young females based on the growth traits subjected to a reproductive trade-off.

4. The accuracy of predictive models ranged from 85.2% to 91.0% across species and traits, indicating that growth is a good predictor of reproductive history. This method is especially useful for population management of species with traits that form permanent visible yearly annuli because they retain a record of annual growth that allows retrospective estimation of reproductive history over multiple years.

5. *Synthesis and applications*. We show that because growth significantly decreased in years of allocation to reproduction, annual growth increments provide insights on reproductive history of young females. Population or temporal differences in reproduction of young females affect demographic rates and sustainable harvest. Growth measures of traits that form yearly annuli, such as teeth and horns, could be easily obtained at a low cost from animals harvested or found dead in multiple species. Thus, predictive models of reproductive history based on annual growth could assist conservation and management in a broad range of species.

1 | INTRODUCTION

In iteroparous species, trade-offs between current and future reproduction should determine the frequency of reproductive events (Stearns, 1992; Williams, 1966). Early reproduction can lead to substantial life-history costs, such as reductions in growth, survival and future reproductive potential (Williams, 1966). Early reproduction before growth completion, however, can be advantageous if delaying primiparity reduces reproductive lifespan or when future reproductive potential is reduced by high mortality (Hechinger, 2010). Thus, early reproduction at a smaller size should be particularly favoured in species with a short and seasonally fixed breeding season for which not reproducing implies surviving a full year before the next potential reproductive event (Dmitriew, 2011).

Reproduction before growth completion forces a trade-off with growth in a broad range of taxa in both plants and animals (Stearns, 1992). When growth is subjected to a reproductive trade-off, individual differences in growth can partly arise from differences in reproductive status. If the negative effect of reproduction on growth is measurable, annual growth could be a proxy of reproductive effort. Given that growth versus reproduction trade-offs have been confirmed in many taxa (Stearns, 1992), traits that preserve measurable annual growth increments could potentially be used to retrospectively estimate reproductive history in several species. For example, annual growth increments in teeth and horns of some mammals may provide information about reproductive history over multiple years. Previous studies have retrospectively assessed female reproductions using length of horn growth increments in Japanese serow *Capricornis crispus* (Miura et al., 1987), and width of tooth cementum annuli in black bears *Ursus americanus* (Allen et al., 2017; Coy & Garshelis, 1992), Asian black bears *Ursus thibetanus* (Tochigi et al., 2018), grizzly bears *Ursus arctos* (Matson et al., 1999), polar bears *Ursus maritimus* (Medill et al., 2010), sea otters *Enhydra lutris kenyoni* (von Biela et al., 2008), ringed seals *Pusa hispida* (Nguyen et al., 2017) and dolphins genus *Stenella* (Klevezal' & Myrick, 1984). Traits that form growth annuli may provide information on reproductive effort over multiple years, but their reliability has seldom been tested with a sample of animals with known reproductive history.

Several confounding factors may affect the detectability of growth versus reproduction trade-offs, partly explaining the limited success of earlier attempts using growth as the sole predictor of reproductive success (Medill et al., 2010; Miura et al., 1987). Reduced accuracy could result from individual heterogeneity in energy allocation to reproduction and growth (Hamel et al., 2009). The growth versus reproduction trade-off can be simplified as:

$$A_i = G_i + R_i \qquad (1)$$

$$G_i = \beta_i A_i \qquad (2)$$

$$R_i = (1 - \beta_i) A_i \qquad (3)$$

where A is the total energy acquired by an individual i, G is the allocation to growth, R is the allocation to reproduction and β is a partitioning parameter bounded between 0 and 1 (van Noordwijk & de Jong, 1986). Based on Equations 2 and 3, the detectability of a trade-off could be diminished by large individual differences in total energy acquired (A_i) and/or in energy partitioning between the two traits (β_i; van Noordwijk & de Jong, 1986). If there are large differences in total energy acquired, individuals with more energy could potentially allocate more to both growth and reproduction than individuals with less energy (van Noordwijk & de Jong, 1986). Possible sources of differences in energy acquisition include changes in population density and environmental conditions, or differences in resource availability within home ranges (Ruf et al., 2006). A factor that can affect energy partitioning is previous growth. Indeed, individuals with reduced growth the previous year could compensate by increasing allocation to current growth (increase β_i; Hector & Nakagawa, 2012).

Accurate models that retrospectively assess reproductive history based on growth measurements are appealing for both applied and fundamental reasons. These models could be used in ecological studies when growth is known, but reproductive history is not. This is particularly interesting for long-term studies in which better model validation could be made through larger sample sizes. Predictive models could also assist species management and conservation. In species for which females are hunted (e.g. bears, seals, bighorn sheep *Ovis canadensis*, mountain goats *Oreamnos americanus*, Japanese serow, ibex *Capra ibex* and chamois *Rupicapra rupicapra*), growth data can be collected from harvested females at low cost and be used for retrospective determination of age at primiparity and reproductive history of young females. Age at primiparity is particularly important in the demography of long-lived species (Gaillard et al., 1998, 2000). Accurate estimates of this parameter could help managers determine appropriate hunting quotas (Skalski et al., 2010). For example, mountain goats are thought to be highly vulnerable to harvest partly because of the late age of primiparity (Festa-Bianchet & Côté, 2008).

Here, we investigated whether mass gain and horn growth accurately predict reproductive events in females of two seasonally breeding mountain ungulates: bighorn sheep and mountain goats. In both species, horn growth stops in winter. When growth resumes the following spring, a distinct annulus is formed, allowing a precise measurement of horn growth each year as the segment between successive annuli. Using longitudinal data on marked individuals, we first fitted exploratory models that investigated potential reproductive costs on growth. This first step was essential as it allowed identifying the growth traits subjected to a reproductive trade-off. Second, we fitted predictive models of reproductive success based

on growth of the traits that suggested a reproductive trade-off while accounting for confounding variables. Finally, we evaluated the predictive accuracy of these models using cross-validation. We focused on females because the occurrence of this trade-off is unlikely in male ungulates because male reproductive effort is mainly during the rut, which happens after the growing season (Pelletier et al., 2006).

2 | MATERIALS AND METHODS

2.1 | Study areas and data collection

2.1.1 | Bighorn sheep

The study area consists of 38 km^2 of subalpine meadows and alpine tundra on Ram Mountain (52°N, 115°W), Alberta, Canada. From 1972 to 2018, sheep were captured in a corral trap baited with salt from late May to late September, and individually marked with ear tags or visual collars. Resighting probability of females was >99% (Festa-Bianchet et al., 2003). Age of all individuals was known because they were first captured as lambs or yearlings. The length of the previous year's horn growth increment was measured at first capture each year, typically in late May or early June. At each capture, mass was measured to the nearest 250 g with a Detecto spring scale. We adjusted repeated masses of all individuals to 15 September using mixed models (Martin & Pelletier, 2011). Annual mass gain was determined by subtracting the mid-September mass of year t_{-1} from that of year t. Reproductive status was determined by observations of ewes nursing a lamb. Only females that incurred some costs of lactation, including those whose lamb died pre-weaning (<5%), were considered reproductive. Ewes whose lamb died at birth were not considered reproductive. Lamb sex was determined at first capture. Density was measured each year in June as the number of adult females (≥2 years old) because of sexual segregation (Ruckstuhl, 1998).

2.1.2 | Mountain goats

Mountain goats were studied at Caw Ridge (54°N, 119°W), Alberta, Canada. The study area consists of c. 28 km^2 of alpine tundra and subalpine open forest. From 1990 to 2018, goats were captured from late May to mid-September with traps baited with salt. Goats ≥3 years were chemically immobilized (Haviernick et al., 1998). All goats were fitted with a visual collar and/or plastic ear tags at first capture. Resighting probability of females exceeded 99% (Festa-Bianchet & Côté, 2008). Age of most goats was known because they were either captured as juveniles or were aged by counting horn annuli, a reliable technique up to about 7 years of age (Stevens & Houston, 1989). The length of all visible horn growth increments was measured at every capture (Côté et al., 1998). Captured individuals were weighted to the nearest 0.5 kg with a spring scale. Beginning in

2001, mass was also recorded to the nearest 0.5 kg using remotely controlled electronic platform scales baited with salt. We adjusted repeated mass measurements of adult females to 15 July using the average rates of summer mass gain for five age classes (3, 4, 5, 6 and ≥7 years old) obtained from linear mixed models (Hamel et al., 2010). Annual mass gain was determined by subtracting mass adjusted to 15 July of year t_{-1} from mass adjusted to 15 July of year t. We did not adjust mass to September as for bighorn sheep because few mass measurements were recorded after July. Reproductive status was determined by observations of females nursing a kid. Only lactating females, including those for which their kid died pre-weaning (<12%), were considered reproductive. Kid sex was determined by observations of the black vulvar patch in females or by urination posture. Population density was measured in June as the number of adult females (≥2 years old; Festa-Bianchet & Côté, 2008).

2.1.3 | Growth data

Only horn growth increments 3–6 were used because later horn growth is negligible or absent (Stevens & Houston, 1989). These increments represented growth when 2–5 years old for bighorn ewes, and when 3–6 years old for female goats because the first increment in goats grows over the first 1.5 years of life. For mass gain models, ages 2–5 were used for bighorn ewes and ages 3–6 for goats, based on the minimum age of primiparity and on when females attain asymptotic mass in each species (Côté & Festa-Bianchet, 2001; Marcil-Ferland et al., 2013).

2.2 | Statistical analyses

2.2.1 | Exploratory growth models

All statistical analyses were performed in R version 3.5.2 (R Core team, 2018). To explore the determinants of annual horn growth and mass gain, we fitted four models, one for each growth trait in each species. Models included five main variables: age, reproductive status, density, North Pacific Index (NPI; Trenberth & Hurrell, 1994) and previous growth. We used the November–March anomalies of the NPI as a global climate index for environmental conditions in winter, with high NPI values representing cold and snowy winters in both study areas (Hamel et al., 2009). The models also included six interactions: reproductive status*age, reproductive status*density, reproductive status*previous growth, reproductive status*North Pacific Index, previous growth*age and density*North Pacific Index. Each model was fitted as a linear mixed effects model using the *lmer* function in the LME4 package (Bates et al., 2014). Age was fitted as a polynomial in all models, using Akaike's information criterion corrected for small sample sizes (AIC$_c$; Burnham & Anderson, 2004) to select the appropriate polynomial degree. To circumvent multicollinearity between age and previous growth, we used the residuals of the regression of

the previous year's total horn length or adjusted mass with age (Dormann et al., 2013). These residuals (hereafter referred to as 'previous growth index') measure the age-independent effect of previous growth, with positive values representing above-average growth for a given age. Previous growth index ranged from −9.54 to 7.26 cm, −17.6 to 15.9 kg, −5.35 to 3.13 cm and −16.9 to 12.5 kg for sheep horn growth, sheep mass gain, goat horn growth and goat mass gain, respectively. We included population density and NPI to account for yearly differences in resource availability. We included year as a random intercept to account for annual variation in unmeasured environmental variables. The model for goat horn growth showed a singular fit estimating the year random intercept at zero. We thus removed the year random intercept for that model. Finally, we added individual identity (ID) as a random intercept to control for non-independence in repeated measurements of the same individuals (362 annual horn growth measures on 186 sheep; 877 annual mass gain measures on 257 sheep; 157 annual horn growth measures on 49 goats and 277 annual mass gain measures on 103 goats).

2.2.2 | Predictive reproductive success models

We modelled 4 sets of 22 competing hypotheses to develop predictive models of past reproductive events that we compared to a null model (Table S1). We fitted generalized linear mixed models with reproductive status as the response variable using the *glmer* function with a binomial family and a logit link function. We attempted to include random intercepts for both year and ID in all models but only retained year because of singular fit. We included the 'previous growth index' described above and calculated a 'current growth index' as the residual of the regression of current horn increment length or mass gain with age. Predictive models included the modulating parameters accounted for in the exploratory growth models, but reproductive status was replaced by current growth index (Table S1). Age was included as a factorial variable in the predictive models.

　　To select the most parsimonious models among each candidate set, we used an AIC_c model selection in which all models within $\Delta AIC_c < 2$ were considered as providing equivalent fit to the data. We then evaluated the predictive accuracy of the selected models using 10-fold block cross-validation (Roberts et al., 2017). Block cross-validation implies separating folds of data strategically rather than randomly (e.g. excluding observations on an individual basis, with all observations from a single individual removed together). Blocking at the individual level was used to avoid overestimation of predictive accuracy from pseudoreplication, and to allow predictions for new individuals as would be typical in a conservation or management context. To optimally classify each prediction, we determined the binary classification threshold that maximized the sum of true positive and true negative rates using the *roc* function of the pROC package (Robin et al., 2011). Model accuracy was determined as the sum of true positives and true negatives over total predictions × 100

with the *confusionMatrix* function of the CARET package (Kuhn, 2008). We selected the model with the best predictive accuracy as the final model. To evaluate age-specific predictive accuracy, we subsampled the data by age and determined accuracy for each age separately. Finally, we compared the accuracy of the selected model to the accuracy of a simpler model that only had fixed effects of age and current growth, without any random effects. This simpler model would be more broadly applicable in the context of conservation and management.

3 | RESULTS

3.1 | Exploratory growth models

3.1.1 | Sheep horn growth

Lactating females had lower horn growth than non-lactating females (Table S2; Figure 1a). The effect of reproduction diminished with age (Table S2; Figure 1a). At age 2, reproductive females grew 1.82 cm (95% confidence intervals [CI]: 1.21, 1.44; ~29%) less horn than non-reproductive females. By age 5, this effect disappeared, with large uncertainty in the difference between reproductive and non-reproductive females (0.41 cm [95% CI: −0.60, 1.43]). The effect of previous growth on current horn growth was negative, independent of age and slightly stronger in lactating ewes (Table S2; Figure S1b,d). The horns of a lactating ewe with a previous growth index of 5 cm grew 1.57 cm [95% CI: 0.12, 0.44] (~43%) less than a lactating ewe with a previous growth index of −5 cm (Figure S1b). Density reduced growth independently of reproductive status (Table S2; Figure S1a).

3.1.2 | Sheep mass gain

Lactating females had a lower annual mass gain than non-lactating females (Table S2; Figure 1c) and the negative effect of reproduction increased with density (Table S2). The predicted difference in mass gain between lactating and non-lactating ewes increased from 2.90 kg [95% CI: 1.95, 3.84] at a density of 20−5.25 kg [95% CI: 4.22, 6.27] at a density of 100 (Figure S2a). Previous mass generally reduced current mass gain, particularly in ewes older than 2 years (Table S2; Figure S2d). The predicted difference in mass gain between ewes with a previous mass gain index of −10 kg and 10 kg increased from 6.79 kg [95% CI: 3.62, 9.95] at age 2 to 7.97 kg [95% CI: 4.58, 11.36] at age 5 (Figure S2d).

3.1.3 | Goat horn growth

Lactating females aged 3 grew 0.95 cm [95% CI: 0.57, 1.33] (~47%) less horn than non-lactating females (Figure 1b). The effect of lactation disappeared starting at age 5, with a difference between lactating and non-lactating females at age 6 of only 0.08 cm [95%: CI

FIGURE 1 Changes in annual horn growth (a: bighorn ewes, b: female mountain goats) and in annual mass gain (c: bighorn ewes, d: female mountain goats) as a function of age and reproductive status. Boxplots with outlier dots represent the raw data (blue full line = no reproduction and grey dashed line = reproduction). Lines with shaded areas represent model predicted values with 95% confidence intervals
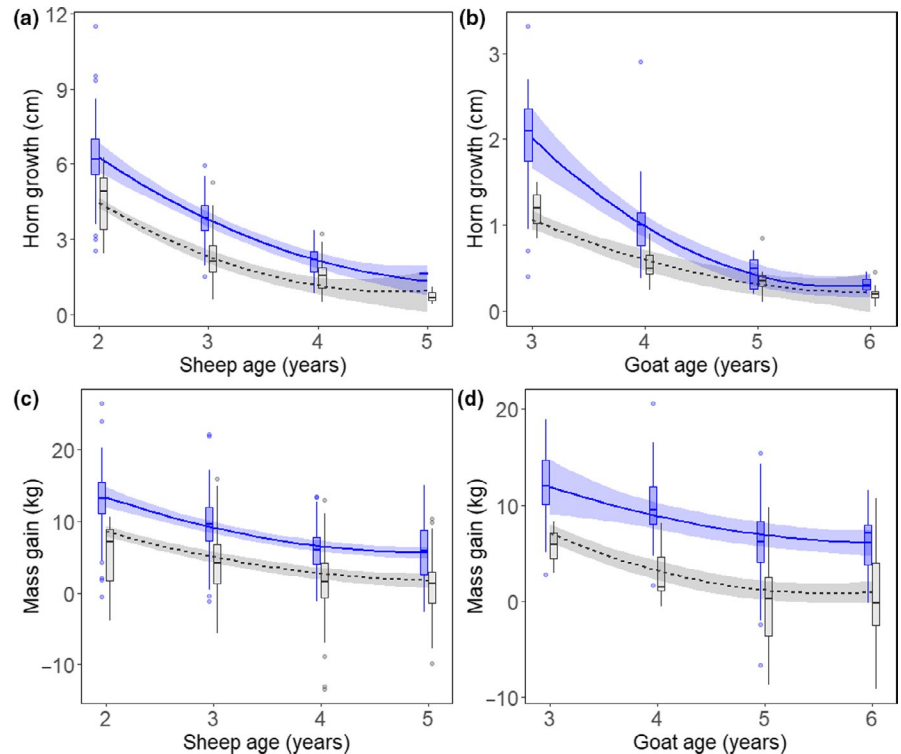
FIGURE 2 Age-specific predictive accuracy (sum of true positives and true negatives over total predictions × 100%) with 95% confidence intervals of models fitted to predict the reproductive status of bighorn ewes (a) and female mountain goats (b). Black dots and errors bars represent accuracy based on annual horn growth; orange dots and error bars represent accuracy based on annual mass gain
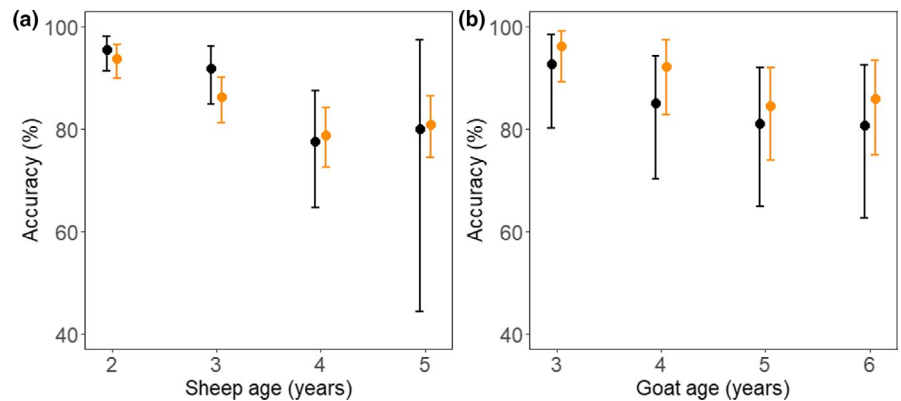
−0.19, 0.36] (Table S3; Figure 1b). The negative effect of reproduction tended to weaken as winter conditions worsened (Figure S3c), but overall, there was little influence of winter conditions, density or previous growth on current growth (Table S3; Figure S3).

3.1.4 | Goat mass gain

Reproduction reduced goat annual mass gain (Table S3; Figure 1d), and this effect varied with density and previous growth in mass (Table S3; Figure S4a,b,d). The predicted difference in mass gain between a lactating and a non-lactating female was negligible at low density but increased to 6.97 kg [95% CI: 5.59, 8.36] at a density of 68 (Figure S4b). Similarly, the predicted difference in mass gain between a lactating and a non-lactating female increased from 4.26 kg [95% CI: 2.05, 6.47] at a previous growth index of −10 kg to 7.49 kg [95% CI: 5.44, 9.54] at a previous growth index of 10 kg (Figure S4b).

Previous mass gain reduced current gain, especially for lactating females older than 3 years (Figure S4b,d).

3.2 | Predictive reproductive success models

3.2.1 | Sheep horn growth

No model of the determinants of ewe reproductive status using horn growth fell within $\Delta AIC_c < 2$ of the model with the lowest AIC_c (model 17; Table S4). The predictive accuracy of model 17 in 10-fold block cross-validation was 91.0% [95% CI: 87.4, 94.1] across all ages. Accuracy was highest at ages 2 and 3, lower at age 4 and uncertain at age 5 (Figure 2a). The accuracy of the simpler model which only included fixed effects of age and current growth index was 87.1% [95% CI: 83.1, 90.4], indicating a small gain in accuracy obtained with the more complex model. The estimates of model 17 show that the

Variables	Horn growth		Mass gain	
Fixed effects	**β**	**95% CI**	**β**	**95% CI**
Intercept	−2.54	[−3.97; −1.11]	−2.82	[−3.98; −1.66]
Age 3	4.14	[2.86; 5.42]	4.16	[3.33; 4.98]
Age 4	4.03	[2.76; 5.30]	4.89	[4.04; 5.75]
Age 5	31.09	[−8,770; 8832]	5.74	[4.84; 6.65]
Previous growth index	0.28	[0.11; 0.45]	0.03	[−0.02; 0.08]
Current growth index	−0.81	[−1.39; −0.22]	−0.46	[−0.54; −0.38]
Population density	−0.04	[−0.06; −0.01]	−0.023	[−0.042; −0.004]
North Pacific Index	−0.77	[−1.29; −0.24]	−0.07	[−0.28; 0.14]
Age 3*current growth index	−1.59	[−2.71; −0.48]		
Age 4*current growth index	−0.69	[−1.98; 0.60]		
Age 5*current growth index	−69.03	[−22,098; 21960]		
Density*North Pacific Index	0.02	[0.01; 0.03]		
Previous growth index*current growth index			0.009	[−0.002; 0.020]
Current growth index*North Pacific Index			−0.028	[−0.058; 0.001]
Random effects	**SD**		**SD**	
Year	0.76		1.75	

TABLE 1 Coefficients (β—on the logit scale) of fixed effects and standard deviations (SD) of random intercepts with corresponding 95% confidence intervals (95% CI) for variables included in models assessing the determinants of reproductive status of bighorn ewes aged 2–5 years at Ram Mountain, Alberta, Canada using annual horn growth and annual mass gain

effect of age on the probability of reproducing varied with current growth index but was generally positive (Table 1). Reproduction decreased with current growth index at all ages (Table 1). For instance, a 3-year-old female with a current growth index of −2 cm had a 0.99 [95% CI: 0.98, 1.00] probability of reproducing, whereas the probability of a female of the same age with a current growth index of 2 cm was 0.006 [95% CI: 0.004, 0.008].

3.2.2 | Sheep mass gain

Three models (11, 12 and 22) of the determinants of ewe reproductive status using mass gain fell within $\Delta AIC_c < 2$ (Table S4). The overall predictive accuracy of models 11, 12 and 22 in cross-validation were 85.6% [95% CI: 82.9, 87.8], 85.5% [95% CI: 82.9, 87.8] and 84.8% [95% CI: 82.1, 87.2], respectively. Because of a slightly greater predictive accuracy, we selected model 11 (Table S4). Accuracy of model 11 was highest at age 2 at 93.8% [95% CI: 89.9, 96.5] and lowest at age 4 at 78.8% [95% CI: 72.6, 84.2] (Figure 2a). The accuracy of a model with only age and current growth index was 77.9% [95% CI: 75.0, 80.6]. The estimates of model 11 show that the probability of reproducing strongly decreased with current growth index, especially when winter conditions were harsh and when previous growth was low (Table 1). For instance, the probability of reproducing

in years with harsh winter conditions (NPI = 3) and high previous growth (previous growth index = 5 kg) decreased from 0.83 [95% CI: 0.67, 0.92] to 0.48 [95% CI: 0.30, 0.67] when current growth increased from low (index = −5 kg) to average (index = 0 kg). For the same winter conditions and the same difference in current growth, however, the probability of reproducing decreased from 0.90 [95% CI: 0.73, 0.95] to 0.32 [95% CI: 0.16, 0.54] when previous growth was low (previous growth index = −5 kg).

3.2.3 | Goat horn growth

Only one model (model 10) of the determinants of female goat reproductive status using horn growth fell within $\Delta AIC_c < 2$ (Table S4). The predictive accuracy of this model in 10-fold block cross-validation was 85.2% [95% CI: 78.2, 91.0] across all ages. Accuracy was highest at age 3, decreased at ages 4 and 5, and then plateaued at 6 (Figure 2b). The accuracy of a model with only age and current growth index was 78.4% [95% CI: 71.1, 84.7]. The estimates of model 10 show that current growth index was correlated with a lower probability of reproducing, particularly at high density and when previous growth was low (Table 2). The probability of reproducing increased from 0.15 [95% CI: 0.04, 0.41] for a current growth index of 0 cm to 0.40 [95% CI: 0.03, 0.93] for a current growth index

TABLE 2 Coefficients (β—on the logit scale) of fixed effects and standard deviations (Std. Dev.) of random intercepts with corresponding 95% confidence intervals (95% CI) for variables included in models assessing the determinants of reproductive status of female mountain goats aged 3–6 years at Caw Ridge, Alberta, Canada using annual horn growth and annual mass gain

Variables	Horn growth		Mass gain	
Fixed effects	**β**	**95% CI**	**β**	**95% CI**
Intercept	−7.40	[−12.37; −2.44]	−7.65	[−7.66; −7.64]
Age 4	5.23	[2.34; 8.12]	2.88	[2.87; 2.88]
Age 5	6.65	[3.39; 9.90]	4.10	[4.09; 4.11]
Age 6	7.41	[4.10; 10.72]	4.48	[4.47; 4.49]
Previous growth index	0.06	[−0.35; 0.46]	−0.17	[−0.18; −0.16]
Current growth index	8.88	[−4.24; 22.00]	−0.54	[−0.55; −0.53]
Population density	0.02	[−0.05; 0.09]	0.05	[0.04; 0.06]
North Pacific Index	−0.06	[−0.48; 0.36]	−0.11	[−0.12; −0.10]
Previous growth index*current growth index	−2.93	[−5.35; −0.52]		
Current growth index*density	−0.33	[−0.61; −0.06]		
Current growth index*NPI			0.02	[0.01; 0.03]
Random effects	**SD**		**SD**	
Year	0.94		0.90	

of −1 cm at a density of 40 and previous growth index of −1 cm. For the same difference in current growth index, but at a density of 60 and a previous growth index of 1 cm, the probability increased from 0.24 [95% CI: 0.09, 0.51] to 1.00 [95% CI: 0.99, 1.00].

3.2.4 | Goat mass gain

Five models (models 2, 5, 6, 8 and 20) of the determinants of female mountain goat reproductive status using mass gain fell within $\Delta AIC_c < 2$ (Table S4). The overall predictive accuracy of models 2, 5, 6, 8 and 20 were 89.2% [95% CI: 84.7, 92.2], 89.2% [95% CI: 84.7, 92.6], 89.8% [95% CI: 85.7, 87.8], 89.5% [95% CI: 85.2, 93.0] and 88.8% [95% CI: 83.9, 93.0], respectively. The selected model was therefore model 6 (Table S4), whose accuracy was highest at age 3 at 96.2% [95% CI: 89.7, 99.2] and lowest at age 5 at 84.5% [95% CI: 74.0, 92.0] (Figure 2b). The accuracy of a model with only age and current growth index was 83.8% [95% CI: 78.9, 87.9]. The estimates show that current growth index had a strong negative effect, especially when winter conditions were good (low NPI; Table 2). The probability of reproducing decreased from 0.50 [95% CI: 0.40, 0.60] for a current growth index of −5 kg to 0.08 [95% CI: 0.06, 0.12] for a current growth index of 0 kg and harsh winter conditions (NPI = 3). For the same difference in current growth index but good winter conditions (NPI = −3), the decrease was from 0.78 [95% CI: 0.70, 0.84] to 0.15 [95% CI: 0.11, 0.20].

4 | DISCUSSION

We found clear evidence of a trade-off between growth and reproduction in young female bighorn sheep and mountain goats,

supporting previous studies (Côté et al., 1998; Gallant et al., 2001; Hamel & Côté, 2009). Horn growth and mass gain were reduced in young lactating females so that all studied growth traits could be used to predict past reproductive events. The overall accuracy of reproductive success predictions in young females was high across species and traits, suggesting that our predictive models could retroactively estimate the reproductive history of young females from measures of annual growth. Accuracy was higher for younger females, indicating that these models would be particularly useful to estimate age at primiparity, a key demographic parameter, from animals harvested, found dead or live-captured. This predictive method could be extended to determine primiparity from annual growth increments in a broad range of mammalian species.

4.1 | Growth and the reproductive trade-off

A substantial growth versus reproduction trade-off was confirmed for both horn growth and mass gain in young females. Confounding factors that influenced total energy acquired (A_i; Equations 2 and 3) and energy partitioning (β_i; Equations 2 and 3) directly affected the strength of this trade-off (Stearns, 1992; Van Noordwijk & de Jong, 1986). First, the negative effect of reproduction on annual growth was greater at high population density, particularly for mass gain. Earlier studies on the same populations reported density-independent growth in females but they did not assess the interaction between reproduction and density as reported here (Festa-Bianchet & Côté, 2008; Martin & Festa-Bianchet, 2010). Second, the negative effect of reproduction on current growth was strongest when previous growth was high for horns in ewes and mass gain in goats. Reproductive females allocated fewer resources

to current growth and more to reproduction if they had already attained a large horn size or mass. Although previous studies reported negative effects of previous growth on current growth (Marcil-Ferland et al., 2013; Martin & Festa-Bianchet, 2010), by differentiating the effect of previous growth according to reproductive status we provide a more nuanced portrait of carryover effects on annual growth. Previous growth generally had a negative effect on current growth, suggesting catch-up growth (Hector & Nakagawa, 2012; Marcil-Ferland et al., 2013). These results highlight the importance of considering factors that may affect not only total energy acquired (A_i; Equations 2 and 3) but also energy partitioning between traits (β_i; Equations 2 and 3). They also underline how the reproductive tactic of iteroparous large mammals is affected by resource availability and allocation decisions over multiple years.

4.2 | Growth as an index of past reproductive success

Our models predicted reproductive success with good accuracy in 10-fold cross-validations using both traits in both species. Based on the exploratory growth models, the probability of reproduction decreased with current growth. Accuracy ranged from 85.2% to 91.0% across species and traits. Previous studies, such as Miura et al. (1987), von Biela et al. (2008) and Medill et al. (2010) reported 77.6%, 83% and 72%, respectively. We determined accuracy from numerous individuals whose reproductive status was confirmed by direct observations, whereas Miura et al. (1987) and von Biela et al. (2008) relied on small sample sizes and determined reproductive status from analyses of ovaries, which are subject to some error. The higher predictive performance we report partially results from considering several confounding effects. Indeed, although the predictive accuracy of simpler models with only fixed effects of age and growth remained reasonable, it dropped by several percentage points. Additional variables such as population density and climate indices are often available to researchers interested in investigating reproductive history from a sample of growth measurements when the year of collection is known. Attempts to reconstruct reproductive history based on growth measures should aim to account for confounding effects whenever possible. Nevertheless, accuracy of simpler models was reasonable, indicating that this method would be robust when performed on populations with fewer data available.

Predictive accuracy decreased with age. For horn growth, the age effect could partially be explained by the constant measurement error (0.05 cm) becoming considerably larger relative to horn increment length with age (Figure 1). This problem is particularly evident for 5- and 6-year-old goats because horn growth is often <0.6 cm at these ages and variance is low. Because of reduced accuracy with age, our models should perform best in determining age at primiparity, but less accurately in determining all reproductions before reaching asymptotic size. Knowing age at primiparity in long-lived species could be very useful for conservation and management. In these species, reproduction probability of young

females is more sensitive to environmental conditions and usually shows larger variability than reproduction probability of prime-aged females (Gaillard et al., 2000; Hadley et al., 2006). Because population recruitment decreases as age at primiparity advances, variation in age at primiparity has considerable effects on demographic rates and harvest sustainability (El Bizri et al., 2019; Mace et al., 2008).

Finally, our results highlight the use of annual growth as a proxy for past reproduction. Using two traits in two species, we show that the method is not trait- or species-specific, and thereby could be used in a broad range of species. Growth data from traits that form annual growth annuli such as horns and teeth already can be collected from harvested female ungulates, ursids, phocids or other taxa at low cost (Allen et al., 2017; Corlatti et al., 2015; Nguyen et al., 2017). Many wildlife management agencies already have decades of measurements of such traits (Douhard et al., 2016).

AUTHORS' CONTRIBUTIONS

B.L., S.H., M.F.-B., F.P. and S.D.C. collected the data; B.L. was responsible for conceived the project, analysed the data and wrote the manuscript; M.F.-B. contributed to conceiving the project and S.H. oversaw analyses; M.F.-B., S.H., F.P. and S.D.C. contributed to writing and revising the manuscript.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.k3j9kd560 (Larue et al., 2020).

ORCID

Benjamin Larue ID https://orcid.org/0000-0002-4608-9288

REFERENCES

Allen, M. L., Kohn, B., Roberts, N., Crimmins, S., & Van Deelen, T. R. (2017). Benefits and drawbacks of determining reproductive histories for black bears (*Ursus americanus*) from cementum annuli techniques. *Canadian Journal of Zoology*, *95*, 991–995.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting linear mixed-effects models using lme4. arXiv preprint arXiv:1406.5823.

Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods*

& *Research*, *33*, 261–304. https://doi.org/10.1177/0049124104 268644

Corlatti, L., Gugiatti, A., & Imperio, S. (2015). Horn growth patterns in Alpine chamois. *Zoology*, *118*, 213–219. https://doi.org/10.1016/j.zool.2015.01.003

Côté, S. D., & Festa-Bianchet, M. (2001). Reproductive success in female mountain goats: The influence of age and social rank. *Animal Behaviour*, *62*, 173–181. https://doi.org/10.1006/anbe.2001.1719

Côté, S. D., Festa-Bianchet, M., & Smith, K. G. (1998). Horn growth in mountain goats (*Oreamnos americanus*). *Journal of Mammalogy*, *79*, 406–414. https://doi.org/10.2307/1382971

Coy, P. L., & Garshelis, D. L. (1992). Reconstructing reproductive histories of black bears from the incremental layering in dental cementum. *Canadian Journal of Zoology*, *70*, 2150–2160. https://doi.org/10.1139/z92-290

Dmitriew, C. M. (2011). The evolution of growth trajectories: What limits growth rate? *Biological Reviews*, *86*, 97–116. https://doi.org/10.1111/j.1469-185X.2010.00136.x

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., & Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, *36*, 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Douhard, M., Festa-Bianchet, M., Pelletier, F., Gaillard, J. M., & Bonenfant, C. (2016). Changes in horn size of Stone's sheep over four decades correlate with trophy hunting pressure. *Ecological Applications*, *26*, 309–321. https://doi.org/10.1890/14-1461

El Bizri, H. R., Fa, J. E., Valsecchi, J., Bodmer, R., & Mayor, P. (2019). Age at sexual maturity, first parturition and reproductive senescence in wild lowland pacas (*Cuniculus paca*): Implications for harvest sustainability. *Animal Reproduction Science*, *205*, 105–114. https://doi.org/10.1016/j.anireprosci.2019.04.009

Festa-Bianchet, M., & Côté, S. D. (2008). *Mountain goats: Ecology, behavior, and conservation of an alpine ungulate*. Island Press.

Festa-Bianchet, M., Gaillard, J. M., & Côté, S. D. (2003). Variable age structure and apparent density dependence in survival of adult ungulates. *Journal of Animal Ecology*, *72*, 640–649. https://doi.org/10.1046/j.1365-2656.2003.00735.x

Gaillard, J. M., Festa-Bianchet, M., & Yoccoz, N. G. (1998). Population dynamics of large herbivores: Variable recruitment with constant adult survival. *Trends in Ecology & Evolution*, *13*, 58–63. https://doi.org/10.1016/S0169-5347(97)01237-8

Gaillard, J. M., Festa-Bianchet, M., Yoccoz, N. G., Loison, A., & Toigo, C. (2000). Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics*, *31*, 367–393. https://doi.org/10.1146/annurev.ecolsys.31.1.367

Gallant, B. Y., Réale, D., & Festa-Bianchet, M. (2001). Does mass change of primiparous bighorn ewes reflect reproductive effort? *Canadian Journal of Zoology*, *79*, 312–318. https://doi.org/10.1139/z00-204

Hadley, G. L., Rotella, J. J., Garrott, R. A., & Nichols, J. D. (2006). Variation in probability of first reproduction of Weddell seals. *Journal of Animal Ecology*, *75*, 1058–1070. https://doi.org/10.1111/j.1365-2656.2006.01118.x

Hamel, S., & Côté, S. D. (2009). Foraging decisions in a capital breeder: Trade-offs between mass gain and lactation. *Oecologia*, *161*, 421–432. https://doi.org/10.1007/s00442-009-1377-y

Hamel, S., Côté, S. D., Gaillard, J. M., & Festa-Bianchet, M. (2009). Individual variation in reproductive costs of reproduction: High-quality females always do better. *Journal of Animal Ecology*, *78*, 143–151. https://doi.org/10.1111/j.1365-2656.2008.01459.x

Hamel, S., Gaillard, J. M., Festa-Bianchet, M., & Côté, S. D. (2009). Individual quality, early-life conditions, and reproductive success in contrasted populations of large herbivores. *Ecology*, *90*, 1981–1995. https://doi.org/10.1890/08-0596.1

Hamel, S., Gaillard, J. M., Yoccoz, N. G., Loison, A., Bonenfant, C., & Descamps, S. (2010). Fitness costs of reproduction depend on life speed: Empirical evidence from mammalian populations. *Ecology Letters*, *13*, 915–935. https://doi.org/10.1111/j.1461-0248.2010.01478.x

Haviernick, M., Côté, S. D., & Festa-Bianchet, M. (1998). Immobilization of mountain goats with xylazine and reversal with idazoxan. *Journal of Wildlife Diseases*, *34*, 342–347. https://doi.org/10.7589/0090-3558-34.2.342

Hechinger, R. F. (2010). Mortality affects adaptive allocation to growth and reproduction: Field evidence from a guild of body snatchers. *BMC Evolutionary Biology*, *10*, 136. https://doi.org/10.1186/1471-2148-10-136

Hector, K. L., & Nakagawa, S. (2012). Quantitative analysis of compensatory and catch-up growth in diverse taxa. *Journal of Animal Ecology*, *81*, 583–593. https://doi.org/10.1111/j.1365-2656.2011.01942.x

Klevezal', G. A., & Myrick Jr., A. C. (1984). Marks in tooth dentine of female dolphins (genus *Stenella*) as indicators of parturition. *Journal of Mammalogy*, *65*, 103–110. https://doi.org/10.2307/1381206

Kuhn, M. (2008). Building predictive models in R using the caret package. *Journal of Statistical Software*, *28*, 1–26.

Larue, B., Pelletier, F., Côté, S. D., Hamel, S., & Festa-Bianchet, M. (2020). Data from: Growth and reproduction trade-offs can estimate previous reproductive history in alpine ungulates. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.k3j9kd560

Mace, G. M., Collar, N. J., Gaston, K. J., Hilton-taylor, C., Akçakaya, H. R., Leader-williams, N., Milner-gulland, E. J., & Stuart, S. N. (2008). Quantification of extinction risk: IUCN's system for classifying threatened species. *Conservation Biology*, *22*, 1424–1442. https://doi.org/10.1111/j.1523-1739.2008.01044.x

Marcil-Ferland, D., Festa-Bianchet, M., Martin, A. M., & Pelletier, F. (2013). Despite catch-up, prolonged growth has detrimental fitness consequences in a long-lived vertebrate. *The American Naturalist*, *182*, 775–785. https://doi.org/10.1086/673534

Martin, J. G., & Festa-Bianchet, M. (2010). Bighorn ewes transfer the costs of reproduction to their lambs. *The American Naturalist*, *176*, 414–423. https://doi.org/10.1086/656267

Martin, J. G. A., & Pelletier, F. (2011). Measuring growth patterns in the field: Effects of sampling regime and methods on standardized estimates. *Canadian Journal of Zoology*, *89*, 529–537. https://doi.org/10.1139/z11-018

Matson, G. M., Casquilho-Gray, H. E., Paynich, J. D., Barnes Jr., V. G., Reynolds III, H. V., & Swenson, J. E. (1999). Cementum annuli are unreliable reproductive indicators in female brown bears. *Ursus*, *11*, 275–280.

Medill, S., Derocher, A. E., Stirling, I., & Lunn, N. (2010). Reconstructing the reproductive history of female polar bears using cementum patterns of premolar teeth. *Polar Biology*, *33*, 115–124. https://doi.org/10.1007/s00300-009-0689-z

Miura, S., Kita, I., & Sugimura, M. (1987). Horn growth and reproductive history in female Japanese serow. *Journal of Mammalogy*, *68*, 826–836. https://doi.org/10.2307/1381560

Nguyen, L., Pilfold, N. W., Derocher, A. E., Stirling, I., Bohart, A. M., & Richardson, E. (2017). Ringed seal (*Pusa hispida*) tooth annuli as an index of reproduction in the Beaufort Sea. *Ecological Indicators*, *77*, 286–292. https://doi.org/10.1016/j.ecolind.2017.02.003

Pelletier, F., Hogg, J. T., & Festa-Bianchet, M. (2006). Male mating effort in a polygynous ungulate. *Behavioral Ecology and Sociobiology*, *60*, 645–654. https://doi.org/10.1007/s00265-006-0208-y

R Core Team. (2018). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Roberts, D. R., Bahn, V., Ciuti, S., Boyce, M. S., Elith, J., Guillera-Arroita, G., Hauenstein, S., Lahoz-Monfort, J. J., Schröder, B., Thuiller, W.,

Warton, D. I., Wintle, B. A., Hartig, F., & Dormann, C. F. (2017). Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. *Ecography*, *40*, 913–929. https://doi.org/10.1111/ecog.02881

Robin, X., Turck, N., Hainard, A., Tiberti, N., Lisacek, F., Sanchez, J. C., & Müller, M. (2011). pROC: An open-source package for R and S+ to analyze and compare ROC curves. *BMC Bioinformatics*, *12*, 77. https://doi.org/10.1186/1471-2105-12-77

Ruckstuhl, K. E. (1998). Foraging behaviour and sexual segregation in bighorn sheep. *Animal Behaviour*, *56*, 99–106. https://doi.org/10.1006/anbe.1998.0745

Ruf, T., Fietz, J., Schlund, W., & Bieber, C. (2006). High survival in poor years: Life history tactics adapted to mast seeding in the edible dormouse. *Ecology*, *87*, 372–381. https://doi.org/10.1890/05-0672

Skalski, J. R., Ryding, K. E., & Millspaugh, J. (2010). *Wildlife demography: Analysis of sex, age, and count data*. Elsevier.

Stearns, S. C. (1992). *The evolution of life histories*. Oxford University Press.

Stevens, V., & Houston, D. B. (1989). Reliability of age determination of mountain goats. *Wildlife Society Bulletin*, *17*, 72–74.

Tochigi, K., Tamatani, H., Kozakai, C., Inagaki, A., Naganuma, T., Myojo, H., Yamazaki, K., & Koike, S. (2018). Reproductive histories of Asian black bears can be determined by cementum annuli width. *Mammal Study*, *43*, 261–268. https://doi.org/10.3106/ms2018-0016

Trenberth, K. E., & Hurrell, J. W. (1994). Decadal atmosphere-ocean variations in the Pacific. *Climate Dynamics*, *9*, 303–319. https://doi.org/10.1007/BF00204745

Van Noordwijk, A. J., & de Jong, G. (1986). Acquisition and allocation of resources: Their influence on variation in life history tactics. *The American Naturalist*, *128*, 137–142. https://doi.org/10.1086/284547

von Biela, V. R., Testa, J. W., Gill, V. A., & Burns, J. M. (2008). Evaluating cementum to determine past reproduction in northern sea otters. *The Journal of Wildlife Management*, *72*, 618–624. https://doi.org/10.2193/2007-218

Williams, G. C. (1966). Natural selection, the costs of reproduction, and a refinement of Lack's principle. *The American Naturalist*, *100*, 687–690. https://doi.org/10.1086/282461

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