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

JOSEFA BLEU1,2*, ANNE LOISON1 and CAROLE TOÏGO3

1CNRS, UMR 5553 Laboratoire d’Écologie Alpine, Université de Savoie, 73376 Le Bourget du Lac, France
2Department of Biology, Centre for Biodiversity Dynamics, Norwegian University of Sciences and Technology, 7491 Trondheim, Norway
3Office National de la Chasse et de la Faune Sauvage (ONCFS), ZI Mayencin, 38610 Gières, France

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Life-history theory predicts trade-offs in energy allocation between different life-history traits when resources are limited, i.e. certain traits should be negatively correlated. However, individuals differ in their ability to acquire resources, which can lead to positive correlations between traits at the population level. Here, we investigated the consequences of the allocation in horn growth and body mass on survival in a bovid (Rupicapra rupicapra) with capture-mark re-sighting data on 161 females. In female ungulates, body mass often covaries positively with demographic performance and the few studies on horn size suggest that this trait could be a signal of individual quality. Thus, we expected to measure positive correlations between the allocation in these traits and female survival. However, body mass was not correlated to female survival and there was only a negative, though marginal, effect of horn growth. Hence, it seems that the allocation in growth is not an indicator of female quality. Future studies could investigate the importance of growth on female reproduction to evaluate its effect on lifetime reproductive success. Moreover, it is important to confirm in other populations our result that suggests a cost of the allocation in horn growth to better understand the presence of horns in female bovids. © 2014 The Linnean Society of London, Biological Journal of the Linnean Society, 2014, 113, 516–521.


INTRODUCTION

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

Here, we investigated the correlations between the allocation in growth and survival in females of a long-lived mammal, the chamois (Rupicapra...
**Rupicapra rupicapra**. We used two variables to describe growth: body mass and horn length. Body mass often covaries positively with demographic performance in ungulates, for example it can be positively correlated with juvenile survival (Côté & Festa-Bianchet, 2001) and negatively with female age at primiparity (Green & Rothstein, 1991). Thus, it seems to be an indicator of female quality and we expect it to covary positively with survival under the ‘individual quality hypothesis’. However, this does not preclude the existence of a delayed cost of growth, which would be revealed by a negative correlation in old females. In boids, such as chamois, horns are permanent and both males and females wear horns. While male horns are known for their role in sexual selection (male–male competition and female choice), the role and putative associated costs of horns are much less studied in females. We aim here to clarify the correlation between horn length and age-specific survival in a female bovid. Given that large-horned females may be dominant over small-horned females (Locati & Lovari, 1991) and attain primiparity at an earlier age (Ruggetti & Festa-Bianchet, 2011), horn size may be a measure of individual quality and thus may covary positively with survival (i.e. support for the individual quality hypothesis). However, horn growth may be energetically costly (e.g. it is adjusted to food availability (Chirichella et al., 2013 and references therein)), and may represent a source of heat loss during winter (Picard et al., 1994). Therefore, large-horned females may bear the cost of their larger horns later in life, in which case we predict a negative covariation between horn growth and old-female survival.

**MATERIAL AND METHODS**

**SITE AND STUDIED SPECIES**

A population of chamois (*Rupicapra rupicapra*, Linnaeus, 1758), a mountain ungulate, has been monitored since the early 1980s in the Game and Wildlife Reserve (GWR) of the Bauges massif (45°40′N, 6°13′E, 5205 ha), in the northern French Alps. This site has been described elsewhere (Loison, Jullien & Menaut, 1999). Chamois are trapped below falling nets baited with salt (June to September). Measurements on captured individuals included body mass, total horn length and horn growth from birth to 3 years of age (we averaged the measures from both horns). Recaptures are rare in this population and thus we used only the measures at first capture. Age was determined by counting horn annuli (Schröder & von Elsner-Schack, 1985). Animals were individually marked with a coloured collar and visually monitored between April and December each year with a varying intensity of observation pressure per year (see supplementary materials). For this study, we considered data from the site Armenaz-Pécloz for females ≥ 3 years of age for which early horn growth (0–3 year increment) was measured. The GWR is a protected area where only guided hunt occurs. We are therefore confident that all marked animals that were shot were reported (N = 20, early horn growth = 162.78 ± 16.14 mm). The data were right-censored (i.e. females were removed from the analyses after being shot) to estimate survivorship independently of any hunting effect (Lebreton et al., 1992).

**STATISTICAL ANALYSES**

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

We tested whether age-specific survival was correlated to early horn growth (0–3 year increment) or body mass at capture, using these two measurements as individual covariates in Capture-Mark-Recapture modelling in E-SURGE (version 1.9.0) (Choquet, Rouan & Pradel, 2009b). We first tested the goodness of fit of the Cormack-Jolly-Seber model using U-CARE (version 2.3.2) (Choquet et al., 2009a). The Cormack-Jolly-Seber model satisfactorily fitted the data ($\chi^2 = 63.70$, $P = 0.382$). There was no transience ($Z = -2.11$, $P = 0.982$), but a strong ‘trap-happiness’ ($Z = -5.26$, $P < 0.001$, see examples of trap-dependence *lato sensu*, i.e. when animals are not physically recaptured, in Pradel & Sanz-Aguilar, 2012). This effect was well accounted for with models taking into account individual heterogeneity in behaviour (e.g. some animals temporarily changing their home range; see supplementary materials). From the model with heterogeneity, we selected the best model describing the time effect in re-sighting probabilities (Table S1). Then, we fitted models on the survival probabilities. We proceeded in two steps. First, we tested for the importance of age and time (year effect). We considered three typical age classes in ungulates: 3–7 years old, 8–12 years old and >12 years old (Loison, Gaillard & Houssin, 1994; Gaillard et al., 2004). Second, we tested for effects of individual covariates: in the best model selected in the first step, we added an effect of early
horn growth (standardized measure) or body mass (corrected measure) on survival of all the age classes or only one age class. Model selection was based on AICc: the model with the strongest support is the one with the lowest AICc. It is considered that two models differ when their difference of AICc is higher than 2 (Burnham & Anderson, 1998). We also calculated the AICc weight of each model (Burnham, Anderson & Huyvaert, 2011).

RESULTS

We gathered data on 161 females captured between 1992 and 2012 aged 3 to 12 years old (Table S2). Horn growth between 0 and 3 averaged 160.7 mm (SE = 14.0 mm, Fig. S1) and accounted for most of total horn length (Fig. 1). There was a positive correlation between early horn growth and total horn length corrected for age (R = 0.61, t = 9.62, df = 158, P < 0.001, Fig. S2). At capture, female body mass averaged 29.23 kg (SE = 3.23 kg, Fig. S3). Early horn growth and body mass corrected for age and capture date were positively correlated (R = 0.18, t = 2.27, df = 153, P = 0.025, Fig. S4). Survival probabilities varied among years and age classes (Table 1). Once these effects were accounted for, the best-fitting model included a negative effect of early horn growth on yearly survival of 8–12 years old females (Fig. 2, model M4 in Table 2). The model with a negative effect on all females also had a similar AICc (model M2 in Table 2). However, the baseline model showed the same support in the data than these two models (Model M0 in Table 2). The best-fitting model M4 is only 1.40 times more likely than model M0. There was no effect of body mass on survival (Table 2). Model M4 is 2.9 times more likely than model M8 which is the model with the lowest AICc within models including an effect of body mass.

DISCUSSION

We investigated the correlation between early horn growth, body mass and survival in adult female chamois. Interestingly, early horn growth and adult body mass were positively correlated, which suggests that these variables can be a measure of some of the

same aspects of female growth. In this population, horn length at age 3 accounted on average for 85% of horn length when older than 8 years old. This confirms some previous results that showed that most horn growth occurs during the first summers of female life in chamois (Bassano, Perrone & Von Hardenberg, 2003; Rughetti & Festa-Bianchet, 2011). Contrary to our predictions and other findings in ungulates (e.g. Gaillard et al., 2000; Poissant et al., 2008), adult body mass was not correlated with annual age-specific survival. We measured body mass only once and the fact that body mass does not seem to be a relevant predictor of annual survival may reflect the inter- and intra-annual variability of this variable. Concerning horn size, the model with most support in the data showed a delayed cost of growing large horns: old females with longer horns tended to have a lower survival than old females with shorter horns. The absence of a highly significant effect may be due to a lack of power because of the sample size and/or because of the large annual variation in survival between years. Indeed, trade-offs are more easily detected in years with overall low survival. Further studies will be needed to better understand the influence of annual variations on horn growth and on the trade-off with survival. Nevertheless, it is surprising to detect a cost, because even in male ungulates with larger horns than chamois, there is no clear pattern linking horn size and survival (e.g. see Table 1 of Bonenfant et al., 2009; Toïgo, Gaillard & Loison, 2013). Further studies in other populations and other species should clarify the existence of such cost in female bovids. For example, there is no correlation between longevity and horn volume in female

Table 1. Effects of age class and year on female survival modelled with Capture-Mark-Recapture data. The estimates of age-specific survival from the ‘A1 + A2 + A3 + year’ model are shown as the average of the estimates for each year with the average confidence intervals

<table>
<thead>
<tr>
<th>Model</th>
<th>k</th>
<th>Deviance</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>AICc weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>A1 + A2 + A3 + year</td>
<td>32</td>
<td>1070.74</td>
<td>1138.05</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Year</td>
<td>30</td>
<td>1086.73</td>
<td>1149.64</td>
<td>11.59</td>
<td></td>
</tr>
<tr>
<td>A1 + A2 + A3</td>
<td>12</td>
<td>1121.04</td>
<td>1145.52</td>
<td>7.47</td>
<td></td>
</tr>
<tr>
<td>Constant survival</td>
<td>10</td>
<td>1149.58</td>
<td>1169.92</td>
<td>31.87</td>
<td></td>
</tr>
</tbody>
</table>

Mean estimates

<table>
<thead>
<tr>
<th></th>
<th>A1</th>
<th>A2</th>
<th>A3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean estimates</td>
<td>0.94 [0.75; 0.99]</td>
<td>0.88 [0.63; 0.96]</td>
<td>0.79 [0.50; 0.93]</td>
</tr>
<tr>
<td>Mean effect size (logit scale)</td>
<td>2.84 [1.09; 4.37]</td>
<td>1.97 [0.54; 3.31]</td>
<td>1.33 [0.01; 2.61]</td>
</tr>
</tbody>
</table>

A1 = 3–7 years old. A2 = 8–12 years old. A3 = >12 years old.

Table 2. Effects of horn growth and body growth on female survival modelled with Capture-Mark-Recapture data. The models with the strongest support in the data are in bold (ΔAICc < 2 and AICc weight > 0.10). The values of the effect size are on the logit scale

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

A1 = 3–7 years old. A2 = 8–12 years old. A3 = >12 years old. BM = corrected body mass (corrected for age and date of capture). HS = standardized early horn growth (horn increment between 0–3 years). HS(A1) = effect of horn size on survival of the individuals of the first age class.
bighorn sheep (Poissant et al., 2008). If our result is confirmed in chamois and females bear a cost of wearing large horns, this suggests that large horns may be counter-selected in females. It would be particularly interesting to know whether the same pattern is observed in males or if selection for this trait is acting in opposite direction in both sexes. However, the presence of horns in females may also be important in other aspects of female life and performance, such as in sociality and reproduction (Locati & Lovari, 1991; Rughetti & Festa-Bianchet, 2011). Accordingly, females with different growth patterns may differ in other life-history traits, such as reproductive effort. In this case, our result may indicate a reproductive cost. To clarify this aspect, future studies will need to investigate the covariation between female phenotype and reproductive trajectory (Hamel et al., 2009, 2010).

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REFERENCES


SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher’s web-site:

**Appendix S1.** Supplementary methods, tables and figures.