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## Is there a trade-off between horn growth and survival in adult female chamois?

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18 **Summary**

19 Life history theory predicts trade-offs in energy allocation between different life history traits  
20 when resources are limited, i.e. certain traits should be negatively correlated. However,  
21 individuals differ in their ability to acquire resources, which can lead to positive correlations  
22 between traits at the population level. Here, we investigated the consequences of the  
23 allocation in horn growth and body mass on survival in a bovid (*Rupicapra rupicapra*) with  
24 capture-mark-resighting data on 161 females. In female ungulates, body mass often covaries  
25 positively with demographic performance and the few studies on horn size suggest that this  
26 trait could be a signal of individual quality. Thus, we expected to measure positive correlations  
27 between the allocation in these traits and female survival. However, body mass was not  
28 correlated to female survival and there was only a negative, though marginal, effect of horn  
29 growth. Hence, it seems that the allocation in growth is not an indicator of female quality.  
30 Future studies could investigate the importance of growth on female reproduction to evaluate  
31 its effect on lifetime reproductive success. Moreover, it is important to confirm in other  
32 populations our result that suggests a cost of the allocation in horn growth to better  
33 understand the presence of horns in female bovids.

34 **Keywords:** horn growth, body mass, trade-off, ungulates, life-history strategies, delayed  
35 costs

36

## 37 **Introduction**

38 The existence of trade-offs is a central pillar of evolutionary theory in general and life history  
39 theory in particular (Roff, 2002). When resources are limited, the allocation of energy to one  
40 function (e.g., survival, reproduction or growth) reduces the amount of energy available to  
41 another, resulting in an observable cost. For example, reproductive costs have been described  
42 in many taxa as a negative correlation between reproductive allocation and survival (Roff,  
43 2002). Similarly, but less studied, we may expect a negative correlation between growth rates  
44 and survival (Mangel & Stamps, 2001). However, especially in the wild, it is not always  
45 straightforward to detect trade-offs because of individual heterogeneity. Indeed, high-quality  
46 individuals may be able to acquire more resources and may thus allocate more energy,  
47 simultaneously, in several traits than low-quality individuals (van Noordwijk & de Jong, 1986;  
48 Wilson & Nussey, 2010). This results in positive correlations at the population level even if an  
49 underlying trade-off exists at the individual level (Hamel *et al.*, 2009) (individual quality  
50 hypothesis). Moreover, the costs of an allocation may only be expressed at later stages: for  
51 example higher growth rates early in life can be correlated with reduced later performance  
52 and shorter lifespans (Metcalfe & Monaghan, 2003).

53 Here, we investigated the correlations between the allocation in growth and survival in  
54 females of a long-lived mammal, the chamois (*Rupicapra rupicapra*). We used two variables  
55 to describe growth: body mass and horn length. Body mass often covaries positively with  
56 demographic performance in ungulates, for example it can be positively correlated with  
57 juvenile survival (Côté & Festa-Bianchet, 2001) and negatively with female age at primiparity  
58 (Green & Rothstein, 1991). Thus, it seems to be an indicator of female quality and we expect  
59 it to covary positively with survival under the 'individual quality hypothesis'. However, this  
60 does not preclude the existence of a delayed cost of growth, which would be revealed by a

61 negative correlation in old females. In bovids, such as chamois, horns are permanent and both  
62 males and females wear horns. While male horns are known for their role in sexual selection  
63 (male-male competition and female choice), the role and putative associated costs of horns  
64 are much less studied in females. We aim here to clarify the correlation between horn length  
65 and age-specific survival in a female bovid. Given that large-horned females may be dominant  
66 over small-horned females (Locati & Lovari, 1991) and attain primiparity at an earlier age  
67 (Rughetti & Festa-Bianchet, 2011), horn size may be a measure of individual quality and thus  
68 may covary positively with survival (i.e., support for the individual quality hypothesis).  
69 However, horn growth may be energetically costly (e.g. it is adjusted to food availability  
70 (Chirichella *et al.*, 2013 and references therein)), and may represent a source of heat loss  
71 during winter (Picard *et al.*, 1994). Therefore, large-horned females may bear the cost of their  
72 larger horns later in life, in which case we predict a negative covariation between horn growth  
73 and old-female survival.

## 74 **Material and methods**

### 75 Site and studied species

76 A population of chamois (*Rupicapra rupicapra*, Linnaeus, 1758), a mountain ungulate, has  
77 been monitored since the early 1980s in the Game and Wildlife Reserve (GWR) of the Bauges  
78 massif (45°40'N, 6°13'E, 5,205 ha), in the northern French Alps. This site has been described  
79 elsewhere (Loison, Jullien, & Menaut, 1999). Chamois are trapped below falling nets baited  
80 with salt (June to September). Measurements on captured individuals included body mass,  
81 total horn length and horn growth from birth to 3 years of age (we averaged the measures  
82 from both horns). Recaptures are rare in this population and thus we used only the measures  
83 at first capture. Age was determined by counting horn annuli (Schröder & von Elsner-Schack,  
84 1985). Animals were individually marked with a coloured collar and visually monitored

85 between April and December each year with a varying intensity of observation pressure per  
86 year (see supplementary materials). For this study, we considered data from the site Armenaz  
87 for females  $\geq 3$  years of age for which early horn growth (0-3 year increment) was measured.  
88 The GWR is a protected area where only guided hunt occurs. We are therefore confident that  
89 all marked animals that were shot were reported ( $n = 20$ , early horn growth =  $162.78 \pm 16.14$   
90 mm). The data were right-censored (i.e. females were removed from the analyses after being  
91 shot) to estimate survivorship independently of any hunting effect (Lebreton *et al.*, 1992).

## 92 Statistical analyses

93 Body mass varies with age and capture date. In all the analyses, we used a corrected measure  
94 of body mass defined as the residuals of a linear regression of  $\log(\text{body mass})$  against capture  
95 date ( $F_{1,154}=15.41$ ,  $P<0.001$ ) and age (linear:  $F_{1,154}=11.26$ ,  $P<0.001$ , quadratic:  $F_{1,154}=6.31$ ,  
96  $P=0.013$ ). The interactions between age (linear and quadratic terms) and capture date were  
97 not included (all  $P>0.70$ ). For early horn growth, we used the standardized (i.e. centered and  
98 reduced) early horn growth and performed a Pearson's correlation with standardized total  
99 horn length and one with corrected body mass. Total horn length was standardized within  
100 each age (except for females aged 10 and more that were pooled).

101 We tested whether age-specific survival was correlated to early horn growth (0-3 year  
102 increment) or body mass at capture, using these 2 measurements as individual covariates in  
103 Capture-Mark-Recapture modelling in E-SURGE (version 1.9.0) (Choquet, Rouan, & Pradel,  
104 2009b). We first tested the goodness-of-fit of the Cormack-Jolly-Seber model using U-CARE  
105 (version 2.3.2) (Choquet *et al.*, 2009a). The Cormack-Jolly-Seber model satisfactorily fitted the  
106 data ( $\chi^2 = 63.70$ ,  $P = 0.382$ ). There was no transience ( $Z = -2.11$ ,  $P = 0.982$ ), but a strong "trap-  
107 happiness" ( $Z = -5.26$ ,  $P < 0.001$ , see examples of trap-dependence *lato sensu*, i.e. when  
108 animals are not physically recaptured, in (Pradel & Sanz-Aguilar, 2012)). This effect was well

109 accounted for with models taking into account individual heterogeneity in behaviour (e.g.  
110 some animals temporarily changing their home range; see supplementary materials). From  
111 the model with heterogeneity, we selected the best model describing the time effect in re-  
112 sighting probabilities (Table S1). Then, we fitted models on the survival probabilities. We  
113 proceeded in two steps. First, we tested for the importance of age and time (year effect). We  
114 considered 3 typical age classes in ungulates: 3-7 years old, 8-12 years old and >12 years old  
115 (Loison, Gaillard, & Houssin, 1994; Gaillard *et al.*, 2004). Second, we tested for effects of  
116 individual covariates: in the best model selected in the first step, we added an effect of early  
117 horn growth (standardized measure) or body mass (corrected measure) on survival of all the  
118 age classes or only one age class. Model selection was based on AICc: the model with the  
119 strongest support is the one with the lowest AICc. It is considered that two models differ when  
120 their difference of AICc is higher than 2 (Burnham & Anderson, 1998). We also calculated the  
121 AICc weight of each model (Burnham, Anderson, & Huyvaert, 2011).

## 122 **Results**

123 We gathered data on 161 females captured between 1992 and 2012 aged 3 to 12 years old  
124 (Table S2). Horn growth between 0 and 3 averaged 160.7 mm (SE = 14.0 mm, Figure S1) and  
125 accounted for most of total horn length (Figure 1). There was a positive correlation between  
126 early horn growth and total horn length corrected for age ( $R = 0.61$ ,  $t = 9.62$ ,  $df = 158$ ,  $P <$   
127  $0.001$ , Figure S2). At capture, female body mass averaged 29.23 kg (SE = 3.23kg, Figure S3).  
128 Early horn growth and body mass corrected for age and capture date were positively  
129 correlated ( $R = 0.18$ ,  $t = 2.27$ ,  $df = 153$ ,  $P = 0.025$ , Figure S4). Survival probabilities varied among  
130 years and age-classes (Table 1). Once these effects were accounted for, the best-fitting model  
131 included a negative effect of early horn growth on yearly survival of 8-12 years old females  
132 (Figure 2, model M4 in Table 2). The model with a negative effect on all females also had a

133 similar AICc (model M2 in Table 2). However, the baseline model showed the same support in  
134 the data than these two models (Model M0 in Table 2). The best-fitting model M4 is only 1.40  
135 times more likely than model M0. There was no effect of body mass on survival (Table 2).  
136 Model M4 is 2.9 times more likely than model M8 which is the model with the lowest AICc  
137 within models including an effect of body mass.

## 138 **Discussion**

139 We investigated the correlation between early horn growth, body mass and survival in adult  
140 female chamois. Interestingly, early horn growth and adult body mass were positively  
141 correlated, which suggests that these variables can be a measure of some of the same aspects  
142 of female growth. In this population, horn length at age 3 accounted on average for 85% of  
143 horn length when older than 8 years old. This confirms some previous results that showed  
144 that most horn growth occurs during the first summers of female life in chamois (Bassano,  
145 Perrone, & Von Hardenberg, 2003; Rughetti & Festa-Bianchet, 2011). Contrary to our  
146 predictions and other findings in ungulates (e.g. Gaillard *et al.*, 2000; Poissant *et al.*, 2008),  
147 adult body mass was not correlated with annual age-specific survival. We measured body  
148 mass only once and the fact that body mass does not seem to be a relevant predictor of annual  
149 survival may reflect the inter- and intra-annual variability of this variable. Concerning horn  
150 size, the model with most support in the data showed a delayed cost of growing large horns:  
151 old females with longer horns tended to have a lower survival than old females with shorter  
152 horns. The absence of a highly significant effect may be due to a lack of power because of the  
153 sample size and/or because of the large annual variation in survival between years. Indeed,  
154 trade-offs are more easily detected in years with overall low survival. Further studies will be  
155 needed to better understand the influence of annual variations on horn growth and on the  
156 trade-off with survival. Nevertheless, it is surprising to detect a cost, because even in male

157 ungulates with larger horns than chamois, there is no clear pattern linking horn size and  
158 survival (e.g., see table 1 of Bonenfant *et al.*, 2009; Toïgo, Gaillard, & Loison, 2013). Further  
159 studies in other populations and other species should clarify the existence of such cost in  
160 female bovids. For example, there is no correlation between longevity and horn volume in  
161 female bighorn sheep (Poissant *et al.*, 2008). If our result is confirmed in chamois and females  
162 bear a cost of wearing large horns, this suggests that large horns may be counter-selected in  
163 females. It would be particularly interesting to know whether the same pattern is observed in  
164 males or if selection for this trait is acting in opposite direction in both sexes. However, the  
165 presence of horns in females may also be important in other aspects of female life and  
166 performance, such as in sociality and reproduction (Locati & Lovari, 1991; Rughetti & Festa-  
167 Bianchet, 2011). Accordingly, females with different growth patterns may differ in other life-  
168 history traits, such as reproductive effort. In this case, our result may indicate a reproductive  
169 cost. To clarify this aspect, future studies will need to investigate the covariation between  
170 female phenotype and reproductive trajectory (Hamel *et al.*, 2009, 2010).

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## 178 **References**

179 **Bassano B, Perrone A, Von Hardenberg A. 2003.** Body weight and horn development in  
180 Alpine chamois, *Rupicapra rupicapra* (Bovidae, Caprinae). *Mammalia* **67**: 65–74.

- 181 **Bonenfant C, Pelletier F, Garel M, Bergeron P. 2009.** Age-dependent relationship between  
182 horn growth and survival in wild sheep. *Journal of Animal Ecology* **78**: 161–171.
- 183 **Burnham KP, Anderson DR. 1998.** *Model selection and inference: a practical information-*  
184 *theoretical approach*. New-York, NY: Springer-Verlag.
- 185 **Burnham KP, Anderson DR, Huyvaert KP. 2011.** AIC model selection and multimodel  
186 inference in behavioral ecology: some background, observations, and comparisons.  
187 *Behavioral Ecology and Sociobiology* **65**: 23–35.
- 188 **Chirichella R, Ciuti S, Grignolio S, Rocca M, Apollonio M. 2013.** The role of geological  
189 substrate for horn growth in ungulates: a case study on Alpine chamois. *Evolutionary Ecology*  
190 **27**: 145–163.
- 191 **Choquet R, Lebreton JD, Gimenez O, Reboulet AM, Pradel R. 2009a.** U-CARE: Utilities for  
192 performing goodness of fit tests and manipulating CAPture-REcapture data. *Ecography* **32**:  
193 1071–1074.
- 194 **Choquet R, Rouan L, Pradel R. 2009b.** Program E-Surge: a software application for fitting  
195 multievent models. In: Thomson DL, Cooch EG, Conroy MJ, eds. *Environmental and*  
196 *Ecological Statistics. Modeling Demographic Processes In Marked Populations*. Springer US,  
197 845–865.
- 198 **Côté SD, Festa-Bianchet M. 2001.** Birthdate, mass and survival in mountain goat kids: effects  
199 of maternal characteristics and forage quality. *Oecologia* **127**: 230–238.
- 200 **Gaillard JM, Festa-Bianchet M, Delorme D, Jorgenson J. 2000.** Body mass and individual  
201 fitness in female ungulates: bigger is not always better. *Proceedings of the Royal Society of*  
202 *London. Series B: Biological Sciences* **267**: 471–477.
- 203 **Gaillard JM, Viallefont A, Loison A, Festa-Bianchet M. 2004.** Assessing senescence patterns  
204 in populations of large mammals. *Animal Biodiversity and Conservation* **27**: 47–58.
- 205 **Green WCH, Rothstein A. 1991.** Trade-offs between growth and reproduction in female  
206 bison. *Oecologia* **86**: 521–527.
- 207 **Hamel S, Côté SD, Gaillard JM, Festa-Bianchet M. 2009.** Individual variation in reproductive  
208 costs of reproduction: high-quality females always do better. *Journal of Animal Ecology* **78**:  
209 143–151.
- 210 **Hamel S, Gaillard JM, Yoccoz NG, Loison A, Bonenfant C, Descamps S. 2010.** Fitness costs of  
211 reproduction depend on life speed: empirical evidence from mammalian populations.  
212 *Ecology letters* **13**: 915–935.
- 213 **Lebreton JD, Burnham KP, Clobert J, Anderson DR. 1992.** Modeling survival and testing  
214 biological hypotheses using marked animals: a unified approach with case studies. *Ecological*  
215 *Monographs* **62**: 67–118.
- 216 **Locati M, Lovari S. 1991.** Clues for dominance in female chamois: age, weight, or horn size?  
217 *Aggressive Behavior* **17**: 11–15.

- 218 **Loison A, Gaillard JM, Houssin H. 1994.** New insight on survivorship of female chamois  
219 (*Rupicapra rupicapra*) from observation of marked animals. *Canadian Journal of Zoology* **72**:  
220 591–597.
- 221 **Loison A, Jullien JM, Menaut P. 1999.** Subpopulation structure and dispersal in two  
222 populations of chamois. *Journal of Mammalogy* **80**: 620.
- 223 **Mangel M, Stamps J. 2001.** Trade-offs between growth and mortality and the maintenance  
224 of individual variation in growth. *Evolutionary Ecology Research* **3**: 583–593.
- 225 **Metcalfe NB, Monaghan P. 2003.** Growth versus lifespan: perspectives from evolutionary  
226 ecology. *Experimental Gerontology* **38**: 935–940.
- 227 **Van Noordwijk AJ, de Jong G. 1986.** Acquisition and allocation of resources: their influence  
228 on variation in life history tactics. *The American Naturalist* **128**: 137–142.
- 229 **Picard K, Thomas DW, Festa-Bianchet M, Lanthier C. 1994.** Bovid horns - an important site  
230 for heat-loss during winter. *Journal of Mammalogy* **75**: 710–713.
- 231 **Poissant J, Wilson AJ, Festa-Bianchet M, Hogg JT, Coltman DW. 2008.** Quantitative genetics  
232 and sex-specific selection on sexually dimorphic traits in bighorn sheep. *Proceedings of the*  
233 *Royal Society B: Biological Sciences* **275**: 623–628.
- 234 **Pradel R, Sanz-Aguilar A. 2012.** Modeling trap-awareness and related phenomena in  
235 capture-recapture studies. *PLoS ONE* **7**: e32666.
- 236 **Roff DA. 2002.** *Life history evolution*. Sunderland, MA: Sinauer Associates.
- 237 **Rughetti M, Festa-Bianchet M. 2011.** Effects of early horn growth on reproduction and  
238 hunting mortality in female chamois. *Journal of Animal Ecology* **80**: 438–447.
- 239 **Schröder W, von Elsner-Schack I. 1985.** Correct age determination in chamois. In: Lovari S,  
240 ed. *The Biology and management of mountain ungulates*. London, UK: Croom Helm, 65–70.
- 241 **Toïgo C, Gaillard JM, Loison A. 2013.** Alpine ibex males grow large horns at no survival cost  
242 for most of their lifetime. *Oecologia* **173**: 1261–1269.
- 243 **Wilson AJ, Nussey DH. 2010.** What is individual quality? An evolutionary perspective. *Trends*  
244 *in Ecology & Evolution* **25**: 207–214.
- 245
- 246

247 **Figure captions**

248 **Figure 1.** Relationship between early horn growth (0-3 year horn increment) and total horn  
249 length for each age at capture. Early horn growth does not include the growth that occurs  
250 after the 3<sup>rd</sup> winter and thus is not equal to total horn length of individuals aged 3 years old.

251

252 **Figure 2.** Relationship between early horn growth (0-3 year horn increment) and survival for  
253 females of the 8-12 age class. The lines represent the average estimates and average  
254 confidence intervals for all years of the model M4 presented in Table 2. The distribution of  
255 early horn growth in our population is at the bottom of the figure.

256

257 **Tables**

258 **Table 1.** Effects of age class and year on female survival modelled with capture-mark-  
 259 recapture data. The estimates of age-specific survival from the “A1 + A2 + A3 + year” model  
 260 are shown as the average of the estimates for each year with the average confidence  
 261 intervals.

Model	k	Deviance	AICc	ΔAICc
<b>A1 + A2 + A3 + year</b>	<b>32</b>	<b>1070.74</b>	<b>1138.05</b>	<b>0</b>
year	30	1086.73	1149.64	11.59
A1 + A2 + A3	12	1121.04	1145.52	7.47
Constant survival	10	1149.58	1169.92	31.87
	A1	A2	A3	
Mean estimates	0.94	0.88	0.79	
	[0.75 ; 0.99]	[0.63 ; 0.96]	[0.50 ; 0.93]	
Mean effect size (logit scale)	2.84	1.97	1.33	
	[1.09 ; 4.37]	[0.54 ; 3.31]	[0.01 ; 2.61]	

262 A1 = 3-7 years old  
 263 A2 = 8-12 years old  
 264 A3 = > 12 years old  
 265

266 **Table 2.** Effects of horn growth and body growth on female survival modelled with capture-  
 267 mark-recapture data. The models with the strongest support in the data are in bold ( $\Delta AICc <$   
 268 2 and AICc weight  $> 0.10$ ). The values of the effect size are on the logit scale.

ID	Model	k	Deviance	AICc	$\Delta AICc$	AICc weight	Effect size
<b>M0</b>	<b>base = A1 + A2 + A3 + year</b>	<b>32</b>	<b>1070.74</b>	<b>1138.05</b>	<b>0.67</b>	<b>0.172</b>	
M1	base + HS(A1) + HS(A2) + HS(A3)	35	1067.75	1141.73	4.35	0.027	
<b>M2</b>	<b>base + HS</b>	<b>33</b>	<b>1068.85</b>	<b>1138.38</b>	<b>1.00</b>	<b>0.146</b>	<b>-0.22 ± 0.16</b>
M3	base + HS(A1)	33	1070.64	1140.16	2.78	0.060	
<b>M4</b>	<b>base + HS(A2)</b>	<b>33</b>	<b>1067.85</b>	<b>1137.38</b>	<b>0</b>	<b>0.241</b>	<b>-0.43 ± 0.27</b>
M5	base + HS(A3)	33	1070.56	1140.09	2.71	0.062	
M6	base + BM(A1) + BM(A2) + BM(A3)	35	1069.51	1143.49	6.11	0.011	
M7	base + BM	33	1070.36	1139.89	2.51	0.069	
M8	base + BM(A1)	33	1069.99	1139.52	2.14	0.083	
M9	base + BM(A2)	33	1070.29	1139.82	2.44	0.071	
M10	base + BM(A3)	33	1070.69	1140.22	2.84	0.058	

269 BM = corrected body mass (corrected for age and date of capture)  
 270 HS = standardized early horn growth (horn increment between 0-3 years)  
 271 A1 = 3-7 years old  
 272 A2 = 8-12 years old  
 273 A3 = > 12 years old  
 274 HS(A1) = effect of horn size on survival of the individuals of the first age class  
 275