

Effects of population density on static allometry between horn length and body mass in mountain ungulates

Christophe Pélabon, Steeve D Côté, Marco Festa-bianchet, Jean-michel Gaillard, Mathieu Garel, Jean-francois Lemaître, Anne Loison, Morgane Tidière, Carole Toïgo

▶ **To cite this version:**

Christophe Pélabon, Steeve D Côté, Marco Festa-bianchet, Jean-michel Gaillard, Mathieu Garel, et al.. Effects of population density on static allometry between horn length and body mass in mountain ungulates. Oikos, 2021, 10.1111/oik.08726 . hal-03452979

HAL Id: hal-03452979
https://cnrs.hal.science/hal-03452979

Submitted on 27 Nov 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution 4.0 International License

OIKOS

Research

Effects of population density on static allometry between horn length and body mass in mountain ungulates

Christophe Pélabon, Steeve D. Côté, Marco Festa-Bianchet, Jean-Michel Gaillard, Mathieu Garel, Jean-Francois Lemaître, Anne Loison, Morgane Tidière and Carole Toïgo

C. Pélabon (https://orcid.org/0000-0002-8630-8983) ✉ (christophe.pelabon@ntnu.no), Dept of Biology, Centre for Biodiversity Dynamics, Norwegian Univ. of Science and Technology, Trondheim, Norway. – S. D. Côté, Dépt de Biologie and Centre d'Etudes Nordiques, Univ. Laval, Québec (QC), Canada. – M. Festa-Bianchet, Dépt de Biologie, Univ. de Sherbrooke, Sherbrooke, Québec, Canada. – J.-M. Gaillard and J.-F. Lemaître, Laboratoire de Biométrie et Biologie Evolutive, UMR5558, Univ. de Lyon, Université Lyon 1, CNRS, Villeurbanne, France. – M. Garel and C. Toïgo, Office Français de la Biodiversité, Unité Ongulés Sauvages, ZI Mayencin, Gières, France. – A. Loison, Univ. Grenoble Alpes, Univ. Savoie Mont-Blanc, CNRS, LECA, Grenoble, France. – M. Tidière, Species360 Conservation Science Alliance, Bloomington, Minnesota, USA and Interdisciplinary Centre on Population Dynamics, Dept of Biology, Univ. of Southern Denmark, Odense M, Denmark.

Oikos
00: 1–10, 2021
doi: 10.1111/oik.08726

Subject Editor: Jessica Abbott
Editor-in-Chief: Dries Bonte
Accepted 8 September 2021

Little is known about the effects of environmental variation on allometric relationships of condition-dependent traits, especially in wild populations. We estimated sex-specific static allometry between horn length and body mass in four populations of mountain ungulates that experienced periods of contrasting density over the course of the study. These species displayed contrasting sexual dimorphism in horn size; high dimorphism in *Capra ibex* and *Ovis canadensis* and low dimorphism in *Rupicapra rupicapra* and *Oreamnos americanus*. The effects of density on static allometric slopes were weak and inconsistent while allometric intercepts were generally lower at high density, especially in males from species with high sexual dimorphism in horn length. These results confirm that static allometric slopes are more canalized than allometric intercepts against environmental variation induced by changes in population density.

Keywords: allometry, bovids, condition dependence, density dependence, horns

Introduction

For morphological traits, allometric relationships describe the proportional increase in size of a trait for a proportional increase in size of the whole organism (Huxley 1932). These relationships are often expressed as a power function of the form $y = ax^b$, where y is trait size and x body size, and where a depends on the initial values of x and y, while b, the allometric exponent, depends on the relative rate of increase of x and y. On a log–log scale, this yields a linear relationship: $\log(y) = \log(a) + b \times \log(x)$, with a slope b and an intercept $\log(a)$. Allometric relationships can be estimated during growth (ontogenetic allometry), among individuals measured at similar age or developmental stage (static allometry) or among populations or species (evolutionary allometry; Cheverud 1982, Klingenberg and Zimmermann 1992).

Static allometries generally display little variation among populations and they have been often considered to represent developmental or genetic constraints (Maynard

© 2021 The Authors. Oikos published by John Wiley & Sons Ltd on behalf of Nordic Society Oikos. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Smith et al. 1985, Pélabon et al. 2014, Voje et al. 2014). In particular, static allometric slopes are less variable than allometric intercepts among populations (Egset et al. 2011, Voje et al. 2014) and they are also more difficult to change by artificial selection (Egset et al. 2012, Bolstad et al. 2015, Stillwell et al. 2016). It remains largely unknown, however, whether static allometric slopes are also less sensitive than allometric intercepts to environmental variation affecting nutrition and growth. Few studies have investigated how nutrition affects the proportional growth rates of different body parts, and they produced inconclusive results. For example, evidence for reprogramming the relative growth of specific body parts following starvation in *Drosophila* (Bergland et al. 2008) suggests that variation in nutrition can affect the allometric slope. Similarly, in an artificial selection on static allometry of a wing character in *Drosophila*, selected changes of the allometric slope vanished when flies were starved during development (Bolstad et al. 2015). On the other hand, Tobler and Nijhout (2010) showed that starvation only affected the intercept of the static allometry between wing mass and body mass in the moth *Manduca sexta*.

Different traits may react differently to changes in nutrition. Because secondary sexual characters are often condition-dependent, they are expected to be more sensitive to variation in resource availability than other traits. Allometric relationships steeper than isometry (slope > 1, characterising hyperallometry) generally observed between secondary sexual characters and body size (Bonduriansky 2007, Voje 2016) confirm this hypothesis, because to a 1% variation of body size corresponds a variation in trait size > 1%. Yet, it remains unclear whether changes in the conditions encountered by a population will only generate changes in the allometric intercept (changes in average trait size compared to average body size, Fig. 1A) or if they may also modify the allometric slope (changes in the increase in trait size relative to the increase in body size; Fig. 1B). Some observations suggest that static allometric slopes of condition-dependent traits can change with nutrition. For example, in the stalk-eyed fly *Cyrtodiopsis dalmanni*, the coefficient of variation of eyespan of flies exposed to poor nutrition increased more than the coefficient of variation in body size (Cotton et al. 2004). On the other hand, Emlen (1997) reported that poor nutrition only affected the intercept of the nonlinear static allometry between horn length and body size in the dung beetle *Onthophagus acuminatus*. That interpretation, however, is partly compromised by the use of an arithmetic scale to quantify allometry.

These considerations underscore that our knowledge of how variation in food availability affects static allometry is limited not only by the low number of studies, but also because they are restricted to laboratory studies of holometabolous insects. To better understand how variation in nutrition affects static allometry of condition-dependent traits, we assessed the effects of population density on the allometry between horn length and body mass in four mountain ungulates with different horn sizes in adult males and contrasting sexual dimorphism both in horn size and body size. In two species, Alpine ibex *Capra ibex* and bighorn sheep *Ovis canadensis*, males are 30–50% heavier than females and develop very large horns that are over 10 times the volume of female horns. In chamois *Rupicapra rupicapra* and mountain

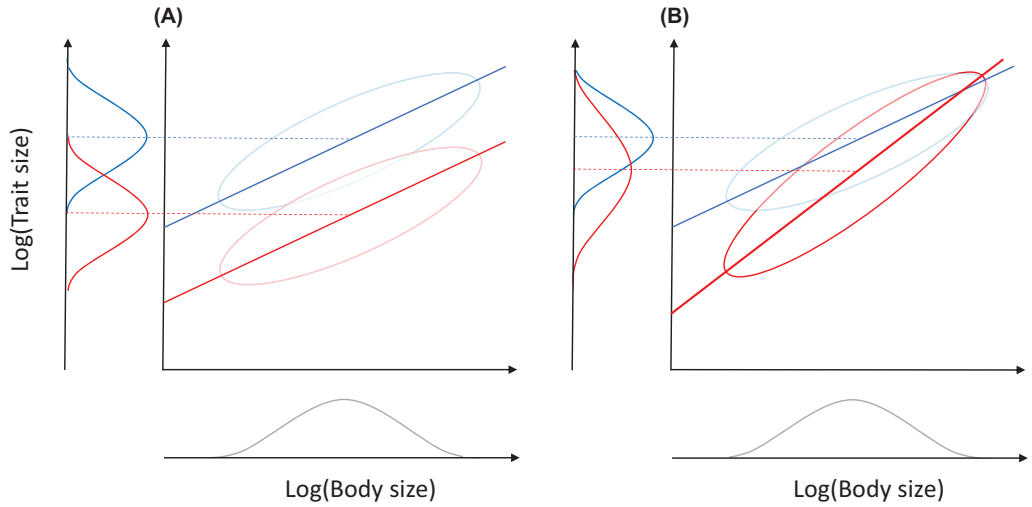


Figure 1. Consequences of a decrease in environmental quality on the static allometry between a condition dependent trait and body size. Blue ellipses and lines represent the bivariate distributions of the trait and body size and the allometric relationships under good environmental conditions (i.e. low density, good nutrition). Red ellipses and lines represent the distributions and allometry under poor environmental conditions (i.e. high density, poor nutrition). (A) The allometric slope is canalized against environmental variation and a decrease in condition generates a similar proportional decline of the average trait size for any body mass. Consequently, a proportional change in mass generates a similar proportional change in trait size under good or poor environmental conditions. For simplicity we present a case where body size is not affected by condition. (B) The decrease in condition generates a stronger proportional decrease in the average trait size for small than for large individuals and an increase in the trait variance. In this case, a change in body mass generates a stronger change in trait size under poor than under good conditions.

goat *Oreamnos americanus*, despite substantial sexual size dimorphism in body mass, males and females display smaller horns with little size differences between sexes (Toïgo et al. 1999, Bassano et al. 2003, Festa-Bianchet et al. 2019). For each species, we obtained data on horn length and body mass from long-term studies during which each population experienced pronounced variation in density that impacted individual performance. We were thus able to estimate static allometry between horn length and body mass under contrasting conditions and compare variation in allometric slopes and intercepts in both sexes of each species.

Methods

Study species and populations

Horn length and body mass data were obtained from the long-term capture–mark–recapture monitoring of Alpine ibex *Capra ibex* on Belledonne-7-Laux Reserve (45°10′N, 05°58′E, France), bighorn sheep *Ovis canadensis* on Ram Mountain (52°02′N, 115°05′W, Alberta, Canada) and mountain goats *Oreamnos americanus* on Caw Ridge (54°N, 119°W, Alberta, Canada). For chamois *Rupicapra rupicapra*, body mass and horn size data were collected from long-term monitoring of animals shot by hunters on the Bauges mountains (45°40′N, 06°13′E, France). The duration of the monitoring, number of individuals measured and the age classes included in analyses are presented in Table 1. We summarize here the methods to measure horn length and body mass, and we present in the Supporting information a detailed description of these methods for each population.

For the three live-monitored populations, captures occurred each year during late spring and summer. Animals were marked with ear tags or collars when first captured. At each capture, body mass and horn length were measured. For animals marked during their first year, the exact age was known. For animals captured as adults, age was determined by counting the visible horn annuli that form each year. Body mass was recorded to the nearest 0.5 kg with spring scales hung from a tripod, and the length of both horns was measured with a tape along the external curvature of the horn. To decrease the effect of age-related horn wear, we retained the measure of the longest of the two horns for analyses.

For chamois, age determination was also based on counts of horn growth annuli (Schröder and Von Elsner-Schak 1985). Measurements of carcass mass were done on complete carcasses, partially eviscerated carcasses (minus digestive tract) or eviscerated carcasses (minus all internal organs, blood and digestive tract). We used chamois for which at least two different measures of mass were taken to establish conversion equations and we transformed measures of all individuals into eviscerated carcass mass (Supporting information).

For Alpine ibex, bighorn sheep and mountain goats, population size and vital rates such as female reproductive success and age-specific survival were obtained from the capture–recapture monitoring scheme. For chamois, population size was estimated by block counts and transects, and a reproductive index (number of offspring/number of females) was calculated each year from groups observed during summer.

Except for small intensively studied populations such as the bighorn sheep population on Ram Mountain or the mountains goats at Caw ridge, population counts in ungulates are generally highly inaccurate and have low informative content (Morellet et al. 2007). Therefore, we defined periods of low and high density based on estimated population size as well as changes in body mass, female reproductive performances or juvenile survival (Supporting information). Periods of low and high density were separated by transition periods to avoid including in the analysis animals that experienced very different densities during their lifespan. For each species, we estimated age- and sex-specific static allometry of horn length on body mass for each period separately.

Statistical analyses

Effects of density on body mass and horn size

We first tested the effect of density on age- and sex-specific body mass and horn length. Density effects have been previously examined in detail for each species (Festa-Bianchet et al. 2004, Toïgo et al. 2007, Hamel et al. 2010, Garel et al. 2011, Douhard et al. 2018). We updated these analyses with additional years.

In each species, we fitted linear mixed-effect models for each sex separately. Body mass or horn length was the response variable, age, period (high versus low density), sampling date (capture or hunting date) and their two-way interactions were the predictor variables. Models also included

Table 1. Summary of data included for each species and sex. Age start: youngest age class included; age end: oldest age class included for analyses of static allometry. The low density and high density columns list the years included in each period; n = number of observations/number of individuals.

Species	Sex	Age start	Age end	Low density	n Obs/ind.	High density	n Obs/ind.
C. ibex	♂	1	5	1984–1998	111/95	2003–2016	358/307
	♀	1	3		58/49		168/158
O. canadensis	♂	1	4	1975–1989	530/153	1992–2010	582/70
	♀	1	4		994/146		1317/112
R. rupicapra	♂	1	5	1982–1997	782	2001–2017	1088
	♀	1	5		444		831
O. americanus	♂	1	5	1988–1996 and 2014–2019	95/54	2001–2011	276/130
	♀	1	5		116/76		187/108

year of measurement and individual identity as random factors, except for chamois where individuals were measured only once when shot. We did not include year of birth as a random factor because it was redundant with the inclusion of age as predictor variable and year of measurement as random variable.

In ibex, bighorn sheep and mountain goats, measurement date was included as a predictor variable to account for effects of seasonal growth on body mass and horn length in spring and summer. We median-centred this predictor variable so that the parameter estimates represent the expected value of body mass or horn length at the median measurement date. Median-centring prevented the few late measurement dates to strongly influence the parameter estimates. We did not include three-way interactions (age × period × capture date) in these models because the low number of observations for some age classes prevented us from fitting such complex models.

For chamois, hunting occurs from 1 September to 27 February. During this period, body mass may first increase and subsequently decrease, especially among adult males due to the combined effects of resource scarcity and rut activity during winter (Mason et al. 2012). Horn length, on the other hand, remains constant during this period. To account for the non-linear response of body mass to hunting date, we included a quadratic effect of hunting date in models testing the effect of density on body mass. Hunting date was also median-centred in these models.

Models were fitted with the R-package lme4 (Bates et al. 2015), and model selection was performed using Akaike information criterion (AIC) on models fitted with maximum likelihood. When the difference in AIC of two competing models was < 2, we retained the model with the lowest number of parameters (principle of parsimony, Burnham and Anderson 2002). Parameter estimates were obtained from the best models fitted with restricted maximum likelihood.

Effects of density on static allometry

All allometric relationship were estimated on a log–log scale, with log-transformed body mass and horn length (see Pélabon et al. 2018 for justification). We limited our analyses of static allometry to age classes with a minimum of 10 observations (Table 1). We fitted mixed-effect models where horn length was the response variable and body mass the covariate, age and period were fixed factors and year of measure and individual identity (except for chamois) were random factors. The full model included all possible interactions. Model selection was based on AICc (AIC corrected for small sample size) of models fitted with maximum likelihood.

We obtained estimates of age-specific static allometry at both density levels by fitting separate models for each period where horn length was the response variable, and body mass, age class and their interaction were the predictor variables. Year of measure and individual identity were random factors, except for chamois where year of measure was the only random factor. In these models, body mass was age-class mean-centred, so that intercepts can be interpreted as the age-specific average horn length for an individual with an average body mass and compared between periods even when the allometric slopes differed. Models were fitted using restricted maximum likelihood for each sex separately. All statistics were performed with R ver. 4.0.2 (<www.r-project.org>).

Results

Density-dependent responses of body mass and horn length

In all species, population density negatively affected body mass and horn length. The factor period was always included in the best models (Supporting information). These effects were stronger for ibex and bighorn sheep males, with an average decrease in mass across age classes of 20% and 8%, respectively, and in horn length of 14% and 12%, respectively. For males of the two other species and for most females, density-dependent responses of both traits were weaker with an average decrease in body mass at high density ranging from 2 to 6%, and an average decrease in horn length ranging from 1 to 6% (Supporting information). Body mass of female ibex, however, strongly decreased (15% on average) at high density.

Density-dependent responses of static allometry

Static allometries were steeper in ibex and bighorn sheep than in chamois and mountain goat and they were generally steeper in males than in females in all species (Fig. 2, Table 2). Additionally, static allometric slopes decreased with increasing age. This effect was particularly pronounced in chamois and mountain goat of both sexes and in ibex and bighorn sheep females for which static allometric slopes were always shallower than isometry (i.e. < 0.3) for individuals older than three years. In ibex and bighorn sheep males, this decrease was weaker and static allometries were always steeper or not different from isometry for all age classes (Table 2).

Model selection provided low statistical support for differences in allometric slopes between low and high density (selected models rarely include period × log(body mass) interactions in the Supporting information). Accordingly, we found no systematic differences in age-specific static allometric slopes between low- and high-density periods (Table 2). The median difference in age-specific static allometric slopes between high and low density was 0.05, ranging from −0.56 to +0.48.

In contrast, with few exceptions, the allometric intercept was lower at high density, when individuals had shorter horns for a given body mass (Table 2). In ibex and mountain goat, however, individuals aged 1- and 2-year had higher allometric intercepts at high density, indicating that for a given body mass, horns were on average longer at high than at low population density in these groups (Fig. 2, Table 2). Remarkably, density-induced differences in allometric intercept were smaller in mountain goat and chamois than in ibex and bighorn sheep of both sexes. Finally, among species and age classes, differences in intercept between low and high density tended to be correlated between males and females (Fig. 3).

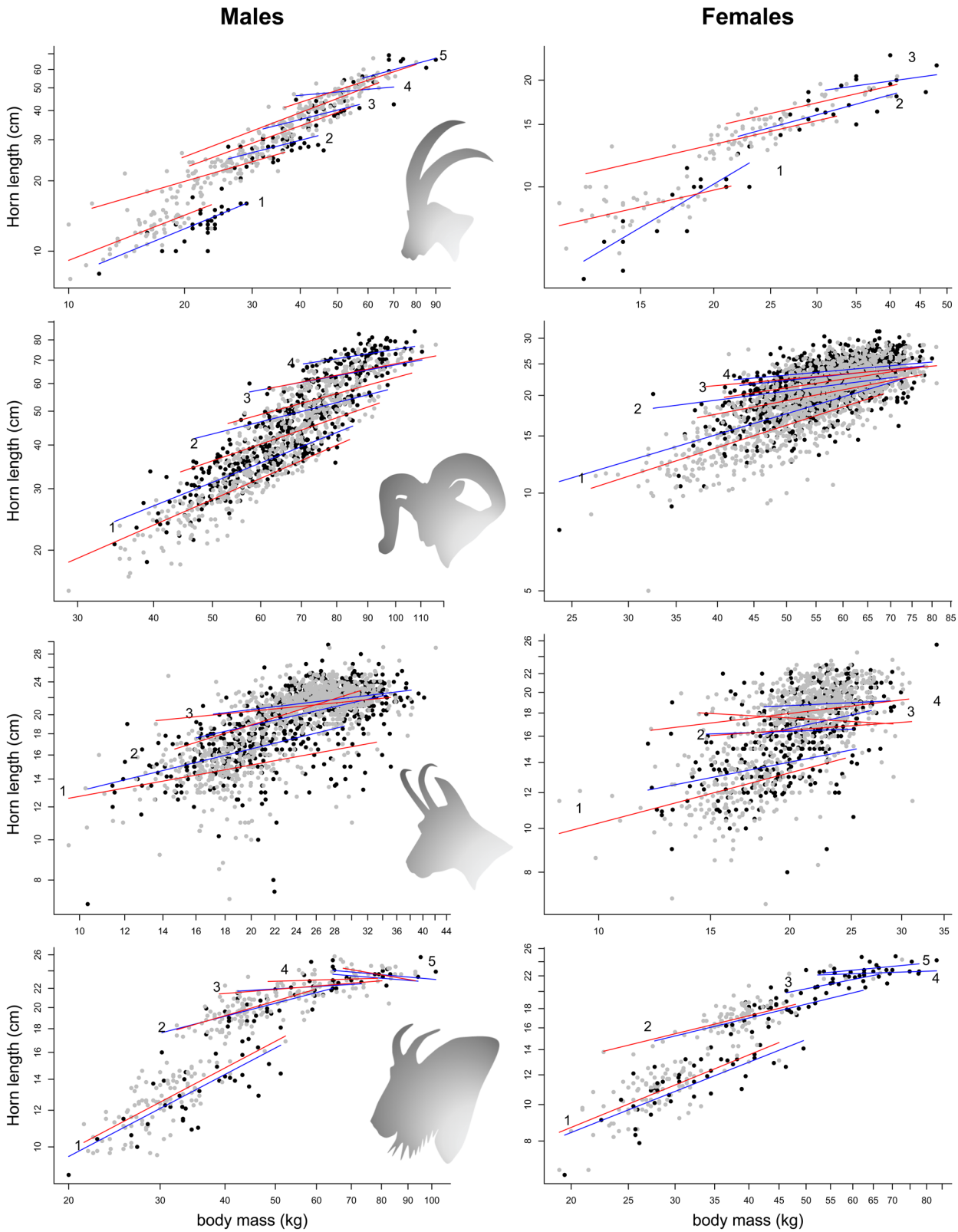


Figure 2. Static allometry between horn length and body mass in males (left) and females (right) of four mountain ungulates (row 1–4: *Capra ibex*, *Ovis canadensis*, *Rupicapra rupicapra* and *Oreamnos americanus*). Black dots and blue lines: low-density period; grey dots and red lines: high-density period. The numbers indicating age classes are placed close to the static allometry for the low-density period. Only age classes with more than 10 observations per period are included. See Table 2 for parameter estimates of the allometric relationships.

Table 2. Parameter estimates for the age-specific static allometry for each sex at low and high density in the four study species. α: intercept; β: slope. Isometry between a length and a mass measurement corresponds to a slope of 0.3. Parameters were estimated by fitting mixed-effect models for each period separately with log(horn length) as the response variable and age-class mean-centred log(body mass), age class and their two-way interaction as predictor variables. Year of measurement and animal identity (except for chamois) were included as random effects.

			Low density		High density	
Species	Sex	Age	α ± SE	β ± SE	α ± SE	β ± SE
C. ibex	♂	1	2.45 ± 0.03	0.68 ± 0.10	2.59 ± 0.01	0.64 ± 0.06
		2	3.24 ± 0.04	0.42 ± 0.12	3.14 ± 0.01	0.48 ± 0.04
		3	3.59 ± 0.03	0.42 ± 0.14	3.52 ± 0.01	0.60 ± 0.05
		4	3.86 ± 0.05	0.15 ± 0.16	3.75 ± 0.01	0.63 ± 0.05
		5	4.01 ± 0.05	0.45 ± 0.23	3.97 ± 0.01	0.54 ± 0.08
	♀	1	2.08 ± 0.04	0.87 ± 0.12	2.18 ± 0.01	0.31 ± 0.08
		2	2.67 ± 0.04	0.41 ± 0.15	2.65 ± 0.01	0.43 ± 0.06
		3	2.93 ± 0.05	0.31 ± 0.22	2.88 ± 0.02	0.36 ± 0.08
O. canadensis	♂	1	3.52 ± 0.01	0.70 ± 0.02	3.41 ± 0.02	0.76 ± 0.02
		2	3.90 ± 0.01	0.44 ± 0.03	3.78 ± 0.02	0.60 ± 0.02
		3	4.13 ± 0.01	0.32 ± 0.04	4.01 ± 0.02	0.48 ± 0.03
		4	4.27 ± 0.01	0.27 ± 0.06	4.16 ± 0.02	0.34 ± 0.03
	♀	1	2.84 ± 0.01	0.66 ± 0.03	2.75 ± 0.02	0.71 ± 0.02
		2	3.06 ± 0.01	0.28 ± 0.03	3.01 ± 0.02	0.42 ± 0.03
		3	3.14 ± 0.01	0.23 ± 0.03	3.11 ± 0.02	0.34 ± 0.03
		4	3.18 ± 0.01	0.20 ± 0.04	3.16 ± 0.02	0.20 ± 0.03
R. rupicapra	♂	1	5.07 ± 0.01	0.34 ± 0.04	4.99 ± 0.01	0.25 ± 0.04
		2	5.28 ± 0.01	0.31 ± 0.08	5.30 ± 0.01	0.43 ± 0.07
		3	5.37 ± 0.02	0.17 ± 0.09	5.35 ± 0.01	0.14 ± 0.06
		4	5.37 ± 0.01	0.14 ± 0.09	5.37 ± 0.01	0.02 ± 0.06
		5	5.47 ± 0.01	0.10 ± 0.06	5.40 ± 0.01	0.14 ± 0.05
	♀	1	4.90 ± 0.01	0.28 ± 0.06	4.83 ± 0.01	0.37 ± 0.05
		2	5.10 ± 0.02	0.04 ± 0.16	5.11 ± 0.02	0.10 ± 0.11
		3	5.14 ± 0.03	0.30 ± 0.23	5.16 ± 0.01	−0.08 ± 0.10
		4	5.24 ± 0.02	0.06 ± 0.16	5.21 ± 0.01	0.17 ± 0.08
		5	5.25 ± 0.01	0.19 ± 0.08	5.28 ± 0.01	0.18 ± 0.05
O. americanus	♂	1	4.82 ± 0.02	0.61 ± 0.06	4.85 ± 0.01	0.60 ± 0.04
		2	5.27 ± 0.02	0.31 ± 0.08	5.28 ± 0.01	0.32 ± 0.05
		3	5.40 ± 0.02	−0.00 ± 0.22	5.40 ± 0.01	0.08 ± 0.06
		4	5.46 ± 0.03	−0.06 ± 0.20	5.44 ± 0.01	0.03 ± 0.09
		5	5.50 ± 0.03	−0.17 ± 0.16	5.47 ± 0.01	−0.17 ± 0.12
	♀	1	4.66 ± 0.02	0.63 ± 0.04	4.69 ± 0.01	0.62 ± 0.05
		2	5.12 ± 0.02	0.38 ± 0.06	5.14 ± 0.01	0.42 ± 0.06
		3	5.33 ± 0.02	0.34 ± 0.17	–	–
		4	5.41 ± 0.02	0.05 ± 0.12	–	–
		5	5.44 ± 0.02	0.16 ± 0.14	–	–

Discussion

We analyzed the effect of population density on static allometry between horn length and body mass in four mountain ungulates to test whether allometric relationships were more sensitive to variation in individual condition in species with large horns, and whether allometric slopes and intercepts were equally sensitive to changes in environmental conditions mostly induced by variation in population density. We showed that density-dependent changes in static allometry mostly resulted from changes in the allometric intercept, thus confirming that allometric slope is canalized against environmental variation. Changes in the allometric intercept further showed that, in most cases, horns were shorter for a given body mass at high density, the differences being more pronounced in species with larger horns, as expected for condition-dependent traits.

Patterns of static allometry between horn length and body mass

In all species static allometry of both sexes was shallower in older individuals. This effect was more pronounced in chamois and mountain goats where it also started at younger age, with static allometric slopes generally not statistically different from zero for individuals older than two years (see Rughetti and Festa-Bianchet 2010 for similar results on the arithmetic scale). In contrast, the static allometry in ibex and bighorn sheep males remained hyperallometric or not different from isometry for all age classes examined. In females, age-specific changes in static allometry were qualitatively similar to those observed in males for each species, although static allometry was systematically shallower than in males.

Shallow static allometries among older individuals do not necessarily imply that the two traits are independent.

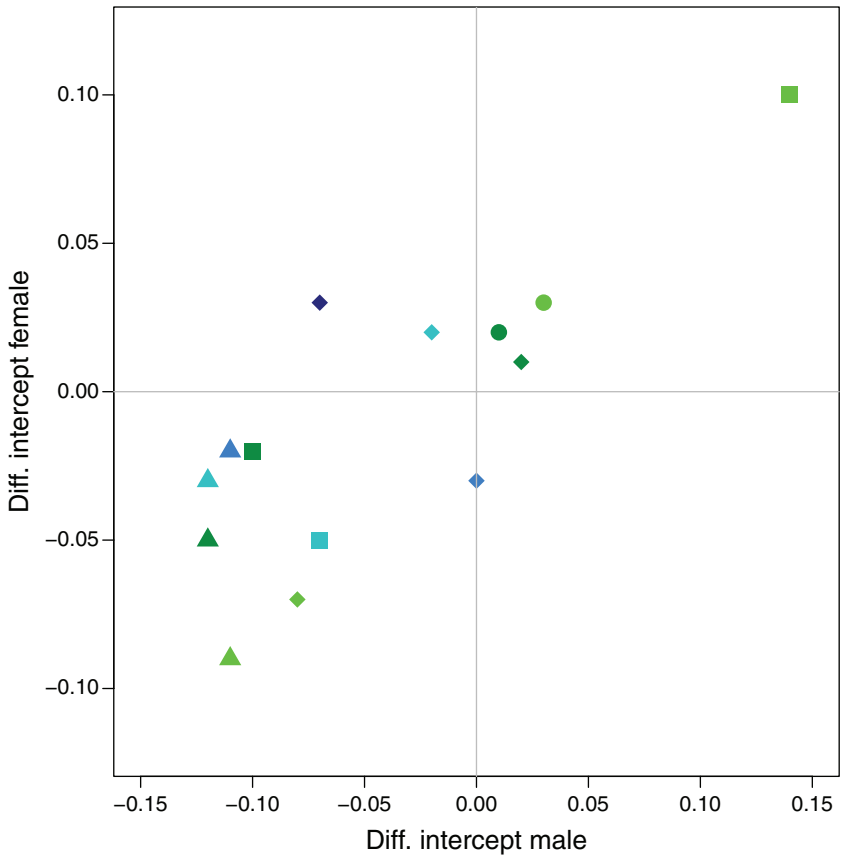


Figure 3. Relationship between sexes in the differences in allometric intercept between density periods (high minus low density) for each age class in the different species ($r^2 = 0.65$, Alpine ibex: squares; bighorn sheep: triangles; chamois: diamonds; mountain goat: dots; light green: 1 year old, dark green: 2 years old, cyan: 3 years old, blue: 4 years old, dark blue: 5 years old).

In capital breeders that accumulate body reserves during the summer to sustain reproduction during periods of low resource availability, body mass fluctuates seasonally, while horn length monotonically increases over time, but at a slower rate at old age. Therefore, for prime-aged individuals, even if heavier animals carry longer horns, the importance of the within-individual variation in body mass becomes larger compared to the among-individual variation in body mass within age class. This generates a biological error on the predictor variable that biases downward estimates of the allometric slope (Hansen and Bartoszek 2012). Unfortunately, the number of recaptures within each year was too low for most species to evaluate the within-year variation in body mass and correct the estimated slopes. Although analyzing allometric relationship between horn length and some skeletal measurement would provide less biased estimates of the allometric slope, data for skeletal measurements are not available for all studied species. More generally, these data are scarce for bovids (Tidière et al. 2020) and they tend to be error prone (Martin et al. 2013).

In ibex and bighorn sheep, the static hyperallometry among prime-age males indicates that horn length provides somewhat reliable cues about age and body mass. In contrast, horn length in females of these two species and in both sexes of chamois and mountain goat conveys little information for conspecifics. These results tend to support the differences in the role of horn length for male mating success in the different species. Indeed, horn length together with body mass and age affect dominance and mating success in both bighorn sheep (Coltman et al. 2002, Pelletier and Festa-Bianchet 2006) and ibex (Bergeron et al. 2010, Willisch et al. 2012, 2015), whereas for chamois, age is the key factor affecting the ability to defend a territory (Corlatti et al. 2015b). In mountain goat males older than two years, mating success is mostly determined by body mass at the time of the rut (Côté et al. 1998, Mainguy and Côté 2008). We note, however, that the stronger covariation between horn size and body mass in ibex and bighorn sheep makes it difficult to assess the relative contribution of each trait to male mating success. Furthermore, in chamois, mountain goats, but also bighorn sheep, dominance among females generally depends on the interaction among age, body mass and horn length, with body mass being the key factor once age is accounted for (Locati and Lovari 1991, Côté 2000, Favre et al. 2008). We found no study documenting how age, horn size and body mass influence dominance rank of ibex females. However, according to the allometric pattern, which is similar among the four species, one can predict that horn size is not a key factor for dominance for ibex females either.

Effects of population density on static allometry

Our results confirm the negative impact of population density on both horn length and body mass in bovids (reviewed by Bonenfant et al. 2009b and Douhard et al. 2017), and they also show that, except for male and female bighorn sheep, this impact is proportionally stronger on body mass than on horn length. Nevertheless, static allometric intercepts were generally lower at high than at low density, indicating that horns grown at high density were shorter for a given body mass than those grown at low density. Note that a change in allometric intercept directly represents the proportional change in the mean of both variables solely when the allometric slope equals 1. In ibex and mountain goats, however, yearling of both sexes showed a higher allometric intercept at high than at low density. This is explained by a particularly strong negative effect of density on body mass compared to horn length (Supporting information). Consequently, while both traits decrease at high density, the decrease in body mass is so pronounced that yearling from both species carry horns that are longer for a given body mass at high than at low density. Remarkably, from two years of age onward, horns grown at high density are again smaller than those grown at low density for a given body mass. This suggests that under poor nutritional conditions generated by high population density, resource allocation to body mass is prioritized possibly at the expense of horn growth. These results confirm the key role of body mass for reproduction in these capital breeder species (Gaillard et al. 2000, Bonenfant et al. 2009b), and also corroborate earlier results by Jorgenson et al. (1998) and Festa-Bianchet et al. (2004) who showed that the effects of density on horn length and body mass mostly affect young age classes.

The absence of statistically significant differences in slope may reflect a lack of statistical power. We note, however, that the differences in static allometric slopes were highly idiosyncratic and inconsistent between sexes within species. Therefore, we propose that changes in static slope between low and high density mostly reflect sampling variance.

The congruence of the density-dependent changes in static allometric intercept between sexes suggests that despite sex differences in horn length and body mass and in the selective pressures resulting from the different function of horns in each sex, the influence of population density and thereby per capita food intake on growth regulation of both traits is similar in both sexes. Whether these similarities reflect the effects of cross-sex genetic correlations (Lande 1980) or the congruent effects of different selection pressures acting on both traits remains an open question.

Conclusions

We found that in four species of mountain ungulates, the effects of population density on the static allometry between horn length and body mass were restricted to changes in the allometric intercept, the changes in the allometric slope being limited and inconsistent. These results suggest that the static allometric slope between horn length and body mass is canalized against deterioration of the environment generated by difference in population density.

Acknowledgements – We would like to thank the OGFH, the Groupement d'Intérêt Cynégétique des Bauges, the Office National des Forêts, hunters and wildlife technicians (T. Chevrier, T. Amblard and J.-M. Jullien) who contributed collecting chamois data.
Funding – Financial support was provided to CP by the Research Council of Norway, FRIPRO program, project 287214, and by the Research Council of Norway through its Centre of Excellence funding scheme, project number 223257. Funding for the bighorn sheep and the mountain goat studies was mainly provided by the Natural Sciences and Engineering Research Council of Canada, and Alberta Conservation Association.
Conflict of interest – The authors declare having no conflict of interest.
Ethics statement – The research presented in this manuscript was done according to the ethical rules of each country.

Author contributions

Christophe Pélabon: Conceptualization (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Writing – original draft (equal). **Steeve D. Cote**: Data curation (equal); Writing – review and editing (equal). **Marco Festa-Bianchet**: Data curation (equal); Writing – review and editing (equal). **Jean-Michel Gaillard**: Writing – review and editing (equal). **Mathieu Garel**: Data curation (equal); Writing – review and editing (equal). **Jean-François Lemaître**: Writing – review and editing (equal). **Anne Loison**: Data curation (equal); Writing – review and editing (equal). **Morgane Tidière**: Writing – review and editing (equal). **Carole Toïgo**: Conceptualization (equal); Data curation (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.f4qrfj6wr> (Pélabon et al. 2021).

References

Bassano, B. et al. 2003. Body weight and horn development in Alpine chamois, *Rupicapra rupicapra* (Bovidae, Caprinae). – Mammalia 67: 65–73.

Bates, D. et al. 2015. Fitting linear mixed-effects models using lme4. – J. Stat. Softw. 67: 1–48.

Bergeron, P. et al. 2010. Secondary sexual characters signal fighting ability and determine social rank in Alpine ibex *Capra ibex*. – Behav. Ecol. Sociobiol. 64: 1299–1307.

Bergland, A. O. et al. 2008. Quantitative trait loci affecting phenotypic plasticity and the allometric relationship of ovariole number and thorax length in *Drosophila melanogaster*. – Genetics 180: 567–582.

Bolstad, G. H. et al. 2015. Complex constraints on allometry revealed by artificial selection on the wing of *Drosophila melanogaster*. – Proc. Natl Acad. Sci. USA 112: 13284–13289.

Bonduriansky, R. 2007. Sexual selection and allometry: a critical reappraisal of the evidence and ideas. – Evolution 61: 838–849.

Bonenfant, C. et al. 2009a. Age-dependent relationship between horn growth and survival in wild sheep. – J. Anim. Ecol. 78: 161–171.

Bonenfant, C. et al. 2009b. Empirical evidence of density-dependence in populations of large herbivores. – Adv. Ecol. Res. 41: 313–357.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference. A practical information-theoretic approach, 2nd edn. – Springer.
Cheverud, J. M. 1982. Relationships among ontogenetic, static and evolutionary allometry. – Am. J. Phys. Anthropol. 59: 139–149.
Coltman, D. W. et al. 2002. Age-dependent sexual selection in bighorn rams. – Proc. R. Soc. B 269: 165–172.
Corlatti, L. et al. 2015a. Horn growth patterns in Alpine chamois. – Zoology 118: 213–219.
Corlatti, L. et al. 2015b. Preliminary analysis of reproductive success in a large mammal with alternative mating tactics, the Northern chamois, *Rupicapra rupicapra*. – Biol. J. Linn. Soc. 116: 117–123.
Côté, S. 2000. Dominance hierarchies in female mountain goats: stability, aggressiveness and determinants of rank. – Behaviour 137: 1541–1566.
Côté, S. D. et al. 1998. Horn growth in mountain goats *Oreamnos americanus*. – J. Mammal. 79: 406–414.
Cotton, S. et al. 2004. Condition dependence of sexual ornament size and variation in the stalk-eyed fly *Cyrtodiopsis dalmanni* (Diptera: Diopsidae). – Evolution 58: 1038–1046.
Douhard, M. et al. 2017. Environmental and evolutionary effects on horn growth of male bighorn sheep. – Oikos 126: 1031–1041.
Douhard, M. et al. 2018. Drivers and demographic consequences of seasonal mass changes in an alpine ungulate. – Ecology 99: 724–734.
Egset, C. K. et al. 2011. Geographical variation in allometry in the guppy *Poecilia reticulata*. – J. Evol. Biol. 24: 2631–2638.
Egset, C. K. et al. 2012. Artificial selection on allometry: change in elevation but not slope. – J. Evol. Biol. 25: 938–948.
Emlen, D. J. 1997. Diet alters male horn allometry in the beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). – Proc. R. Soc. B 264: 567–574.
Favre, M. et al. 2008. Determinants and life-history consequences of social dominance in bighorn ewes. – Anim. Behav. 76: 1373–1380.
Festa-Bianchet, M. et al. 2004. Relative allocation to horn and body growth in bighorn rams varies with resource availability. – Behav. Ecol. 15: 305–312.
Festa-Bianchet, M. et al. 2019. Long-term studies of bighorn sheep and mountain goats reveal fitness costs of reproduction. – J. Anim. Ecol. 88: 1118–1133.
Gaillard, J.-M. et al. 2000. Temporal variation in fitness components and population dynamics of large herbivores. – Annu. Rev. Ecol. Syst. 31: 367–393.
Garel, M. et al. 2011. Population abundance and early spring conditions determine variation in body mass of juvenile chamois. – J. Mammal. 92: 1112–1117.
Hamel, S. et al. 2010. Maternal characteristics and environment affect the costs of reproduction in female mountain goats. – Ecology 91: 2034–2043.
Hansen, T. F. and Bartoszek, K. 2012. Interpreting the evolutionary regression: the interplay between observational and biological errors in phylogenetic comparative studies. – Syst. Biol. 61: 413–425.
Huxley, J. 1932. Problem of relative growth. – Johns Hopkins Univ. Press, Baltimore.
Jorgenson, J. T. et al. 1998. Effects of population density on horn development in bighorn rams. – J. Wildl. Manage. 62: 1011–1020.
Klingenberg, C. P. and Zimmermann, M. 1992. Static, ontogenic and evolutionary allometry – a multivariate comparison in 9 species of water-striders. – Am. Nat. 140: 601–620.
Lande, R. 1980. Sexual dimorphism, sexual selection and adaptation in polygenic characters. – Evolution 34: 292–305.
Locati, M. and Lovari, S. 1991. Clues for dominance in female chamois: age, weight or horn size? – Aggress. Behav. 17: 11–15.
Mainguy, J. and Côté, S. D. 2008. Age- and state-dependent reproductive effort in male mountain goats, *Oreamnos americanus*. – Behav. Ecol. Sociobiol. 62: 935–943.
Martin, J. G. A. et al. 2013. Detecting between-individual differences in hind-foot length in populations of wild mammals. – Can. J. Zool. 91: 118–123.
Mason, T. H. et al. 2012. Intraseasonal variation in reproductive effort: young males finish last. – Am. Nat. 180: 823–830.
Maynard Smith, J. M. et al. 1985. Developmental constraints and evolution: a perspective from the Mountain Lake conference on development and evolution. – Q. Rev. Biol. 60: 265–287.
Morellet, N. et al. 2007. Indicators of ecological change: new tools for managing populations of large herbivores. – J. Appl. Ecol. 44: 634–643.
Pélabon, C. et al. 2014. Evolution of morphological allometry. – Ann. N. Y. Acad. Sci. 1320: 58–75.
Pélabon, C. et al. 2018. Modelling allometry: statistical and biological considerations – a reply to Packard. – Biol. J. Linn. Soc. 125: 664–671.
Pélabon, C. et al. 2021. Data from: Effects of population density on static allometry between horn length and body mass in mountain ungulates. – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.f4qrfj6wr>.
Pelletier, F. and Festa-Bianchet, M. 2006. Sexual selection and social rank in bighorn rams. – Anim. Behav. 71: 649–655.
Rughetti, A. and Festa-Bianchet, M. 2010. Compensatory growth limits opportunities for artificial selection in Alpine chamois. – J. Wildl. Manage. 74: 1024–1029.
Schröder, W. and Von Elsner-Schak, I. 1985. Correct age determination in chamois. – In: Lovari, S. (ed.), The biology and management of mountain ungulates. Croom Helm, London, pp. 65–70.
Stillwell, R. C. et al. 2016. Tipping the scales: evolution of the allometric slope independent of average trait size. – Evolution 70: 433–444.
Tidière, M. et al. 2020. Variation in the ontogenetic allometry of horn length in bovids along a body mass continuum. – Ecol. Evol. 10: 4104–4114.
Tobler, A. and Nijhout, H. F. 2010. Developmental constraints on the evolution of wing-body allometry in *Manduca sexta*. – Evol. Devel. 12: 592–600.
Toïgo, C. et al. 1999. Cohort affects growth of males but not females in alpine ibex *Capra ibex ibex*. – J. Mammal. 80: 1021–1027.
Toïgo, C. et al. 2007. Sex- and age-specific survival of the highly dimorphic Alpine ibex: evidence for a conservative life-history tactic. – J. Anim. Ecol. 76: 679–686.
Voje, K. L. 2016. Scaling of morphological characters across trait type, sex and environment: a meta-analysis of static allometries. – Am. Nat. 187: 89–98.
Voje, K. L. et al. 2014. Allometric constraints and the evolution of allometry. – Evolution 68: 866–885.
Willisch, C. S. et al. 2012. Male reproductive pattern in a polygynous ungulate with a slow life-history: the role of age, social status and alternative mating tactics. – Evol. Ecol. 26: 187–206.
Willisch, C. S. et al. 2015. Horn growth and reproduction in a long-lived male mammal: no compensation for poor early-life horn growth. – Evol. Biol. 42: 1–11.