

Antler growth as a cost of reproduction in female reindeer

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¹ Author contribution statement

¹ LEL, SA, AS, JI, VV and ER manage the long-term Svalbard reindeer project, collected the data and conceived the idea for the study. GP and LEL did the analyses. LEL, AM and PEG wrote the first draft of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

1 **Abstract**

2 The costs of reproduction are important in shaping individual life histories, and hence
3 population dynamics, but the mechanistic pathways of such costs are often unknown. Female
4 reindeer have evolved antlers possibly due to interference competition on winter-feeding
5 grounds. Here we investigate if variation in antler size explains part of the cost of
6 reproduction in late winter mass of female reindeer. We captured 440 individual Svalbard
7 reindeer a total of 1426 times over 16 years and measured antler size and body mass in late
8 winter, while presence of a ‘calf-at-heel’ was observed in summer. We found that
9 reproductive females grew smaller antlers and weighed 4.3 kg less than non-reproductive
10 females. Path analyses revealed that 14% of this cost of reproduction in body mass was
11 caused by the reduced antler size. Our study is therefore consistent with the hypothesis that
12 antlers in female *Rangifer* have evolved due to interference competition and provides
13 evidence for antler growth as a cost of reproduction in females. Antler growth was
14 constrained more by life history events than by variation in the environment, which contrasts
15 markedly with studies on male antlers and horns, and hence increases our understanding of
16 constraints on ornamentation and life history trade-offs.

17

18 **Keywords** Horn • interference competition • Rangifer • Svalbard reindeer • trade off

19

20 Introduction

21 Horns and antlers of ungulates are among the most extravagant ornamentations seen in
22 nature, and their large variation in form, size and function has intrigued natural historians for
23 centuries (Gould 1992). Today, the evolution of horns and antlers in male ungulates is
24 attributed to sexual selection (Bro-Jørgensen 2007; Clutton-Brock 1982; Geist 1966). In
25 polygynous species, male reproductive success is limited by access to mates (Clutton-Brock
26 et al. 1988). Antlers are honest signals of body size, and potentially fighting ability, and are
27 decisive for the outcome of male-male combats determining dominance rank and access to
28 mates (Bro-Jørgensen 2007; Clutton-Brock et al. 1980; Clutton-Brock et al. 1982). As
29 expected for an honest signal of competitive ability, the production of antlers is costly and
30 may account for as much as 1/3 of summer energy intake (Moen et al. 1999). In contrast to
31 males, female reproductive success is limited by the energy available to allocate to offspring.
32 The absence of female mate contests and high cost of growing antlers may be the main reason
33 why female cervids typically, are antlerless. The presence of antlers in female reindeer and
34 caribou (*Rangifer tarandus* ssp.) stands out as an intriguing exception, and the function and
35 consequences of antlers for female life history remains poorly documented.

36 Arguably, reindeer are the most social cervid species inhabiting harsh alpine and
37 Arctic environments. During winter, they dig craters to access forage under the snow, a
38 process which is energetically costly and increasingly so with more snow (Fancy and White
39 1985). Access to craters, therefore, may often lead to interference competition (Espmark
40 1964). While adult males cast antlers shortly after the autumn rut, females retain them
41 throughout winter. Further, population level studies have found a higher proportion of
42 antlered females in areas with deep snow in winter (Schaefer and Mahoney 2001). Several
43 mechanisms have been suggested to explain the fitness benefits of horns in female ruminants

44 (Packer 1983; Roberts 1996; Stankowich and Caro 2009), but the function of antlers in
45 female reindeer is currently understood in terms of interference competition (Espmark 1964).

46 Antler growth in *Rangifer* females starts after calving in June and continues
47 throughout the summer and autumn. This coincides with the period of lactation and peak
48 energy allocation in offspring (Espmark 1971). The amount of energy allocated to horn and
49 antler growth depends on quality and quantity of plant biomass (Festa-Bianchet et al. 2004;
50 Mysterud et al. 2005; Smith 1998; Thalmann et al. 2015) and population density (Prichard et
51 al. 1999; Schmidt et al. 2001; Vanpé et al. 2007) during the antler development period.
52 Presumably, the additional cost associated with the production of antlers during lactation is
53 compensated by the benefit of antlers during winter improving relative fitness. However, to
54 date no study has followed individual female reindeer over multiple years to investigate
55 constraints and energy allocation trade off associated with antler production and the
56 consequences for body mass and reproductive success in the next breeding event. This is the
57 aim of the current study.

58 We use a unique longitudinal data set of 440 female Svalbard reindeer (*Rangifer*
59 *tarandus platyrhynchus*) repeatedly captured between 2002 and 2017. Plant biomass
60 measured in early August, shortly before senescence, varies two-fold between years as a
61 function of July temperature (van der Wal and Stien 2014). During the last two decades there
62 has been significant warming in both summer and winter (Albon et al. 2017) and the study
63 population size has nearly doubled (Lee et al. 2015). In winter, food is often restricted to
64 small patches on wind-blown ridges where reindeer aggregates, especially when deep snow
65 or rain-on-snow (ROS), which can lead to the formation of ice-encrusted pastures, limits
66 access elsewhere (Hansen et al. 2010). Consequently, our study provides a unique
67 opportunity to explore first, the limiting factors on antler growth, and second, the impact of
68 female antlers on fitness traits, under rapidly changing environmental conditions.

69 We predict that, **(P1a)**, antler size is resource limited and positively affected by warm
70 summers with higher plant biomass (van der Wal and Stien 2014), **(P1b)**, early plant
71 phenology in spring (due to longer plant growth season), and **(P1c)**, low population size
72 (decreased intraspecific competition for resources). We expect a trade off in energy allocation
73 between antler growth and provisioning for a calf, both energy-draining processes occurring
74 in summer. Thus, we predict that **(P2)** provisioning for a calf in summer reduces
75 contemporary antler growth. Previously, we have documented that rearing a calf has a
76 negative effect on body mass lasting until the end of the next winter (Albon et al 2017).
77 Because small antlers are expected to inhibit the competitive abilities on the winter-feeding
78 grounds, we predict **(P3)** that some of the cost of reproduction in late winter body mass is
79 caused by reduced antler growth.

80

81 **Materials and methods**

82 **Study area and the reindeer population**

83 The study was conducted in Nordenskiöld Land, Spitsbergen, Svalbard. The study area
84 (77°50'N-78°20'N, 15°00'E-17°30'E) of about 150 km² includes the three interconnected
85 valleys Reindalen, Semmeldalen and Colesdalen with adjoining side valleys (Fig. S1). At this
86 high latitude, there is 4 months of midnight sun and 4 months of polar night. Mean air
87 temperature (1981-2010) for the warmest (July) and for the coldest month (February) was 5.8
88 °C and -13 °C respectively (Nordli et al. 2014). Snow covers the area from
89 October/November until mid-June, but varies considerably between years. The vegetation is
90 classified as middle Arctic tundra zone (Elvebakk 2005). The valley floors are mainly
91 vegetated by acidic mires bryophytes, graminoids and herbs (Elvebakk 2005). Ridge habitats,

92 often wind-blown and exposed in winters, and snow-free early in spring, are dominated by
93 the dwarf shrubs *Dryas octopetala* and *Salix polaris* (van der Wal and Stien 2014).

94 The population of Svalbard reindeer in our study area has varied from 750 to around
95 1750, with an increasing trend between 1994 and 2014 (estimate only of females and calves;
96 Lee et al. 2015). In summer, the reindeer forage on widely dispersed and easily accessible
97 graminoids and herbs on lower ground, while in winter they concentrate on wind-blown
98 ridges, depending on snow and ice conditions. Like in many other *Rangifer* populations
99 restricted food patches and cratering behaviour creates an opportunity for interference
100 competition over forage (Schaefer and Mahoney 2001), although Svalbard reindeer are less
101 gregarious than other subspecies of *Rangifer*. The mean late winter body mass of adult
102 females vary between years from ca 40 to 57 kg (Albon et al. 2017) depending on ROS and
103 autumn temperature. Antler mass ranges from about 120 gram for a pair with 3 tines per
104 beam to 350 gram for a set with 6 tines, a difference of about 200-250 grams (Brage B.
105 Hansen unpublished results). The annual antler cycle depends on sex, age and fertility status
106 (Bergerud 1976; Espmark 1971). Unlike prime-aged males, which clean their antlers in
107 August, and cast them shortly after the rut, females possess their antlers through the winter
108 and, if pregnant, cast the antlers a week or two after giving birth. Non-pregnant females
109 usually cast their antlers a few weeks earlier (Espmark 1971; Weladji et al. 2005). Antler
110 growth starts immediately after the old ones are cast, and in females the velvet is cleaned
111 after the rutting season in October and early November (length of rutting season is not well
112 known; Skogland 1989). A highly synchronized calving season takes place during c. 10 days
113 in early June (Tyler 1987). Svalbard reindeer is the only large herbivore in the archipelago,
114 and predation by polar bears (*Ursus maritimus*) is a very rare cause of mortality (Derocher et
115 al. 2000).

116

117 **Reindeer data**

118 The Svalbard reindeer population in the study area has been monitored by capture-mark-
119 recapture since 1994 (Albon et al. 2017) and measurements of antlers have been collected
120 since 2002. During the study period, female adults, yearlings and calves of both sexes were
121 captured in February (2007-2011 only) and/or late winter (late March-April all years) using
122 two snowmobiles and a hand held net (see Omsjø et al. 2009 for detailed description of the
123 methodology). A total of 1426 captures of 440 different adult females (of known age and
124 antler status) were made between 2002 and 2017, with a median of 79 per year; range 59-122.
125 All individuals included in this study were of known age, because they were either captured
126 as calves (at 10-11 months of age; 91.3%), as yearlings (22-23 months of age; 5%), or aged
127 after death (3.7%) based on counts of cementum annuli (Reimers and Nordby 1968). Most
128 individuals were only captured once per year (April), but a subset of 164 adult females were
129 captured both in February and April the same year (mean interval=57 days; range 49-71)
130 between 2007 and 2011. In cases where the antlers were measured more than once per winter
131 the first measurement was used (antlers do not grow from February to April). At first capture
132 individuals were fitted with numbered plastic collars and ear tags. Captured individuals were
133 restrained manually, and weighed to the closest 0.5 kg. The number of tines on each antler
134 beam was recorded, and from 2014, the length of antlers was recorded with a soft tape
135 measure following the outer curve of the main antler beam. The practical field definition of
136 an antler tine was that it needs to be long, and pointed enough to be able to hold a thin camera
137 strap.

138 Of the 431 individuals captured twice or more, 52 individuals were observed without
139 antlers on at least one occasion. Of these, 42 (9.7% of all individuals) had antlers in other
140 years while only 10 individuals (2.3%) were always observed antlerless as adults (median
141 number of captures of antlerless females=4.5; range 2-12). This suggests that being antlerless

142 one or a few years is rather common, and only a small subset of females are permanently
143 antlerless. Antler size of zero was therefore included in the analysis and treated as part of a
144 continuum of allocation in antlers.

145 Observations of calf status took place in July and August each year during a census of
146 the study area, registering whether marked females had a ‘calf-at-heel’, or not. The animals
147 were not captured at this time and summer body mass is unknown. Not all marked individuals
148 were observed in consecutive summer and winter, and therefore, there is only partial overlap
149 between individuals captured in winter and seen the following summer.

150

151 **Environmental data**

152 Meteorological data were collected at Svalbard airport (78°25’N, 15°46’E, 28 m altitude)
153 approximately 20-40 km north of the study area, and were available from the Norwegian
154 Meteorological Institute (www.eklima.no; Fig. S1). ROS was calculated as the amount of
155 precipitation that fell when mean daily temperature was above 1 °C between November 1st
156 and April 30th (Stien et al. 2012). ROS events occurring in the winter immediately prior to the
157 birth of an individual (ROS *in utero*) was used to test for a cohort effect on adult antler
158 growth (Douhard et al. 2016). The Enhanced Vegetation Index (EVI) was used as a proxy for
159 plant phenology in spring (Tveraa et al. 2013; Veiberg et al. 2017), while mean July
160 temperature was used as a proxy for peak annual plant biomass (van der Wal and Stien 2014),
161 which together with estimates of annual population size (Albon et al. 2017) was used to test
162 for resource limitation in antler growth.

163

164 **Matching the reindeer and environmental data in time**

165 The antlers produced in the summer of calendar year t_0 were measured in the subsequent winter
166 in calendar year t_1 . When testing for effects of resource limitation, we therefore use
167 environmental variables (including population size) measured in year t_0 (prediction P1) as
168 predictors of antler sizes measured in year t_1 . Similarly, the effects of calf production in year t_0
169 (cost of reproduction) on antler sizes, is modelled with respect to antler sizes measured in year
170 t_1 (P2). When investigating the direct and indirect (through antlers) cost of reproduction on
171 subsequent winter body masses, the model included calf status in year t_0 , antler size measured
172 in year t_1 and April body mass measured in year t_1 (P3; Fig. 1).

173

174 **Statistical analyses**

175 We document the overall age-related development in number of antler tines in Svalbard
176 reindeer females from age 0 (calves of 10 months) and onwards (Fig. 2). However, since 2
177 year olds are the youngest age of first reproduction in female Svalbard reindeer, calves and
178 yearlings are not included in subsequent analyses. All statistical analyses were performed
179 using R version 3.3.1 (R Core Team 2016).

180 We first investigated if number of tines was an adequate proxy for antler size, as
181 found in other cervids (Clutton-Brock et al. 1982, page 159: $r=0.62$; Mysterud et al. 2005:
182 $r=0.57$). We fitted a generalized additive model (GAM) using the mgcv package in R (Wood
183 2006) to assess a potential non-linear relationship between length and number of tines. In
184 adult females (≥ 2 years of age) the number of antler tines correlated with antler length
185 ($r=0.54$, $p<0.001$) in the subset of data where both measures were recorded ($n=355$). The
186 close to linear relationship (Fig. 3) suggests that the number of tines is a suitable proxy for
187 antler size, and the number of tines is used because it was recorded over a longer time period
188 (16 years versus 4 years). We used the average number of antler tines of left and right beam

189 (average=3.5, sd=1.8, range=0-9) and this measure is henceforth referred to as antler size.
190 Neither antler length, nor the number of antler tines, are perfect metrics of energy allocation
191 to antlers, and also they describe two partly different antler dimensions (which could explain
192 the relatively low correlation). Measuring antler volume, which would have been the best
193 metric, was not feasible during our handling of live, captured reindeer.

194 *Factors affecting antler size*

195 Variation in annual antler size of individuals was analysed with linear mixed models using
196 the functions “lmer” with a Gaussian error structure and the identity link function (Bates et al.
197 2015). Residual plots suggested that linear models with a Gaussian error structure fitted the
198 data better than log-linear Poisson regression models. Metatarsus length (hind leg length) was
199 included as fixed effect and not subjected to model simplification to account for static
200 allometry between antler size and skeletal size. Statistical significance of all other model
201 parameters was assessed using likelihood ratio tests (LRT) with cut-off value $p=0.05$
202 (Pinheiro and Bates 2000). Preliminary analyses using age classes resulted in more
203 parsimonious models than using a full factorial age factor (AIC 1475 vs 1485). The most
204 complex model, included the following candidate reindeer variables as fixed effects: leg
205 length (measured in mm), age category (2-3, 4-6, 7-13 years old; grouped according to
206 previous life history work in Douhard et al. 2016), ‘calf-at-heel’ in August (yes or no). The
207 following environmental variables were also included as fixed effects: ROS *in utero* (high or
208 low, with a cut off at 15mm in line with Stien et al. 2012), plant phenology (EVI), population
209 size (only available up to 2015; Lee et al 2015) and mean July temperature. Also, we
210 included July temperature residuals: the residuals from a regression between mean July
211 temperature and population size. This measure is an index of per capita forage availability.
212 Finally, we selected a random effect structure, where a model with individual ID as random
213 effect, was selected over a model with both year and ID and a model without any random

214 effect (LRT: $p < 0.001$). All continuous predictor variables were standardised at mean 0 and
215 variance 1 to facilitate model convergence and direct comparison of effect sizes.

216 *Cost of reproduction on next winters' body mass*

217 To estimate the average cost of reproduction on body mass at the end of the next winter, we
218 fitted a linear mixed model with body mass in April in year t_1 as response variable, presence
219 of a 'calf-at-heel' (coded as 0=no or 1=yes) in August year t_0 and age as the only fixed
220 effects. Year and individual were fitted as crossed random intercepts; year to account for
221 unexplained annual variation and individual to account for individual heterogeneity
222 (assuming a normal distribution of individual 'quality'). After this initial step we proceeded
223 by separating the direct and indirect (through antler size) cost of reproduction using a path
224 analysis. The starting point of our path model is presence of a 'calf-at-heel' in August year t_0
225 and the end point body mass in April in year t_1 (ca 8 months later). A total of $n=580$ had
226 observed calf status year t and April mass in year t_1 , a prerequisite for being included in the
227 analyses. We defined the following paths:

- 228 1) Antler size $_{t1}$ as a function of 'calf-at-heel' $_{t0}$
- 229 2) April mass $_{t1}$ as a function of 'calf-at-heel' $_{t0}$ (direct cost of reproduction)
- 230 3) April mass $_{t1}$ as a function of antler size $_{t1}$ (indirect cost of reproduction)
- 231 4) 'Calf-at-heel' $_t$ as a function of body size (adult leg length)
- 232 5) Antler size $_{t1}$ as a function of body size
- 233 6) April mass $_{t1}$ as a function of body size

234 To test the fit of the model, we used the direct separation approach ("D-sep", Shipley 2016)
235 which provides a flexible way to test the implied conditional independences of the path
236 model while accounting for the hierarchical nature of the data. We begin by testing the null
237 probability (P) associated with all k mutually independent claims of independence that must

238 be true for the structure of the hypothesized path model to be correct using linear mixed
239 models. We then used these k probabilities obtained to calculate Fisher's C statistic (-2Σ
240 $\ln(P)$). Fisher's C statistic follows a chi-square distribution with $2k$ degrees of freedom. A D-
241 separation test with a p -value ≤ 0.05 indicates that the proposed correlation structure of the
242 model differs from that observed in the data, and the path model is therefore rejected. Path
243 models were tested using the piecewise SEM package (Lefcheck 2016). Age was included as
244 a covariate as a full-factorial variable as this was more parsimonious than using age classes in
245 the body mass sub-models (AIC=1163.5 vs 1164.2). Both year and ID were fitted as random
246 effects in all regressions. The complete path model cannot be rejected given that all
247 endogenous variables are conditionally dependent. Therefore, we tested the sub model
248 excluding the indirect cost of reproduction (path 3 above). We report the un-standardized
249 path coefficients and associated p -values for the paths in the supplementary material (Table
250 S1 and S2). We multiplied the coefficients composing each path to obtain the direct and
251 indirect cost of reproduction on body mass (Shiple 2016). The proportion of the cost due to
252 indirect effect can then be obtained by dividing this cost by the sum of direct and indirect
253 effects.

254 The motivation for two modelling choices needs further reasoning. First, we did not
255 extend the path analyses to 'calf-at-heel'₁₁ mainly because of reduced sample size (inclusion
256 only of individuals observed in two consecutive summers and captured in the intervening
257 winter; reducing sample size by 43%). However, when extending the path analyses to 'calf-
258 at-heel'₁₁ for this subset of individual-years ($n=328$) the indirect antler effect remained
259 significant ($p<0.001$), explaining 12% of the variation in the probability to have a calf-at-
260 heel. This is expected because body mass explains 92% of variation in the probability to have
261 a calf at heel (Veiberg et al. 2017). The combination of severe sample size reduction and the
262 known, strong relationship between body mass and reproduction were our reasons for

263 keeping late winter body mass as the end point in the path analyses. Second, we included
264 individual as a random intercept to account for potential confounding effect of individual
265 heterogeneity. Still, as an additional test, we added late winter body mass t_0 to the path
266 analyses as a variable that could affect both antler growth t_0 and body mass t_1 . Although
267 reducing sample size (n=315), the indirect antler effect remained statistically significant
268 ($p < 0.001$), explaining 9.6% of the variation in late winter body mass. To avoid sample size
269 reduction, coefficients for models including body mass t_0 are only provided as supplementary
270 material (Table S3-S4).

271

272 *Effect of antler size on winter mass loss*

273 The effect of antler size on mass loss from February to April was investigated for the subset
274 of individuals captured twice per winter. Mass loss per month ((February mass – April mass)
275 / observation interval in days) x 30 days was used as the response variable in a linear mixed
276 model. February mass and antler size (number of tines) were candidate fixed effects and year
277 and ID random effects. The statistical significance of antler size on mass loss was evaluated
278 using a LRT as described above.

279

280 **Results**

281 Contrary to prediction P1, antler size was not affected by any of the proxies for forage
282 abundance and level of competition in summer (EVI, July temperatures, population size and
283 July temperature residuals; all LRT: $p \geq 0.20$; Table S5). Only age and calf status explained a
284 significant amount of variation in antler size of adult females (Table 1; Fig 4a). Antlers
285 reached full size from age 4 and showed signs of senescence beyond age 13 (Fig 2). Females

286 rearing a calf grew about one tine less per antler beam than females without a calf (Table 1;
287 Fig 4a) supporting our prediction of a cost of reproduction in antler growth (P2). No second
288 order interactions were statistically significant (All LRT: $p \geq 0.33$; Table S5). Although there
289 was detectable annual variation in antler size (LRT: $p < 0.001$), the effect of year was no
290 longer included in the best model when controlling for calf status. This is in line with the
291 strong negative population level correlation between the annual mean antler size and
292 proportion of females with a ‘calf-at-heel’ ($r = -0.69$; $p = 0.003$, Fig 4b).

293 Females with a ‘calf-at-heel’ in August year t_0 were on average 4.3 kg (SE=0.31)
294 lighter than non-reproducing individuals at the end of next winter (April in year t_1 ; ca 8
295 months later). The path analyses confirmed both a direct negative (- 3.8 kg) and an indirect
296 negative (- 0.6 kg) effect of reproductive success on late winter body mass (Fig 5), with the
297 indirect antler effect accounting for 14 % of the total cost of reproduction on body mass
298 (supporting P3; Fig 5). Path models excluding the indirect antler effect on body mass were
299 rejected ($p < 0.001$). The strength of the indirect antler effect was not affected by age (neither
300 the effect of calving on antler size nor the effect of antler size on body mass changed with age
301 class; LRT: $p = 0.358$ and $p = 0.090$ respectively).

302 Contrary to expectation, antler size did not affect mass loss between February and
303 April for the much smaller subset of individuals weighed twice per winter (LRT: $p = 0.11$), but
304 large antlers tended to reduce mass loss. Winter mass loss was on average 6 kg per month for
305 a female weighing 60 kg in February (95% CI [5.4, 6.6]; Table S6). Mean mass loss was
306 reduced by 0.10 kg (95% CI = [-0.02, 0.23]) per month for each extra tine. This implies for
307 example a 0.8 kg difference (over the 4 winter months from December to March before we
308 capture them) between an individual with a 4 tine antler (the 75% quantile) and one with 2
309 tines (the 25% quantile), which is comparable to the result from the path analysis.

310

311 Discussion

312 Our study of the role of antlers in female reindeer, the only cervid where females routinely
313 grow antlers, provides the first quantitative evidence that a cost of reproduction on antler
314 growth has carry-over effects on late winter body mass. The negative effect of small antlers
315 on late winter mass lends support to the long-held view that antlers in female *Rangifer* have
316 evolved due to interference competition (see Espmark 1971). Antler size was constrained
317 more by life history events (raising a calf reduced antler size), than annual variation in the
318 environment, which is in marked contrast to studies on male antlers (Mysterud et al. 2005)
319 and horns (Douhard et al. 2017; Festa-Bianchet et al. 2004).

320

321 **Cost of reproduction in mass is partly caused by reduced antler growth**

322 About 14% of the cost of reproduction on late winter body mass was likely to be the result of
323 lactating females growing smaller antlers. This provides rare evidence for a cost of
324 reproduction in mass operating partly through a secondary trait. The rationale behind this
325 argument is first, that due to a trade off in energy allocation (Hamel and Côté 2009), females
326 produce smaller antlers in summers, when they suckle a calf. Such reduced allocation in
327 horns and antlers has previously been found in lactating bovids (mountain goats *Oreamnos*
328 *americanus*; Côté et al. 1998) as well as in reindeer (Prichard et al. 1999). Second, small
329 antlers potentially constrain competitive abilities on the winter feeding-grounds, resulting in
330 lower body mass at the end of the next winter. Third, lower body mass is associated with
331 reduced performance at the next breeding event (Albon et al. 2017; Veiberg et al. 2017),
332 suggesting that stunted antlers not only have cost for late winter mass but also for the next

333 breeding event. Other studies have reported on a simple direct cost of reproduction in body
334 mass (Festa-Bianchet et al. 1998) and the majority of the cost of reproduction in mass (the
335 remaining 86%) was attributed to such a direct effect also in our study.

336

337 **Female antler size not linked to environmental variation**

338 Theory predicts that because sexually selected traits are honest signals of condition and male
339 quality, they are sensitive to environmental conditions (Andersson 1994). Consistent with this
340 theory, the size of antlers in cervids (Mysterud et al. 2005; Schmidt et al. 2001), including
341 female reindeer (Thomas and Barry 2005) and horns in male bovids (Festa-Bianchet et al.
342 2004) vary as a function of climate and population density, and tend to do so more than body
343 mass. In contrast, we found no link between antler size and environmental conditions in
344 female reindeer. This is particularly surprising since both plant biomass (van der Wal and
345 Stien 2014) and population size has varied two-fold during the study (Lee et al. 2015) and
346 affected summer body mass gain (Albon et al. 2017). Although the effect of increasing
347 density and plant biomass to some extent may cancel each other in the long-term (i.e.
348 increased carrying capacity), there is considerable annual fluctuations in both variables.

349 Female antlers are much smaller than male antlers and they carry them through the
350 energy-limited winter season. Carrying large antlers through snowy winters with high
351 locomotion cost may clearly act as a selective force against substantially larger antlers. Also,
352 the primary role of female antlers may be in intersexual competition with males that are
353 antlerless in winter (Holand et al. 2004), suggesting that presence/absence of antlers is more
354 important than absolute size. Nevertheless, the positive effect of antler size on late winter mass,
355 makes it surprising that females do not grow even larger antlers in summers when resources
356 are plentiful and competition low.

357

358 **The function of female weaponry**

359 Our study provides the first evidence that some of the cost of reproduction in an ungulate
360 species is due to reduced antler growth. Our results support the hypothesis that interference
361 competition is the selective force for evolution of antlers in female *Rangifer*. This highlights
362 not only that the function of antlers in male and female cervids differs, but also, that they
363 respond differently to environmental variability. A phylogenetic analysis of weaponry in
364 female bovids found that presence of horns was associated with large body size and open
365 habitat (Stankowich and Caro 2009). The clear link to exposure, i.e. the shoulder height
366 relative to habitat openness, suggested that an inability to rely on crypsis or take refuge in
367 dense vegetation has driven the evolution of horns for defense against predators in most
368 female bovids. Hence, weapons can also give a benefit in terms of a high dominance rank
369 related to interference competition either for a territory or directly for food. In addition to our
370 study, such a view is consistent with results from Soay sheep (*Ovis aries*), where females
371 with larger horns were more likely to initiate and win aggressive interactions during the
372 lambing period over access to food, and more so at high local density (Robinson and Kruuk
373 2007). Female Soay sheep without horns suffered from reduced longevity, and thus reduced
374 lifetime breeding success, relative to other horn morphs (Robinson et al. 2006). Since the
375 Soay sheep, like Svalbard reindeer lack contemporary predators, they provide one more case
376 where competition plays a role in the evolution of female weaponry.

377

378 **Acknowledgements**

379 We thank the Governor of Svalbard for permission to undertake the research. We are
380 especially grateful to Steve Coulson, Mads Forchhammer and the logistical and technical

381 staff at the University Centre in Svalbard (UNIS) for supporting the field campaigns. The
382 work was supported mainly by grants from U.K. Natural Environment Research Council
383 (GR3/1083), the Norwegian Research Council (POLARPROG project 216051 and
384 KLIMAFORSK 267613) and the Macaulay Development Trust. We are grateful to Brage B.
385 Hansen for providing antler mass data, and to Jean-Michel Gaillard, Mark Hewison and one
386 anonymous referee for providing valuable comments that greatly improved an earlier version
387 of the manuscript.

388

389 **Ethical approval**

390 All applicable institutional and national guidelines for the care and use of animals were
391 followed. Captures and handling of Svalbard reindeer was approved by the Norwegian Food
392 Safety Authority (permission number 17/237024) and by the Governor of Svalbard
393 (permission number 16/01632- 9).

394

395 **Data Accessibility Statement**

396 Data will be archived on Dryad (<http://datadryad.com/>) following acceptance.

397

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520

Table 1. The selected model explaining variation in number of antler tines in female Svalbard reindeer as a function of age class and calf status as additive effects. The standard deviation of the individual level random effect was 1.13. The age category 2-3 year olds and no calf is the reference level for the age and calf effects, respectively. Leg length (measured in mm) is included a priori to account for static allometry between body size and antler size.

	Estimate	SE	t	p
Intercept	-3.17	3.54	-0.895	0.37
Age 4-6 yr vs 2-3 yr	1.09	0.16	6.7	<0.001
Age 7-13 yr vs 2-3 yr	1.33	0.17	7.8	<0.001
Calf (yes vs no)	-0.96	0.13	-7.3	<0.001
Leg length (mm)	0.022	0.013	1.7	0.08

Figure captions

Figure 1. A conceptual figure showing how the term cost of reproduction (abbreviated C.O.R in the figure) is used in our study. The effects of giving birth and provisioning for a calf causes reduced contemporary antler growth, termed cost of reproduction in antler growth. Giving birth to a calf also causes a cost of reproduction in next winter body mass. This effect can be direct (termed direct cost of reproduction in body mass) or operate through reduced antler size (termed indirect cost of reproduction in body mass).

Figure 2. Antler size in female Svalbard reindeer plotted against age in one-year increments. Estimates are means and error bars are $\pm 1SE$. The estimates are extracted from a linear mixed model adjusting for repeated measurements of individuals over years.

Figure 3. Relationship between antler length (in centimetre) and number of antler tines per antler beam in female Svalbard reindeer. The unbroken lines represent the predicted relationship from a GAM model and dashed lines represent 95% CI. Average number of tines per beam in female reindeer was 3.2 and the average length of the antlers was 33 cm.

Figure 4. a) Relationship between the average number of antler tines, age and calf status in female Svalbard reindeer. Points represent the observed mean values for the different combinations of age class and calf status (open circle: no calf; filled circle with calf) and error bars are 95% confidence limits. Lines represent predicted mean values from the additive model for the effect of age class and calf status that best explain variation in number of antler tines. **b)** Relationship between the annual mean number of antler tines and proportion of

females with a calf at heel in the previous summer, for all marked females 2 year and older. The estimates of mean number of antler tines are corrected for annual variation in age composition and repeated observations of individuals, but uncorrected estimates are very similar ($r=0.96$) and show essentially the same pattern.

Figure 5. Graphical representation of the path model. Effect of reproductive success (Calf) on next winter body mass (Mass) is mediated through a direct effect and an indirect effect of antler size (Antler). Static allometry is accounted for by linking skeletal size (leg length) to antler size and body mass. Also, size is allowed to influence probability of calving. The values on the arrows are the standardized path coefficient with SE in brackets and are effectively correlation coefficients. The width of the arrow is proportional to the strength of the effect. Black paths (red in online version) indicate negative correlations and grey paths (green in online version) indicate positive correlations. Unbroken lines are statistically significant while dotted lines represent non-significant correlations. The direct cost of reproduction is the Calf-to-Mass path coefficient (-0.61). The indirect cost of reproduction is the product of the path coefficients for Calf-to-Antler (-0.55) and Antler-to-Mass (0.18), which is -0.10. The indirect effect account for 14% of the total effect ($-0.10 / (-0.61 + -0.10) * 100$).

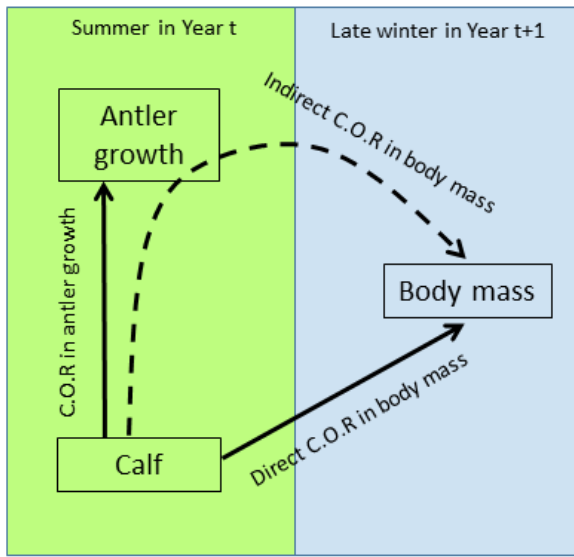


Fig 1

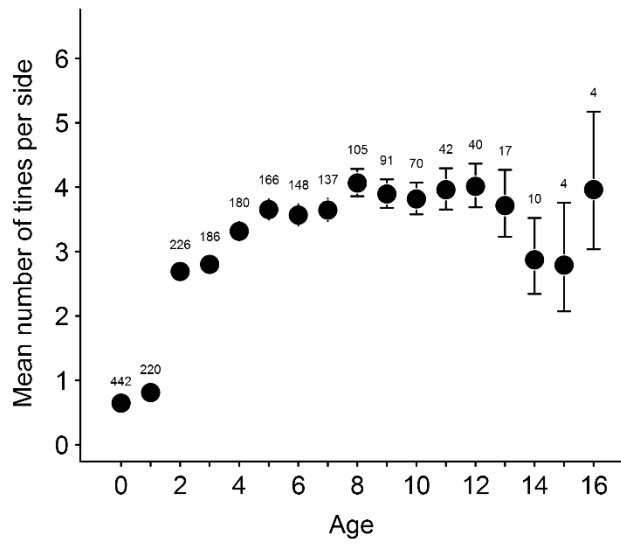


Fig 2

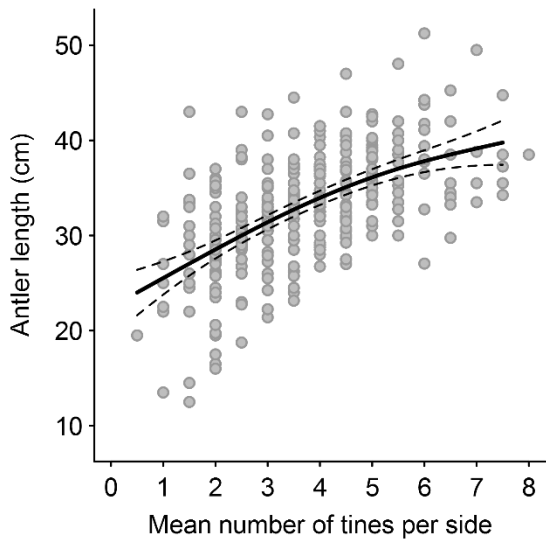


Fig 3

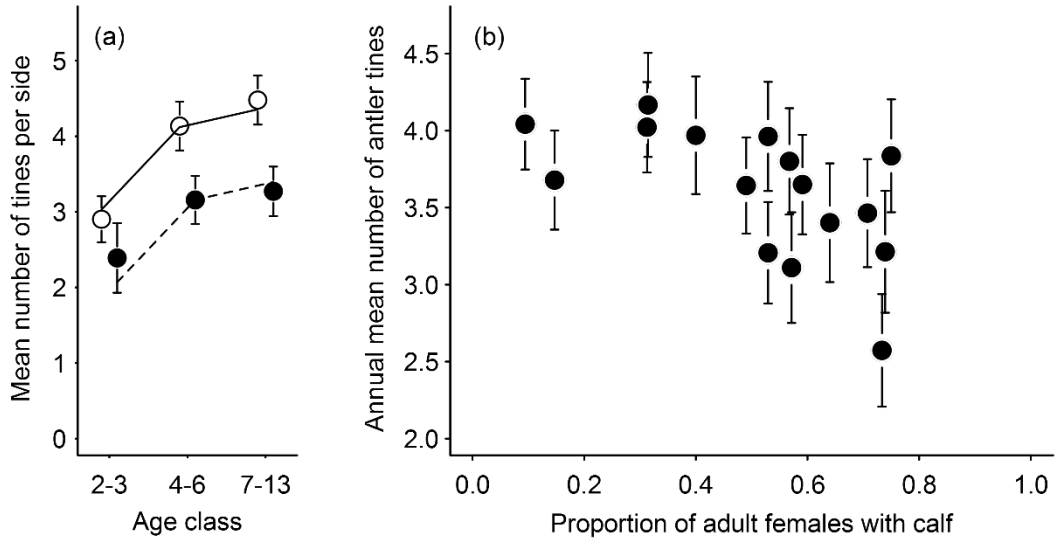


Fig 4

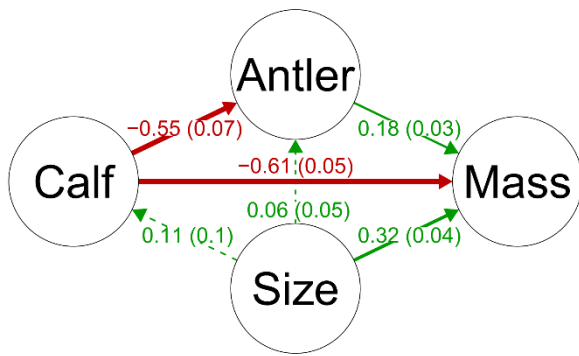


Fig 5