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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 ≥ 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 ± 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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- 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 3rd 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
A1 + A2 + A3 + year	32	1070.74	1138.05	0
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
M0	base = A1 + A2 + A3 + year	32	1070.74	1138.05	0.67	0.172	
M1	base + HS(A1) + HS(A2) + HS(A3)	35	1067.75	1141.73	4.35	0.027	
M2	base + HS	33	1068.85	1138.38	1.00	0.146	-0.22 ± 0.16
M3	base + HS(A1)	33	1070.64	1140.16	2.78	0.060	
M4	base + HS(A2)	33	1067.85	1137.38	0	0.241	-0.43 ± 0.27
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