

Another one bites the dust: Does incisor-arcade size affect mass gain and survival in grazing ungulates?

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Abstract: Incisor-arcade size affects foraging efficiency in grazing ungulates and should be under strong selective pressure. We investigated individual variation in incisor-arcade size and its relationship with body mass and survival in bighorn sheep (*Ovis canadensis*) at Ram Mountain, Alberta, Canada, over 9 years. In adult ewes, incisor-arcade breadth and depth decreased with age, probably as a result of tooth wear. We found no effects of incisor-arcade size on survival of lambs or adult ewes. In adult ewes, an apparent positive effect of incisor-arcade size on survival disappeared when age was accounted for. Incisor-arcade breadth and depth had no effect on summer mass gain in lambs or adult ewes. Although linear models suggested that arcade breadth in lambs was correlated with summer mass gain, a latent variable path analysis model revealed that the correlation was due to an allometric relationship of arcade breadth with body size. Variation in incisor-arcade size in bighorn sheep appears to be due to individual variation in body size and age rather than to directional selection.

Résumé : Puisque la taille de l'arcade incisive affecte l'efficacité de la quête de nourriture chez les ongulés brouteurs, elle doit subir une forte pression sélective. Nous avons étudié la variation individuelle de la taille de l'arcade incisive et sa relation avec la masse corporelle et la survie chez le mouflon d'Amérique (*Ovis canadensis*) à Ram Mountain, Alberta (Canada), durant 9 années. Chez les brebis adultes, la largeur et la profondeur de l'arcade décroissent avec l'âge, probablement à cause de l'usure des dents. Il n'y a pas d'effet de la taille de l'arcade sur la survie des agneaux, ni sur celle des brebis adultes. Chez les brebis adultes, un effet positif apparent sur la survie disparaît lorsque l'âge est pris en compte. La largeur et la profondeur de l'arcade n'ont aucun effet sur le gain de masse durant l'été chez les agneaux, ni chez les brebis adultes. Bien que des modèles linéaires semblent indiquer que la largeur de l'arcade chez les agneaux est en corrélation avec le gain de masse en été, un modèle d'analyse des pistes avec variables latentes démontre que la corrélation est due à une relation allométrique entre la largeur de l'arcade et la taille du corps. La variation de la taille de l'arcade incisive chez le mouflon d'Amérique semble donc s'expliquer par les variations individuelles de la taille du corps et de l'âge, plutôt que par la sélection directionnelle.

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Introduction

Individual variation in traits directly affecting foraging efficiency should have considerable fitness consequences. For example, beak morphology determines foraging efficiency in granivorous birds and variability in this trait can be maintained through oscillating selection following recurrent changes in environmental conditions (Gibbs and Grant 1987; Smith 1987, 1990). Few studies, however, have investigated individual variation in mouth morphology in mammals.

Illius and Gordon (Illius and Gordon 1987; Gordon and Illius 1988; Illius et al. 1995; Gordon et al. 1996) suggested that incisor-arcade breadth (IAB; the distance between the outer edges of the last incisors on the left and right rami) is

under strong selective pressure in grazing ungulates. They argued that individuals with wider incisor arcades are able to grasp more forage per bite and thus have higher fitness than those with a smaller muzzle. A wide mouth should be advantageous especially when forage is scarce at high herbivore density. In an island population of feral sheep, Illius et al. (1995) claimed that during a winter population crash due to starvation, survival increased with IAB. Despite an apparent strong selection gradient against narrow arcades, however, IAB retained considerable variability in the population. Illius et al. (1995) speculated that narrow-mouthed sheep may benefit at low population density, being able to forage selectively on swards dominated by mature and senescent grass. Coarse grassland of low digestibility, requiring selec-

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tive grazing, dominates swards when grazing pressure is low. Based on those results, Fryxell et al. (1999) presented a simple Mendelian genetic model showing how variability in incisor-arcade size could be maintained in populations characterized by dynamic instability, when the fitness advantage of arcade size varies with time among different genotypes.

Later, however, the same research group (Milner et al. 1999) recognized that some individuals had been erroneously assigned in the survival analysis, invalidating the results of Illius et al.'s (1995) study. The hypothesis of direct selection on incisor-arcade size in grazing ungulates is thus poorly tested.

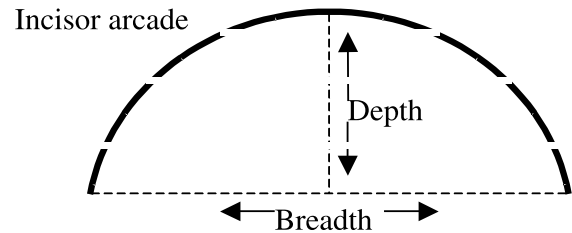
The idea of a selection gradient on a morphological trait directly involved in foraging efficiency is intuitively appealing but presents a major methodological problem. Both incisor-arcade size and body mass depend on the overall body size of an animal: larger individuals weigh more and have a bigger muzzle. Body size, particularly of young ungulates, is often positively correlated with survival (Festa-Bianchet et al. 1997; Milner et al. 1999; Gaillard et al. 2000). Selection on body size may thus appear to act on incisor-arcade size even in the absence of selective pressure on arcade size. This is a classic example of confusing "selection of" a trait (a trait and survival are correlated) and "selection for" a trait (survival is affected by the trait) (Sober 1984). Even if there is a selection gradient, IAB and survival may simply share a common cause (large body size) that is itself the target of selection (Kruuk et al. 2002).

If selection acts directly on incisor-arcade size, individuals with larger arcades for a given body size should have greater foraging efficiency at high population density, and thus gain more mass than individuals with relatively smaller arcades. This assumption has never been tested.

To test this idea, one could experimentally manipulate incisor-arcade size and compare the mass gains of individuals of the same body size. Such an experiment cannot be performed in a wild ungulate population. Traditional statistical methods, like multiple regression, are also of limited usefulness because they cannot distinguish between a correlation due to a third unmeasured variable and one due to a causal relationship. A series of recently developed statistical methods called "structural-equation modelling" are appropriate for solving this problem because they permit testing of hypotheses involving explicit causal relationships (Shipley 2000). The rationale behind these methods is that while correlation does not necessarily involve a cause-effect relationship, causation necessarily implies a series of partial correlations and constraints on the pattern of covariation between variables (Shipley 1999). It is thus possible to test whether the matrix of covariation between test variables fits the predicted covariation matrix of a specific causal model.

Here we investigate individual variation in incisor-arcade size, body mass, and survival in a free-ranging population of bighorn sheep (*Ovis canadensis*) over 9 years. We first analyze the variation in incisor-arcade size with age in adult ewes and test whether this variation might be ascribed to natural selection. We then explore the relationship between incisor-arcade size, mass gain, and survival of lambs and adult ewes. Finally, we use a structural-equation model (SEM) to test the hypothesis of a direct causal relationship between incisor-arcade size and mass gain in lambs.

Fig. 1. Variables measured on incisor arcades of bighorn sheep (*Ovis canadensis*) ewes and lambs. The incisor impressions left by the sheep on dental wax are represented.



Materials and methods

We collected data at Ram Mountain (52°N, 115°W; elevation 1082–2173 m), Alberta, Canada, from 1994 to 2000. Bighorns were captured in a corral trap from late May to early October. Adult ewes were marked with canvas collars and lambs were tagged with coloured Safeflag plastic strips attached to numbered metal Ketchum ear tags. All adult ewes and lambs were marked, and were weighed to the nearest 250 g using a Detecto spring scale at each capture. Spring mass (SW) and autumn mass (AW) are the mass of each sheep adjusted to 5 June (15 June for lambs) and 15 September, respectively, using repeated mass measurements of each individual each year (for more details about mass adjustment see Festa-Bianchet et al. 1996).

Impressions of the incisor arcades of captured sheep were collected on dental wax. IAB was the distance between the outer edges of the last incisors on the left and right rami, measured with a precision calliper (Fig. 1) (Gordon and Illius 1988). Following Gordon and Illius (1988), incisor-arcade depth (IAD) was defined as the perpendicular distance between a line connecting the two outermost incisors and the front of the first incisors (Fig. 1).

IAB of lambs increases substantially during summer. Therefore, IAB of lambs that were captured at least twice was adjusted to 10 August (midsummer) using each lamb's own IAB growth rate. For lambs with only one IAB measurement during summer, IAB was adjusted to midsummer using the mean IAB growth rate of lambs for which we had at least two measurements in that year. Because IAD was not significantly correlated with capture date, no adjustment was applied for that variable. For lambs with more than one IAD measurement in the same year, we used the mean of those measurements. IAB and IAD measurements of adult ewes were not adjusted for capture date, and all incisor-arcade measurements were collected between 25 May and 30 June.

Data analysis

To assess measurement error, we took two dental-wax impressions for each individual during the first capture in 1999, and each impression was measured once. This procedure estimated not only the measurement error due to the use of the calliper, but also potential inaccuracies in the dental-wax impressions. Repeatability of measurements was estimated with the intraclass correlation coefficient (Lessels and Boag 1987; Sokal and Rohlf 1995). Because of differences in trait dimensions among age-sex classes, we performed the analysis separately for lambs and adult females

(>4 years old). We analyzed incisor arcades of 122 lambs and 75 adult ewes.

IAB and IAD increase until bighorn sheep are 4 years of age. Two new incisors (one for each side of the symmetry plane) replace the corresponding milk teeth each year until the full set of adult teeth is completed at age 4. Because the relationship of age with the incisor size variables is not linear, and because tooth replacement often left gaps in the wax impressions, we only considered ewes older than 4 years. We included 75 ewes for which we had at least 2 years of data in the analysis. We excluded ewes with broken or missing incisors.

We used linear mixed effects (LME) models (Pinheiro and Bates 2001) to examine the effects of age on incisor-arcade size and explore the relationship between arcade size and summer mass gain in adult ewes. Fitting individual identity as a random grouping factor, LME models estimate the effects of age on an individual scale and avoid pseudoreplication due to repeated measurements of the same individual at different ages. All the LME models were fitted by maximum likelihood and the significance of fixed terms was assessed with conditional *F* tests. Goodness-of-fit and distributional assumptions were checked by examining the residuals graphically (Pinheiro and Bates 2001).

As lambs were considered only in the year of birth, no repeated individual measures were used, therefore generalized linear models (GLMs) were fitted to explore the relationship between incisor-arcade size and summer mass gain in lambs. GLMs with a binomial distribution and a logit link function were also fitted to explore the effects of incisor-arcade size, population density, and body mass on lamb survival. We modelled survival in adult ewes with generalized linear mixed models (GLMMs), using penalized quasi-likelihood (Venables and Ripley 2002; Wolfinger and O'Connell 1993) to account for repeated measurements of the same individuals in different years. All models were fitted using S-PLUS 2000 (MathSoft Inc.).

To test the hypothesis of a direct causal link between incisor-arcade size and summer mass gain we built a latent variable path analysis model using a SEM approach (Shipley 2000). Briefly, the qualitative causal relationships between the variables, as specified in our hypothesis, was specified as a system of linear equations with free and fixed parameters following this multivariate hypothesis. We then derived the constraints on the predicted covariance matrix that must exist in the data if the qualitative multivariate hypothesis is correct, fit the free parameters of the structural equations to the data by maximizing the likelihood, and then compared the observed and predicted covariance matrices using the maximum-likelihood χ^2 statistic. This statistic is distributed as a χ^2 distribution with appropriate degrees of freedom if the observed and predicted covariance matrices are equivalent up to random sampling variation. Path models were built using EQS 5.7 for Windows.

To avoid problems with non-normally distributed data, we tested the goodness of fit of the SEM models, testing for the significance of the Santorra–Bentler scaled χ^2 value rather than the normal χ^2 value (Shipley 2000). When the χ^2 value is not significant, the null hypothesis cannot be rejected and the corresponding model is considered to fit the data. Nested models, including direct causal links between IAB or IAD

Table 1. Repeatability analysis of measurements of the incisor arcades of bighorn sheep (*Ovis canadensis*) at Ram Mountain, Alberta, taken in 1999.

	df	<i>F</i> ratio	Repeatability <i>r</i>
Incisor-arcade breadth (IAB)			
Lambs	15	7.68***	0.77
Adult ewes	31	34.50***	0.94
Incisor-arcade depth (IAD)			
Lambs	15	7.78***	0.77
Adult ewes	31	23.16***	0.92

Note: A significant *F* ratio indicates that within-individual variability (measurement error) is less than between-individual variability.

****p* < 0.0001.

and AW were tested using the χ^2 difference testing procedure proposed by Santorra and Bentler (1999). The resulting Santorra–Bentler scaled χ^2 difference test follows a χ^2 distribution, and a significant *p* value indicates a better fit of the nested model against the basic model. More details on model-fitting procedures are provided with the results.

Results

Measurement error

Variability within individuals (measurement error), estimated on the repeated incisor impressions taken in 1999, was significantly smaller than variability among individuals. Repeatability was high for both ewes and lambs and for both IAB and IAD (Table 1). Variability in IAB and IAD among individuals was thus not due to measurement error.

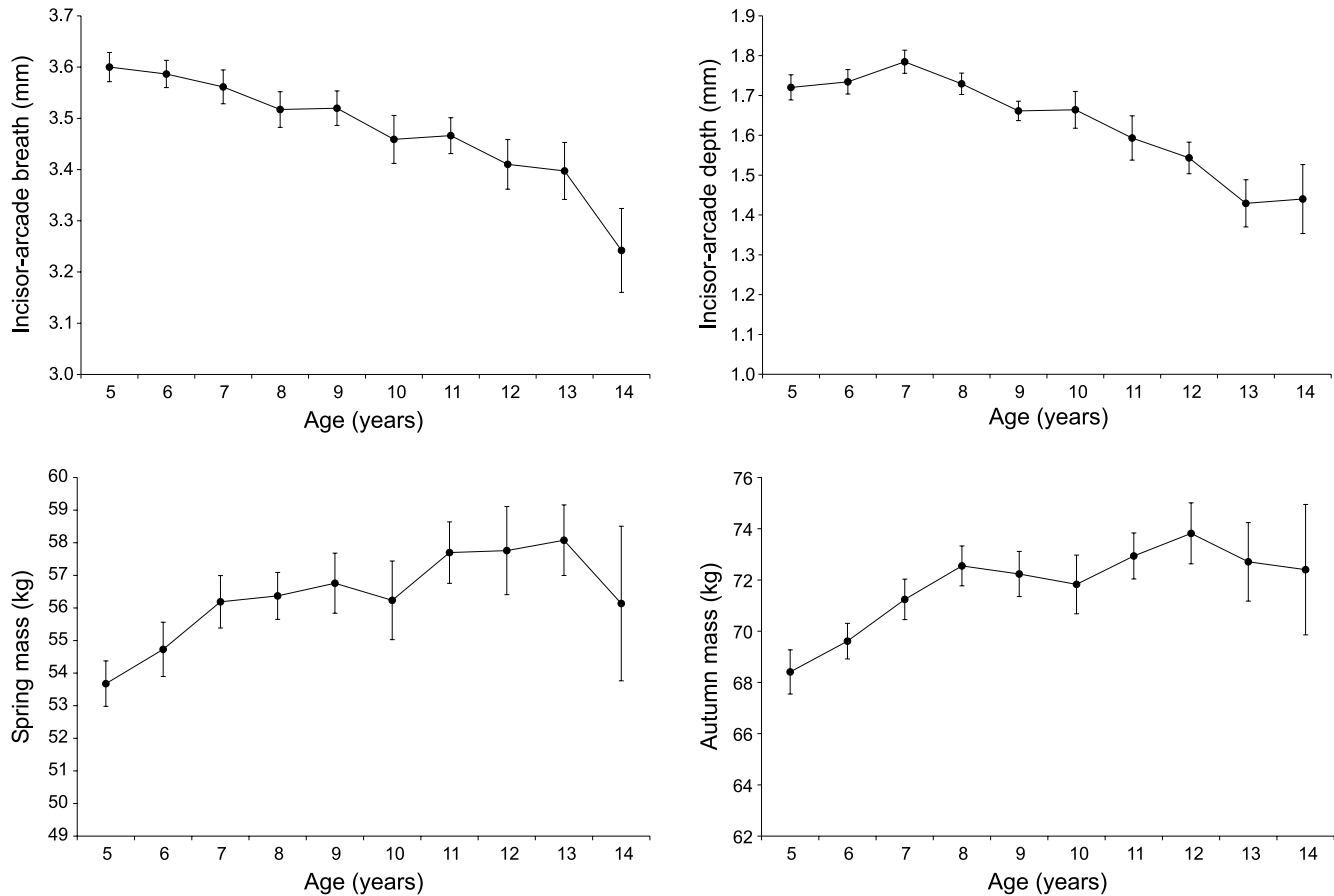
Variation in incisor-arcade size with age

In adult ewes, IAB and IAD appeared to decrease with age (Fig. 2). The apparent effect of age on incisor-arcade size could be due to either selective mortality (if ewes with small arcades are more likely to survive than ewes with large arcades) or tooth wear. To explore the relationship between IAB and IAD and age, we used a LME model fitting individual identity as the random grouping factor. This design corresponds to an analysis of covariance with individual identity as a random factor, IAB or IAD as the dependent variable, and age as a covariate. If the decrease in incisor-arcade size occurs within individuals (and thus is probably due to tooth wear), there should be a significant within-individual negative regression with age. Indeed, both IAB and IAD decreased with age within individuals (IAB: $\beta = -0.031$, $F_{[1,201]} = 82.29$, $p < 0.0001$; IAD: $\beta = -0.037$, $F_{[1,201]} = 71.1$, $p < 0.0001$).

Effects of incisor-arcade size on summer mass gain

We explored the effects of IAB, IAD, density, and age on summer mass gain in adult ewes using LME models with individual identity as a random factor. We fitted AW as the dependent variable and SW as a fixed covariate. Consequently, any effects of arcade size on AW would have been due to effects on summer mass gain. Age was fitted as a quadratic function (Bérubé et al. 1999). As expected, age and SW had positive effects on AW (age: $\beta = 2.27$, $F_{[1,196]} = 15.08$, $p = 0.0001$; age²: $\beta = -0.1$, $F_{[1,196]} = 11.21$, $p = 0.001$; SW: $\beta = 0.31$, $F_{[1,197]} = 47.67$, $p < 0.0001$). Density had no effect on

Fig. 2. Variation with age in the four morphological traits of adult bighorn ewes at Ram Mountain, Alberta, analyzed in this paper.



mass gain ($F_{[1,196]} = 0.30$, $p = 0.58$), nor did IAB ($F_{[1,196]} = 2.19$, $p = 0.14$) or IAD ($F_{[1,196]} = 2.19$, $p = 0.14$).

The effects of IAB, IAD, sex, and density on summer mass gain of lambs were explored with GLMs. AW in lambs was a function of SW ($\beta = 0.71$, $F_{[1,71]} = 1.70$, $p = 0.02$), population density ($\beta = -0.06$, $F_{[1,71]} = 12.79$, $p = 0.0006$), and IAB ($\beta = 13.64$, $F_{[1,71]} = 12.79$, $p < 0.0001$). IAD ($F_{[1,72]} = 1.03$, $p = 0.36$) and sex ($F_{[1,71]} = 0.02$, $p = 0.89$) did not contribute significantly to the model, although when a larger sample was considered, male lambs were about 10% heavier than female lambs (Festa-Bianchet et al. 1996). IAB thus appeared to have a strong positive effect on mass gain in lambs.

Effects of incisor-arcade size on survival

The GLM showed no evidence of an effect of IAB and IAD on lamb survival. Sex had an effect on survival, while AW was almost significant (final GLM: survival \sim sex + AW; sex: $\beta = -0.2$, deviance = 5.84, df = 1,120, $p = 0.02$; AW: $\beta = 0.11$, deviance = 3.3, df = 1,118, $p = 0.07$; rejected terms: IAB: deviance = 0.13, df = 1,117, $p = 0.71$; IAD: deviance = 0.14, df = 1,116, $p = 0.71$). Within this sample, male lamb survival to 1 year of age was 29.9%, while female lamb survival was 45.2%.

For adult ewes, when age was ignored, IAB and IAD appeared to have an effect on survival, while SW and AW did

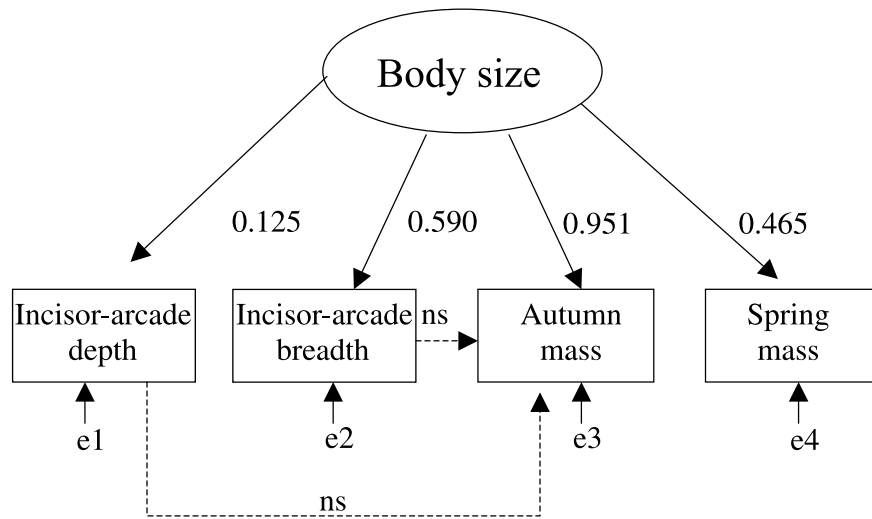
not (final GLMM: survival \sim IAB + IAD; IAB: $\beta = 2.44$, df = 201, $t = 2.99$, $p = 0.003$; IAD: $\beta = 2.38$, df = 201, $t = 3.21$, $p = 0.001$; rejected terms: AW: df = 200, $t = -0.48$, $p = 0.63$; SW: df = 198, $t = -0.98$, $p = 0.33$). When we included age, however, IAB and IAD dropped out from the final model (final GLMM: survival \sim age; age: $\beta = -0.61$, df = 200, $t = -8.89$, $p < 0.0001$; rejected terms: IAB: df = 200, $t = 1.54$, $p = 0.12$; IAD: df = 200, $t = 1.33$, $p = 0.18$), suggesting that IAB and IAD were just proxies for age.

Testing for a causal relationship between incisor-arcade size and mass gain in lambs

We first tested a basic measurement model using a SEM approach, including body size as a latent variable and IAB, IAD, AW, and SW of lambs as dependent variables (Fig. 3). The basic model adequately describes the relationships among these variables (goodness-of-fit test: Santorra-Bentler $\chi^2 = 0.404$, df = 2, $p = 0.82$). The path coefficients of the accepted measurement model are reported in Fig. 3. AW showed the highest correlation with latent body size ($r^2 = 0.905$). The other observable variables had the following determination coefficients with the latent variable body size: SW, $r^2 = 0.216$; IAB, $r^2 = 0.348$; IAD, $r^2 = 0.016$.

We then tested for the significance of two nested models, relaxing the constraints between IAB or IAD and AW, and therefore testing for possible direct causal links between incisor-arcade size and mass gain independent of body size

Fig. 3. Path-analysis diagram for body-size components in bighorn sheep lambs. The solid arrows represent the basic measurement model with body size as a latent variable. The numbers beside the long solid arrows are path coefficients. Broken arrows represent nested models testing for the hypothesized causal links between incisor-arcade breadth (IAB) or incisor-arcade depth (IAD) and autumn mass (AW). The significance of the nested models is indicated above the broken arrows. The error terms are e1, e2, e3, and e4.



(Fig. 3). If there was an effect of IAB or IAD and AW that was not already explained by the common allometric effect of body size, the addition of these direct effects would significantly improve the fit of the model. Neither the nested model including a causal link between IAB and AW nor the one with a causal link between IAD and AW significantly improved the basic measurement model (Table 2). There is therefore no evidence for such direct effects and this supports the hypothesis that the association between IAB or IAD and AW is due simply to a general allometric relationship with body size.

Discussion

Both in our study and in other studies (Illius et al. 1995; Gordon et al. 1996; Milner et al. 1999), dental-wax impressions were taken on live animals in field conditions that were not optimal. The accuracy of measurements made on these impressions may thus be questioned. Estimation of measurement error is very important for traits hypothesized to be under direct selective pressure, because biologically significant patterns could be masked by measurement error. For bighorn sheep, variability in arcade size within individuals (measurement error) was smaller than variability among individuals, and repeatability was high for both IAB and IAD. Variability in IAB and IAD among individuals was thus not simply due to measurement error. Dental-wax impressions, therefore, yield reliable measurements of IAB and IAD in wild ungulates captured and processed under field conditions.

We found no evidence of a direct effect of natural selection on incisor-arcade size in bighorn sheep. Arcade size decreased with age in adult ewes. Such a decrease might be due to a selection gradient against larger incisor arcades. A directional selection gradient against a large incisor arcade could in theory develop at low density, when swards are high and sheep with a narrow muzzle may be able to better select

Table 2. Chi-square difference test of possible direct causal links between incisor-arcade measurements (IAB and IAD) and mass gain in bighorn sheep lambs.

Model	<i>c</i>	<i>cd</i>	<i>Trd</i>	<i>p</i>
Basic model	0.658			
+ IAD → AW	0.564	0.752	0.270	0.60
+ IAB → AW	0.625	0.691	0.003	0.96

Note: Following Santorra and Bentler (1999), *c* is the scaling correction factor, *cd* is the difference test scaling correction, and *Trd* is the Satorra-Bentler scaled χ^2 difference test. A significant *p* value would indicate that the nested model provides a better fit than the basic measurement model.

the most nutritious plant parts (Illius et al. 1995). Indeed, density declined dramatically at Ram Mountain, the number of adult ewes decreasing by half during this study. The age-related decrease in incisor-arcade size, however, occurred only within individuals, and thus was most probably due to tooth wear. Tooth wear with age is well known in ruminants, and is even used to estimate age (Hewison et al. 1999). To date, in virtually all studies of free-ranging ungulates, wear of molars has been analyzed, but wear of incisors should also be expected. Veterinarians use incisors to estimate age of domestic sheep and cattle (Fraser et al. 1991). The outer incisors (actually incisiform canines) of sheep have a typical conic form, with the cone pointing towards the palate. A reduction in height of the incisors due to wear would reduce the dimensions of the incisor arcade, as documented in this study. Our results emphasize how tooth wear with age should be considered in studies of selection on incisor-arcade size. Ignoring the age effect may lead to spurious interpretations.

There was no effect of IAB or IAD on lamb survival, which, however, was affected by AW, in accordance with the results of previous studies on lamb survival (Festa-Bianchet et al. 1997). In this sample we also found a lower survival rate for male than for female lambs.

In adult ewes, also in accordance with the results of previous studies (Festa-Bianchet et al. 1997), only age influenced survival, survival decreasing with age. IAB and IAD did not appear to affect survival. Interestingly, when we fitted IAB and IAD without including age in the model, both variables appeared to affect survival, while body mass did not. When age was included in the model, the effect of incisor-arcade size disappeared. Because age is negatively related to incisor-arcade size, ewes with larger incisor arcades survive better simply because they are younger and survival decreases with age (Loison et al. 1999). Illius et al. (1995) showed an effect of IAB on survival of adult feral sheep, but they did not consider age in their analyses, thus not accounting for possible tooth wear with age. In food-limited populations such as the Soay sheep studied by Illius et al. (1995), tooth wear with age could be particularly strong. Skogland (1988) found that in wild reindeer (*Rangifer tarandus*), tooth wear with age in food-limited females occurred twice as fast as among well-fed females. Moreover, Illius et al. (1995) pooled yearlings and adults in the same analysis, despite reporting that yearlings have a lower survival rate and smaller IAB values than adults.

One assumption of the hypothesis that incisor-arcade size is under a selective gradient is that it influences foraging efficiency (Gordon et al. 1996). Using linear models we showed how IAB is related to summer mass gain in lambs but not in adult ewes. This result must be interpreted with caution, however, because of the collinearity among fixed effects. When we explored these relationships further using a latent variable path analysis model with a SEM approach, the best fit was given by a basic measurement model with body size as a latent variable that was the single common cause of all observed variables. AW was the variable most correlated with body size. Adding explicit causal links between IAB or IAD and AW, independently of body size, did not improve the model. We therefore conclude that the relationships between incisor-arcade size and body mass are just due to an allometric relationship with body size. We found no causal relationship between incisor-arcade size and mass gain. Big sheep survive better than small ones, but incisor-arcade size appears not to be under directional selection in this population. Possibly the morphology of the incisor arcades in our study population reflects adaptation to highly variable environmental conditions. Bighorn ewes on Ram Mountain experience much annual variability in food availability over their life-span of 8–15 years. In addition to changes in population density that affect forage availability, ewes switch seasonally from browsing to grazing and feed on swards of different heights. Our results suggest that variability in incisor-arcade size among individual bighorn sheep is mostly due to variation in body size and age.

In conclusion, researchers studying natural selection on morphological traits should be cautious in inferring directional selection on a trait from patterns of covariance with survival. A third variable, such as body size or age in this study, could be the common cause of the variation both in survival and in the size of the trait, leading to a spurious correlation between the trait and survival. Mixed models, which account for intra-individual variability, and SEMs, which explicitly model causal links among variables, are powerful

tools for identifying real patterns of selection acting on correlated traits.

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