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1 **Maternal longevity and offspring sex in wild ungulates**

2

3 Mathieu Douhard^{1,5}, Marco Festa-Bianchet¹, Sandra Hamel², Daniel H. Nussey³, Steeve D.

4 Côté⁴, Josephine M. Pemberton³, and Fanie Pelletier¹

5

6 ¹Département de biologie, Université de Sherbrooke, Sherbrooke, QC J1K 2R1, Canada.

7 ²Department of Arctic and Marine Biology, UiT The Arctic University of Norway, 9037

8 Tromsø, Norway.

9 ³Institute of Evolutionary Biology, University of Edinburgh, Edinburgh EH9 3FL United

10 Kingdom.

11 ⁴Département de biologie et centre d'études nordiques, Université Laval, Québec, QC G1V

12 0A6, Canada.

13 ⁵E-mail: mathieu.douhard@gmail.com

14

15 **Abstract**

16 In species with sexual size dimorphism, offspring of the larger sex usually have greater
17 energy requirements and may lead to greater fitness costs for parents. The effects of offspring
18 sex on maternal longevity, however, have only been tested in humans. Human studies
19 produced mixed results and considerable debate mainly due to the difficulty of distinguishing
20 the effects of sexual dimorphism from sociocultural factors. To advance this debate, we
21 examined how the relative number of sons influenced maternal longevity in four species of
22 free-living ungulates (Soay sheep *Ovis aries*; bighorn sheep, *Ovis canadensis*; red deer,
23 *Cervus elaphus*; mountain goat, *Oreamnos americanus*), with high male-biased sexual size
24 dimorphism but without complicating sociocultural variables. We found no evidence for a
25 higher cumulative cost of sons than of daughters on maternal longevity. For a given number
26 of offspring, most females with many sons in all four populations lived longer than females
27 with few sons. The higher cost of sons over daughters on maternal lifespan reported by some
28 human studies may be the exception rather than the rule in long-lived iteroparous species.

29 **Keywords:** cost of reproduction, disposable soma, lifespan, mammals, sex ratio, trade-offs.

30

31 **1. Introduction**

32 Trade-offs play a fundamental role in life-history theory [1]. Organisms allocate acquired
33 energy among several functions including growth, reproduction and maintenance. When
34 resources are limited, energy allocated to one function reduces allocation to others [2].
35 Therefore, increasing reproductive effort should reduce the energy available for somatic
36 maintenance, possibly decreasing longevity [3]. Because longevity is a major source of
37 variation in lifetime reproductive success and fitness among long-lived species [4],
38 knowledge of the processes driving variation in longevity is essential to understand
39 population dynamics and evolutionary ecology.

40 Longevity costs of reproduction may vary with sex of both parents [5] and offspring
41 [6]. Sex differences in energy intake and growth of juveniles are common in sexually size-
42 dimorphic species [7]. In humans, despite weak sexual dimorphism [8], the energy intake of
43 pregnant women is about 10% higher when they are expecting a boy rather than a girl [9]. In
44 dimorphic species where sons grow faster than daughters and thus require greater parental
45 energy expenditure, the fitness costs of rearing sons are typically expected to be greater than
46 those of rearing daughters [7]. In many mammals, only mothers provide parental care, and
47 there is suggestive evidence that short-term fitness costs of reproduction (how reproduction at
48 time t affects survival or reproduction at time $t + 1$) are greater for females when rearing a son
49 than a daughter [10–17]. Most of these studies are indicative rather than conclusive because
50 correlation does not imply causation. Experimental manipulation of postnatal offspring sex
51 ratio has only been performed in bank voles (*Myodes glareolus*) [17,18] and tammar
52 wallabies (*Macropus eugenii*) [19,20]. This type of experiment is unfortunately impracticable
53 with most mammals, in part due to maternal refusal of cross-fostered offspring [20].

54 Beyond short-term fitness costs of reproduction, the accumulation of physiological
55 costs over multiple reproductive events may have long-term effects on future performance

56 [3,21]. Most studies testing early-late life trade-offs measured early reproductive effort as the
57 number of offspring produced or reared during a predefined time period [21], ignoring
58 offspring sex. Thus, we know little about the long-term cumulative fitness costs to females of
59 producing and rearing sons versus daughters. The only exceptions are investigations in
60 humans, which provide mixed support for the hypothesis that sons reduce maternal post-
61 menopausal lifespan more than daughters (see mini-review in [22]). Furthermore, the
62 differential effects of sons and daughters on post-reproductive lifespan in human mothers may
63 be due to sociocultural rather than biological mechanisms [23–25]. For instance, in several
64 societies, daughters provide more help than sons for elderly parents [25,26].

65 Here, we examine the long-term impact of producing and rearing more sons relative to
66 daughters on maternal longevity in four intensively monitored populations of free-living
67 ungulates: Soay sheep (*Ovis aries*), bighorn sheep (*Ovis canadensis*), red deer (*Cervus*
68 *elaphus*) and mountain goat (*Oreamnos americanus*). These species show a marked male-
69 biased sexual size dimorphism and a relatively simple social system compared to humans. In
70 all species except Soay sheep, rearing a son lowers maternal reproductive performance the
71 following year more than rearing a daughter [11,13,27,28]. We expected to find a negative
72 effect of producing and rearing relatively more sons than daughters on maternal longevity,
73 especially in bighorn sheep, red deer and mountain goats.

74

75 **2. Materials and Methods**

76 ***(a) Study populations***

77 We studied bighorn sheep at Ram Mountain (38 km²) and mountain goats at Caw Ridge (28
78 km²), Alberta, Canada. The red deer and Soay sheep populations are respectively located in
79 the North Block (12 km²) of the Isle of Rum and in the Village Bay area (2.3 km²) on the

80 island of Hirta, St Kilda, both off the west coast of Scotland, UK. Study areas are unfenced
81 and thus open to movements, but female dispersal is rare in all four populations [29–32].

82 ***(b) Capturing and marking***

83 The study populations have been the subject of detailed individual-based monitoring for 3 or
84 4 decades (table 1). For all species except mountain goats, most individuals were first
85 captured, weighed, sampled for genetic analysis, and marked near birth. Female bighorn
86 sheep, red deer and mountain goats can produce a single offspring in May-June. Female Soay
87 sheep can give birth to either singletons or twins in March-April (mean twinning rate 15%,
88 [33]). In red deer and Soay sheep, all females are monitored for parturition on a daily basis
89 during the spring, and offspring are caught within a few days of birth. In bighorn sheep, age at
90 first capture in a corral trap varies from 1 week to 4 months, but most are captured within a
91 few weeks of birth. Since 1998, female goats with their offspring are not captured owing to
92 the risk of abandonment, so most individuals are aged 1 year or older when first caught in box
93 traps [34]. The age of female mountain goats not marked as yearlings (1 year old) was
94 determined by counting the number of horn annuli, a technique reliable up to 7 years of age
95 [32]. Animals are marked with colored ear tags and/or visual collars for individual
96 identification at a distance (fig. S1 in electronic supplementary information). Techniques used
97 to capture, mark and monitor individuals are described in detail elsewhere [32,33,35,36].

98 ***(c) Longevity***

99 Regular censuses of the study areas are conducted from May to September for bighorn sheep
100 and mountain goats and throughout the year for red deer and Soay sheep. Longevity for red
101 deer and Soay sheep is based on the date an animal was found dead in ~ 70 and 85% of cases
102 or on date of last sighting in the remaining cases [33,36]. In bighorn sheep and mountain
103 goats, 1 and 17% of carcasses were found respectively but the date of last sighting is a reliable
104 indicator of age at death since there is almost no record of female emigration [32,37]. The

105 annual likelihood of missing a female if she is alive is very low in all systems (re-sighting
106 probability: 0.99 for both bighorn sheep [29] and mountain goats [32], 0.95 for red deer [30],
107 and 0.93 for Soay sheep [31]). Our analyses included only resident females that reproduced at
108 least once before natural death (excluding hunter kills in red deer, removals for scientific
109 purposes and capture mortalities). Possible causes of natural mortality included starvation
110 [38] especially at high population density, adverse weather, parasitism, disease, as well as
111 predation in bighorn sheep [39] and mountain goats [32].

112 *(d) Reproduction*

113 Intensive observations took place every summer to determine mother-offspring associations
114 and offspring survival. Weaning success was measured by offspring survival to 15 September
115 in bighorn sheep and mountain goats, 1 August in Soay sheep and 1 October in red deer.
116 Although mountain goat kids were not marked, they tightly follow and bed next to their
117 marked mothers, providing an accurate determination of their fate until weaning, and often
118 until one year old ([32] and fig. S1). In mountain goats, offspring sex was determined by
119 observations of urination posture and the vulvar patch in females. In the other species,
120 offspring sex was determined at capture or, occasionally, through observation of urination
121 posture.

122 *(e) Models*

123 We ran two types of models to examine the effects of sons on maternal longevity. First, in the
124 context of early-late life trade-offs, we assessed whether the number of sons born and weaned
125 during early life influenced maternal lifespan later in life. We defined ‘early life’ at the
126 population level as between minimum age at first parturition and age at onset of actuarial
127 senescence (see [40,41] for a similar approach and table 1 for definition of actuarial
128 senescence). ‘Early life’ overlapped the latest age at which any females started breeding (table
129 1). Actuarial senescence is well documented in all four populations [30–32,42]. We only

130 included females that survived beyond the onset of actuarial senescence in this first approach
131 (see tables 2 and 3 for sample sizes). Second, we examined correlations between the lifetime
132 number of sons born or weaned and maternal longevity using all data (see tables 4 and 5 for
133 sample sizes). The reasons for this second approach include the fact that longevity costs of
134 producing and rearing sons may not be confined to older mothers [43]. The proportion of sons
135 produced or weaned, on average, during early life or lifetime is presented in the electronic
136 supplementary information, table S1.

137 In all models, we controlled for the number of offspring produced/weaned during early
138 life or lifetime. Thus, we investigated whether for females with the same number of offspring,
139 having more sons affected longevity, thereby accounting for variation in reproductive
140 potential that may mask costs of sons. In Soay sheep, we accounted for the number of twin
141 pairs because females that produced twins tended to die younger [44]. Our models included
142 interactions between the number of offspring and the number of sons because costs of
143 reproduction may be greater in females with lower reproductive potential [45–47]. We tested
144 the effects of both the number of offspring born and weaned on maternal longevity to
145 determine the importance of gestation and lactation in generating reproductive costs.

146 All analyses were performed in R (ver. 3.5.0) [48]. Maternal longevity was analyzed in
147 generalized linear mixed models with the package ‘glmmTMB’ [49], using the Conway-
148 Maxwell-Poisson distribution to deal with under-dispersion [50]. The distribution of longevity
149 for each species is shown in figure S2. Year of birth was included as a random effect to
150 account for non-independence of mothers born in the same year and variation in longevity
151 among cohorts. Females were born between 1973 and 2004 in bighorn sheep, 1984 and 2003
152 in mountain goats, 1968 and 2004 in red deer, and 1985 and 2007 in Soay sheep. Regression
153 coefficients (β) and their standard errors (SE) are shown for all fixed covariates, along with
154 statistical significance based on Wald Z statistic. To assess effect sizes, we reported

155 standardized regression coefficients obtained by centring and scaling all continuous
156 explanatory variables (mean = 0, variance = 1). Centring enables interpretation of the main
157 effects involved in an interaction [51]. Thus, we presented the estimates and SE from full
158 models [52]. Variance inflation factors for all explanatory variables in our models were less
159 than 5, indicating no multicollinearity problems [53].

160 *(f) Multiple imputation*

161 The sex of each offspring born was known for most, but not all, female-years (68% in bighorn
162 sheep, 90% in mountain goats, 94% in red deer, 97% in Soay sheep; see table 1 for raw
163 numbers). In bighorn sheep, the sex of lambs that died at birth or within a few days of birth
164 was unknown because no lamb was seen but milk or colostrum was expressed by the mother
165 at capture. Yearly weaning success of female red deer and Soay sheep was missing in 6% and
166 2% of cases. We used multiple imputation to predict these two kinds of missing values. We
167 created multiple “complete” datasets where the missing values were imputed based on
168 information from all variables in the dataset. We used multiple imputation by chained
169 equation (function mice in the package ‘mice’, [54]) because this method is robust and allows
170 categorical variables to be imputed [55]. Differences in the imputed values between the
171 multiple datasets reflect imputation uncertainty. We generated ten imputed datasets for each
172 species as recommended by [56], and calculated the number of sons born/weaned in each
173 dataset. We obtained ten different estimates and their standard errors for each effect of
174 producing/weaning sons (one from each imputed dataset) and used conventional multiple
175 imputation rules for combining results [57]. When comparing the relationships between early-
176 life reproduction and longevity in later life obtained by multiple imputation with those from
177 datasets in which all females with missing values were excluded, we obtained similar patterns
178 (table S2 and S3). In the main text, we only present results based on multiple imputations

179 because of greater statistical power and the risk of biasing effect sizes when excluding
180 missing values [58].

181

182 **3. Results**

183 *(a) Early-life reproduction and lifespan later in life*

184 In Soay sheep, we found an interaction between the number of offspring and sons weaned
185 during early life on later life span ($\beta = 0.024 \pm 0.008$, $P = 0.002$) and there was a similar,
186 though non-significant, interaction between the number of offspring and sons born (rather
187 than weaned, $\beta = 0.016 \pm 0.009$, $P = 0.09$). The relationship between number of sons and
188 maternal lifespan was increasingly negative as number of lambs produced/weaned during
189 early life decreased (fig. 1). However, the cost of sons in terms of subsequent longevity was
190 small and not statistically significant even for females that produced ≤ 5 lambs (post-hoc
191 analysis: $\beta = -0.021 \pm 0.005$, $P = 0.16$, $N = 176$) or weaned ≤ 4 lambs ($\beta = -0.016 \pm 0.015$, $P =$
192 0.29 , $N = 175$) during early life. There were no significant interactions between the number of
193 offspring and sons born or weaned in any other species (tables 2 and 3). In all species except
194 mountain goats, the number of offspring produced during early life was positively associated
195 with lifespan later in life (table 2). For a given number of offspring born, female bighorn
196 sheep, red deer and mountain goats with many sons did not die sooner or later than females
197 with few sons (table 2). Repeating the analysis using the number of sons weaned did not
198 change the results except in bighorn sheep where the positive estimate was slightly stronger
199 and more precise, resulting in confidence intervals that did not overlap 0 (table 3). For
200 bighorn females that weaned 3 lambs during early life (the observed mean), longevity later in
201 life increased from 10.2 to 12.2 years as the number of sons weaned increased from 0 to 3.

202 *(b) Lifetime reproduction and adult lifespan*

203 In all species, we found significant interactions between the lifetime number of offspring and
204 sons on adult longevity regardless of whether reproductive performance was measured at birth
205 (table 4) or weaning (table 5). All these interactive effects acted in the same direction: the
206 relationship between number of sons and maternal longevity was increasingly positive as
207 number of offspring produced/weaned during lifetime decreased (fig. 2). Post-hoc analyses
208 did not show a negative effect of sons on longevity for females producing ≥ 10 offspring in
209 Soay sheep ($\beta = -0.004 \pm 0.010$, $P = 0.70$, $N = 94$) or ≥ 8 offspring in mountain goats ($\beta = -$
210 0.011 ± 0.038 , $P = 0.78$, $N = 19$) and red deer ($\beta = 0.003 \pm 0.011$, $P = 0.79$, $N = 114$).

211

212 **4. Discussion**

213 Our study tested for a trade-off between cumulative reproductive effort, incorporating
214 offspring number and sex ratio, and maternal longevity in non-human animals. Helle and
215 colleagues showed that post-menopausal longevity of pre-industrial Sami women decreased
216 by 0.65 years for each son born, while it increased by 0.44 years for each daughter [6].
217 However, the generality of these findings in pre-industrial humans has been questioned
218 [59,60]. Cesarini and co-workers warned of widespread publication bias in favor of positive
219 results in this area and pointed out the need for more replication studies on independent
220 samples [61]. Our analyses of four intensively monitored populations of free-living ungulates
221 do not support higher costs of sons than daughters to maternal lifespan.

222 Our study is based on correlational evidence: we could not manipulate offspring sex
223 ratio. Thus, the positive relationship between the relative number of sons weaned during early
224 life and maternal longevity in bighorn sheep may reflect the influence of physiological or
225 genetic factors on these two variables, rather than causation *per se*. Although evolutionary
226 theories of ageing predict that early allocation to reproduction should be favored by natural
227 selection at the cost of reduced late-life traits [3,62], trade-offs are often not visible in

228 correlational studies because individuals vary in resource acquisition [63]. According to the
229 van Noordwijk and De Jong [64] model, trade-offs between life-history traits should be
230 apparent only when inter-individual variation in resource allocation exceeds variation in
231 resource acquisition. The variation in reproductive potential (often referred to as “quality”,
232 [65]) that results from variation in resource acquisition may therefore mask the fitness costs of
233 reproduction at the population level [66]. In our study, some females combined a high
234 reproductive success during early life with long lifespans, whereas others had few offspring
235 and relatively short lifespans, suggesting large differences in individual reproductive
236 potential. We found no evidence for a negative effect of number of sons during early life on
237 subsequent maternal longevity even after accounting for differences in the number of
238 offspring. Nevertheless, other characteristics that affect the amount of resources available to
239 individuals, such as metabolic efficiencies [64] and social rank [67], may explain why we
240 failed to find any negative associations between the number of sons and maternal longevity.

241 We examined the effects of number of sons during early life on maternal longevity,
242 using data from females that survived beyond the onset of actuarial senescence. Recent
243 simulations [43] showed that restricting analyses to post-menopausal women underestimates
244 the potential trade-off between reproduction and lifespan. Our second approach avoids
245 potential sample selection problems by considering all adult females. These analyses
246 produced positive rather than negative correlations between the lifetime number of sons and
247 maternal longevity.

248 It could be argued that the overall lack of association between relative number of sons
249 and maternal longevity was due to a lack of statistical power in our analyses. However, our
250 sample size, at least in red deer and Soay sheep, was comparable to that in the study on
251 preindustrial Sami women that found a longevity cost of sons [6]. To maximize sample sizes,
252 we used multiple imputation to handle missing values for females with incomplete

253 reproductive histories. Unlike data deletion where cases containing at least one missing value
254 are excluded from the analysis, multiple imputation neither produces biased parameter
255 estimates nor reduces statistical power [58]. We also chose not to apply corrections for
256 multiple testing because Bonferroni and similar methods reduce statistical power and there is
257 no consensus for when multiple-testing adjustment is necessary [68,69]. We therefore believe
258 it is unlikely that lack of statistical power could explain the absence of positive results.

259 Differences in the energetic costs of sons and daughters are not necessarily limited to
260 the period of offspring nutritional dependence. In mammals, daughters are usually less prone
261 to disperse than sons [70], and are therefore more likely to compete for resources with their
262 mothers after nutritional independence [71]. In red deer on Rum, daughters typically occupy
263 core areas overlapping that of their mother and resource competition between female relatives
264 reduced the reproductive success of adult females [72]. Although the higher energetic costs of
265 sons before weaning might be balanced by post-weaning competition with daughters in red
266 deer [7], we can discard this explanation in other species. The social system of sheep does not
267 include strong post-weaning mother-daughter association [73,74]. In mountain goats, mother-
268 yearling associations were common but a recent study suggests that the post-weaning costs of
269 sons exceed those of daughters [27]. The likelihood of “helping” by one sex of mature
270 offspring may influence maternal longevity in some mammals. In pre-industrial human
271 societies, daughters typically helped in domestic and caregiving responsibilities while sons
272 simply increased maternal workload by working outside the home but living with parents
273 [75]. This sociocultural sexual division of labor offers an alternative explanation for
274 differential effects of sons and daughters on maternal longevity that are often attributed to sex
275 differences in offspring demand during pregnancy [24,75]. One advantage of our study
276 species is that offspring do not help mothers rear the next progeny.

277 There are at least two mechanisms by which females can recover from the higher
278 energetic costs of rearing sons in the short term to avoid cumulating these costs. First, females
279 can take reproductive pauses when their body reserves are insufficient. All the species studied
280 here are capital breeders that use stored energy for reproduction in contrast to income
281 breeders that rely on short-term food acquisition to finance reproduction [76]. There is
282 evidence in red deer that reproductive pauses depend on the sex of the previous offspring.
283 Indeed, female red deer that gave birth to a son are less likely to give birth the following
284 spring than mothers that had a daughter [13]. Although this effect accounted for only 1% of
285 the total variation in hind fecundity [13], it was primarily observed in low ranking mothers
286 [12]. In bighorn sheep, lambs born the year following the weaning of a son had lower survival
287 to weaning than lambs born after a daughter, particularly at high density [11]. Second,
288 mothers with low capacity to provide care, either because of low body condition, social status,
289 or experience, may produce the cheaper sex to reduce fitness costs [12,77,78]. For example,
290 the year after weaning a son bighorn sheep females in poor condition were more likely to
291 produce a daughter than a son [77].

292 A review of empirical studies of free-living mammals [79] reported that short-term
293 survival costs of reproduction are infrequent in ungulates, which exhibit high reproductive
294 variability and low variance in adult survival. Our results suggest that this pattern also holds
295 for cumulative costs of reproduction. Future studies of other groups of mammals (*e.g.* non-
296 human primates, elephants, marsupials) are needed before we can conclude that the higher
297 cost of sons over daughters on maternal longevity reported by some human studies is the
298 exception rather than the rule in long-lived mammal species. Detailed longitudinal data on
299 short-lived species, such as rodents, are also needed to test whether higher cumulative costs of
300 rearing sons on maternal longevity are more likely to be found in short-lived than long-lived
301 species.

302

303 **Ethics.** Ethical approval for the research on Rum's red deer and Soay sheep has been granted
304 by the appropriate UK Home Office licences. The marking and handling of bighorn sheep at
305 Ram Mountain and mountain goats at Caw Ridge were approved by the Animal Care
306 Committee of the Université de Sherbrooke (protocols MFB2009-01 and FP2012-01) and the
307 Université Laval (protocols 115513, 2018-033), both affiliated to the Canadian Council on
308 Animal Care.

309 **Data accessibility.** Data used in this paper are available in Dryad
310 (doi:10.5061/dryad.p0544hn).

311 **Competing interests.** We declare we have no competing interests.

312 **Author's contributions.** MD conceived the study and conducted all analyses with inputs
313 from all co-authors. All authors edited the manuscript, provided critical reviews and gave
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326

327 **References**

- 328 1. Stearns SC. 1992 *The evolution of life histories*. New-York, USA: Oxford University
329 Press.
- 330 2. Cody ML. 1966 A general theory of clutch size. *Evolution (N. Y)*. **20**, 174–184.
- 331 3. Kirkwood TBL, Rose MR. 1991 Evolution of senescence: late survival sacrificed for
332 reproduction. *Philos. Trans. R. Soc. London B Biol. Sci.* **332**, 15–24.
- 333 4. Clutton-Brock TH. 1988 *Reproductive success: studies of individual variation in*
334 *contrasting breeding systems*. Chicago, USA: University of Chicago Press.
- 335 5. Penn DJ, Smith KR. 2007 Differential fitness costs of reproduction between the sexes.
336 *Proc. Natl. Acad. Sci. USA* **104**, 553–558. (doi:10.1073/pnas.0609301103)
- 337 6. Helle S, Lummaa V, Jokela J. 2002 Sons reduced maternal lifespan in pre-modern
338 humans. *Science* **296**, 1085.
- 339 7. Clutton-Brock TH. 1991 *The evolution of parental care*. Princeton, N. J.: Princeton
340 University Press.
- 341 8. Plavcan JM. 2012 Sexual size dimorphism, canine dimorphism, and male-male
342 competition in primates where do humans fit in ? *Hum. Nat.* **23**, 45–67.
343 (doi:10.1007/s12110-012-9130-3)
- 344 9. Tamimi RM, Lagiou P, Mucci LA, Hsieh C-C, Adami H-O, Trichopoulos D. 2003
345 Average energy intake among pregnant women carrying a boy compared with a girl.
346 *Br. Med. J.* **326**, 1245–1246. (doi:10.1136/bmj.326.7401.1245)
- 347 10. Hogg JT, Hass CC, Jenni DA. 1992 Sex-biased maternal expenditure in Rocky
348 Mountain bighorn sheep. *Behav. Ecol. Sociobiol.* **31**, 243–251.
349 (doi:10.1007/BF00171679)
- 350 11. Bérubé CH, Festa-Bianchet M, Jorgenson JT. 1996 Reproductive costs of sons and
351 daughters in Rocky Mountain bighorn sheep. *Behav. Ecol.* **7**, 60–68.

- 352 (doi:10.1093/beheco/7.1.60)
- 353 12. Gomendio M, Clutton-Brock TH, Albon SD, Guinness FE, Simpson MJ. 1990
354 Mammalian sex ratios and variation in costs of rearing sons and daughters. *Nature* **343**,
355 261–263.
- 356 13. Froy H, Walling CA, Pemberton JM, Clutton-Brock TH, Kruuk LEB. 2016 Relative
357 costs of offspring sex and offspring survival in a polygynous mammal. *Biol. Lett.* **12**,
358 20160417. (doi:10.1098/rsbl.2016.0417)
- 359 14. Lee PC, Moss CJ. 1986 Early maternal investment in male and female African elephant
360 calves. *Behav. Ecol. Sociobiol.* **18**, 353–361.
- 361 15. Wolff JO. 1988 Maternal investment and sex ratio adjustment in American bison
362 calves. *Behav. Ecol. Sociobiol.* **23**, 127–133. (doi:10.1007/BF00299896)
- 363 16. Nichols HJ, Fullard K, Amos W. 2014 Costly sons do not lead to adaptive sex ratio
364 adjustment in pilot whales, *globicephala melas*. *Anim. Behav.* **88**, 203–209.
365 (doi:10.1016/j.anbehav.2013.12.015)
- 366 17. Rutkowska J, Koskela E, Mappes T, Speakman JR. 2011 A trade-off between current
367 and future sex allocation revealed by maternal energy budget in a small mammal. *Proc.*
368 *R. Soc. B Biol. Sci.* **278**, 2962–2969. (doi:10.1098/rspb.2010.2654)
- 369 18. Koskela E, Mappes T, Niskanen T, Rutkowska J. 2009 Maternal investment in relation
370 to sex ratio and offspring number in a small mammal - A case for Trivers and Willard
371 theory? *J. Anim. Ecol.* **78**, 1007–1014. (doi:10.1111/j.1365-2656.2009.01574.x)
- 372 19. Robert KA, Schwanz LE, Mills HR. 2010 Offspring sex varies with maternal
373 investment ability: empirical demonstration based on cross-fostering. *Biol. Lett.* **6**,
374 242–245. (doi:10.1098/rsbl.2009.0774)
- 375 20. Schwanz LE, Robert KA. 2016 Costs of rearing the wrong sex: Cross-fostering to
376 manipulate offspring sex in tammar wallabies. *PLoS One* **11**, 1–14.

- 377 (doi:10.1371/journal.pone.0146011)
- 378 21. Lemaître J-F, Berger V, Bonenfant C, Douhard M, Gamelon M, Plard F, Gaillard J-M.
379 2015 Early-late life trade-offs and the evolution of ageing in the wild. *Proc. R. Soc. B*
380 *Biol. Sci.* **282**, 20150209. (doi:10.1098/rspb.2015.0209)
- 381 22. Helle S, Lummaa V, Jokela J. 2010 On the number of sons born and shorter lifespan in
382 historical Sami mothers. *Proc. R. Soc. B, Biol. Sci.* **277**, 2909–2911.
383 (doi:10.1098/rspb.2009.2114)
- 384 23. Helle S, Lummaa V. 2013 A trade-off between having many sons and shorter maternal
385 post-reproductive survival in pre-industrial Finland. *Biol. Lett.* **9**, 20130034.
386 (doi:10.1098/rsbl.2013.0034)
- 387 24. Van De Putte B, Matthijs K, Vlietinck R. 2004 A social component in the negative
388 effect of sons on maternal longevity in pre-industrial humans. *J. Biosoc. Sci.* **36**, 289–
389 297. (doi:10.1017/S0021932003006266)
- 390 25. Pham-Kanter G, Goldman N. 2012 Do sons reduce parental mortality? *J. Epidemiol.*
391 *Community Health* **66**, 710–715. (doi:10.1136/jech.2010.123323)
- 392 26. Grigoryeva A. 2017 Own gender, sibling's gender, parent's gender: The division of
393 elderly parent care among adult children. *Am. Sociol. Rev.* **82**, 116–146.
394 (doi:10.1177/0003122416686521)
- 395 27. Charest Castro K, Leblond M, Côté SD. 2018 Costs and benefits of post-weaning
396 associations in mountain goats. *Behaviour* **155**, 295–326. (doi:10.1163/1568539X-
397 00003490)
- 398 28. Clutton-Brock TH, Stevenson IR, Marrow P, McColl ADC, Houston AI, MacNamara
399 JM. 1996 Population fluctuations, reproductive costs and life-history tactics in female
400 Soay sheep. *J. Anim. Ecol.* **65**, 675–689.
- 401 29. Jorgenson JT, Festa-Bianchet M, Gaillard J-M, Wishart WD. 1997 Effects of age, sex,

- 402 disease and density on survival of bighorn sheep. *Ecology* **78**, 1019–1032.
- 403 30. Catchpole EA, Fan Y, Morgan BJT, Clutton-Brock TH, Coulson T. 2004 Sexual
404 dimorphism, survival and dispersal in red deer. *J. Agric. Biol. Environ. Stat.* **9**, 1–26.
- 405 31. Catchpole EA, Morgan BJT, Coulson TN, Freeman SN, Albon SD. 2000 Factors
406 influencing Soay sheep survival. *J. R. Stat. Soc. Ser. C* **49**, 453–472.
- 407 32. Festa-Bianchet M, Côté SD. 2008 *Mountain goats: Ecology, behavior, and*
408 *conservation of an Alpine ungulate*. Washington, USA: Island Press.
- 409 33. Clutton-Brock TH, Pemberton JM. 2004 *Soay sheep : dynamics and selection in an*
410 *island population*. Cambridge: Cambridge University Press.
- 411 34. Côté SD, Festa-Bianchet M, Fournier F. 1998 Life-history effects of chemical
412 immobilization and radiocollars on mountain goats. *J. Wildlife Manag.* **62**, 745–752.
- 413 35. Festa-Bianchet M, Jorgenson JT, Réale D. 2000 Early development, adult mass, and
414 reproductive success in bighorn sheep. *Behav. Ecol.* **11**, 633–639.
- 415 36. Clutton-Brock TH, Guinness FE, Albon SD. 1982 *Red deer : behavior and ecology of*
416 *two sexes*. Chicago, USA: University of Chicago Press.
- 417 37. Gaillard J-M, Festa-Bianchet M, Delorme D, Jorgenson J. 2000 Body mass and
418 individual fitness in female ungulates: bigger is not always better. *Proc. R. Soc. Ser. B*
419 **267**, 471–477.
- 420 38. Clutton-Brock TH, Illius AW, Wilson K, Grenfell BT, MacColl ADC, Albon SD. 1997
421 Stability and instability in ungulate populations: an empirical analysis. *Am. Nat.* **149**,
422 195–219.
- 423 39. Festa-Bianchet M, Coulson TN, Gaillard J-M, Hogg JY, Pelletier F. 2006 Stochastic
424 predation events and population persistence in bighorn sheep. *Proc. R. Soc. B, Biol.*
425 *Sci.* **273**, 1537–1543. (doi:10.1098/rspb.2006.3467)
- 426 40. Nussey DH, Kruuk LEB, Morris A, Clutton-Brock TH. 2007 Environmental conditions

- 427 in early life influence ageing rates in a wild population of red deer. *Curr. Biol.* **17**,
428 R1000–R1001.
- 429 41. Panagakis A, Hamel S, Côté SD. 2017 Influence of early reproductive success on
430 longevity and late reproductive success in an alpine ungulate. *Am. Nat.* **189**, 667–683.
431 (doi:10.1086/691388)
- 432 42. Loison A, Festa-bianchet M, Gaillard J-M, Jorgenson JT, Jullien J-M. 1999 Age-
433 specific survival in five populations of ungulates: evidence of senescence. *Ecology* **80**,
434 2539–2554.
- 435 43. Helle S. 2017 Selection bias in studies of human. *Proceeding R. Soc. B* **284**, 20172104.
436 (doi:10.1098/rspb.2017.2104)
- 437 44. Hayward AD, Wilson AJ, Pilkington JG, Clutton-Brock TH, Pemberton JM, Kruuk
438 LEB. 2013 Reproductive senescence in female Soay sheep : variation across traits and
439 contributions of individual ageing and selective disappearance. *Funct. Ecol.* **27**, 184–
440 195. (doi:10.1111/1365-2435.12029)
- 441 45. Hamel S, Côté SD, Gaillard J-M, Festa-Bianchet M. 2009 Individual variation in
442 reproductive costs of reproduction: high-quality females always do better. *J. Anim.*
443 *Ecol.* **78**, 143–151.
- 444 46. Robert A, Paiva VH, Bolton M, Jiguet F, Bried J. 2012 The interaction between
445 reproductive cost and individual quality is mediated by oceanic conditions in a long-
446 lived bird. *Ecology* **93**, 1944–1952. (doi:10.1890/11-1840.1)
- 447 47. Debeffe L, Poissant J, McLoughlin PD. 2017 Individual quality and age but not
448 environmental or social conditions modulate costs of reproduction in a capital breeder.
449 *Ecol. Evol.* **7**, 5580–5591. (doi:10.1002/ece3.3082)
- 450 48. R Development Core Team. 2015 R: A language and environment for statistical
451 computing.

- 452 49. Magnusson A, Hans S, Nielsen A, Berg C, Kristensen K, Maechler M, van Benthman
453 K, Bolker B, Brooks M. 2018 glmmTMB: Generalized linear mixed models using
454 template model buildere.
- 455 50. Lynch HJ, Thorson JT, Shelton AO. 2014 Dealing with under-and over-dispersed count
456 data in life history, spatial, and community ecology. *Ecology* **95**, 3173–3180.
457 (doi:10.1890/13-1912.1)
- 458 51. Schielzeth H. 2010 Simple means to improve the interpretability of regression
459 coefficients. *Methods Ecol. Evol.* **1**, 103–113. (doi:10.1111/j.2041-210X.2010.00012.x)
- 460 52. Forstmeier W, Schielzeth H. 2011 Cryptic multiple hypotheses testing in linear
461 models : overestimated effect sizes and the winner's curse. *Behav. Ecol. Sociobiol.* **65**,
462 47–55. (doi:10.1007/s00265-010-1038-5)
- 463 53. O'Brien RM. 2007 A caution regarding rules of thumb for variance inflation factors.
464 *Qual. Quant.* **41**, 673–690. (doi:10.1007/s11135-006-9018-6)
- 465 54. Buuren S van, Groothuis-Oudshoorn K. 2011 mice : multivariate imputation by
466 chained equations in R. *J. Stat. Softw.* **45**. (doi:10.18637/jss.v045.i03)
- 467 55. Penone C, Davidson AD, Shoemaker KT, Di Marco M, Rondinini C, Brooks TM,
468 Young BE, Graham CH, Costa GC. 2014 Imputation of missing data in life-history trait
469 datasets: Which approach performs the best? *Methods Ecol. Evol.* **5**, 1–10.
470 (doi:10.1111/2041-210X.12232)
- 471 56. Schafer JL. 1999 Multiple imputation: A primer. *Stat. Methods Med. Res.* **8**, 3–15.
472 (doi:10.1191/096228099671525676)
- 473 57. Honaker J, King G, Blackwell M. 2011 AMELIA II : A program for missing data. *J.*
474 *Stat. Softw.* **45**, 1–54. (doi:10.1.1.149.9611)
- 475 58. Nakagawa S, Freckleton RP. 2008 Missing inaction : the dangers of ignoring missing
476 data. *Trend Ecol. Evol.* **23**, 592–596. (doi:10.1016/j.tree.2008.06.014)

- 477 59. Beise J, Volland E. 2002 Effect of producing sons on maternal longevity in premodern
478 populations. *Science* **298**, 317. (doi:10.1126/science.298.5592.317a)
- 479 60. Cesarini D, Lindqvist E, Wallace B. 2009 Is there an adverse effect of sons on maternal
480 longevity? *Proc. R. Soc. B Biol. Sci.* **276**, 2081–2084.
- 481 61. Cesarini DA, Lindqvist E, Wallace B. 2010 Reply to Helle et al. *Proc. R. Soc. B Biol.*
482 *Sci.* **277**, 2913–2914. (doi:10.1098/rspb.2010.0983)
- 483 62. Williams GC. 1957 Pleiotropy, natural selection and the evolution of senescence.
484 *Evolution (N. Y.)*. **11**, 398–411.
- 485 63. Reznick D. 1992 Measuring the costs of reproduction. *Trends Ecol. Evol.* **7**, 42–45.
- 486 64. van Noordwijk AJ, de Jong G. 1986 Acquisition and allocation of resources: their
487 influences on variation in life history tactics. *Am. Nat.* **128**, 137–142.
- 488 65. Bergeron P, Baeta R, Pelletier F, Réale D, Garant D. 2011 Individual quality: tautology
489 or biological reality? *J. Anim. Ecol.* **80**, 361–364. (doi:10.1111/j.1365-
490 2656.2010.01770.x)
- 491 66. Lim JN, Senior AM, Nakagawa S. 2014 Heterogeneity in individual quality and
492 reproductive trade-offs within species. *Evolution (N. Y.)*. **68**, 2306–2318.
493 (doi:10.1111/evo.12446)
- 494 67. Ceacero F, García AJ, Landete-Castillejos T, Bartošová J, Bartoš L, Gallego L. 2012
495 Benefits for dominant red deer hinds under a competitive feeding system: Food access
496 behavior, diet and nutrient selection. *PLoS One* **7**, 1–9.
497 (doi:10.1371/journal.pone.0032780)
- 498 68. Moran MD. 2003 Arguments for rejecting the sequential bonferroni in ecological
499 studies. *Oikos* **100**, 403–405. (doi:10.1034/j.1600-0706.2003.12010.x)
- 500 69. Nakagawa S. 2004 A farewell to Bonferroni: The problems of low statistical power and
501 publication bias. *Behav. Ecol.* **15**, 1044–1045. (doi:10.1093/beheco/arh107)

- 502 70. Greenwood PJ. 1980 Mating systems, philopatry and dispersal in birds and mammals.
503 *Anim. Behav.* **28**, 1140–1162.
- 504 71. Clark AB. 1978 Sex ratio and local resource competition in a prosimian primate.
505 *Science* **201**, 163–165.
- 506 72. Clutton-Brock TH, Albon SD, Guinness FE. 1982 Competition between female
507 relatives in a matrilocaI mammal. *Nature* **300**, 178–180. (doi:10.1038/300178a0)
- 508 73. Festa-Bianchet M. 1991 The social system of bighorn sheep: grouping patterns, kinship
509 and female dominance rank. *Anim. Behav.* **42**, 71–82. (doi:10.1016/S0003-
510 3472(05)80607-4)
- 511 74. Lawrence AB. 1990 Mother-daughter and peer relationships of Scottish hill sheep.
512 *Anim. Behav.* **39**, 481–486. (doi:10.1016/S0003-3472(05)80412-9)
- 513 75. Harrell CJ, Smith KR, Mineau GP. 2008 Are girls good and boys Bad for parental
514 longevity? : tthe effects of sex composition of offspring on parental mortality past age
515 50. *Hum. Nat.* **19**, 56–69. (doi:10.1007/s12110-008-9028-2)
- 516 76. Stephens PA, Boyd IL, McNamara JM, Houston AI. 2009 Capital breeding and income
517 breeding: their meaning, measurement, and worth. *Ecology* **90**, 2057–2067.
- 518 77. Douhard M, Festa-Bianchet M, Pelletier F. 2016 Maternal condition and previous
519 reproduction interact to affect offspring sex in a wild mammal. *Biol. Lett.* **12**,
520 20160510. (doi:10.1098/rsbl.2016.0510)
- 521 78. Martin JGA, Festa-Bianchet M. 2011 Sex ratio bias and reproductive strategies: What
522 sex to produce when? *Ecology* **92**, 441–449. (doi:10.1890/09-2413.1)
- 523 79. Hamel S, Gaillard J-M, Yoccoz NG, Loison A, Bonenfant C, Descamps S. 2010
524 Fitness costs of reproduction depend on life speed: empirical evidence from
525 mammalian populations. *Ecol. Lett.* **13**, 915–935.

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528 **Table captions**

529 Table 1. The four study populations of female ungulates. Age-related variation in survival is
530 well documented in each population [30–32,42]. Survival rates are high and constant for adult
531 females, then decrease after species-specific age thresholds marking the onset of actuarial
532 senescence. Information about age at first parturition, longevity and offspring sex is from data
533 analyzed here.

534

535 Table 2. Effects of the relative number of sons produced during early life on later lifespan for
536 females of four ungulate species. Interactions are denoted by ×.

537 Table 3. Effects of the relative number of sons weaned during early life on later lifespan for
538 females of four ungulate species. Interactions are denoted by ×.

539 Table 4. Effects of the relative number of sons produced during lifetime on maternal longevity
540 in four ungulate species. Interactions are denoted by ×. Sample sizes are larger compared to
541 previous analyses (table 2) because here we considered all adult females.

542 Table 5. Effects of the relative number of sons weaned during lifetime on maternal longevity
543 in four ungulate species. Sample sizes are larger compared to previous analyses (table 3)
544 because here we considered all adult females.

545

546

Table 1

Species	Soay sheep	Bighorn sheep	Mountain goat	Red deer
Population	Hirta	Ram Mountain	Caw Ridge	Rum
Start of the study	1985	1971	1988	1971
Onset of actuarial senescence	6 yr	7 yr	9 yr	9 yr
Early life	1-6 yr	2-7 yr	3-9 yr	3-9 yr
Mean age at first parturition (min, max)	1.5 yr (1, 6)	3.4 yr (2, 7)	4.7 yr (3, 8)	4.1 yr (3, 7)
Mean longevity for adults (sample size)	6.35 yr (N= 703)	9.4 yr (N= 173)	10.7 yr (N= 92)	12.2 yr (N=344)
Number of offspring of each sex at or shortly after birth	1783 ♀ 1762 ♂ 131 unknown	415 ♀ 392 ♂ 377 unknown	209 ♀ 204 ♂ 46 unknown	960 ♀ 967 ♂ 139 unknown

Species	N	Effect	Slope	SE	Z	P
Soay sheep	357	No. offspring born early	0.040	0.017	2.32	0.02
		No. twins born early	-0.030	0.017	-1.81	0.07
		No. sons born early	-0.021	0.012	-1.84	0.06
		No. offspring born early × No. sons born early	0.016	0.009	1.71	0.09
Bighorn sheep	118	No. offspring born early	0.069	0.028	2.46	0.01
		No. sons born early	0.035	0.033	1.06	0.29
		No. offspring born early × No. sons born early	0.017	0.022	0.76	0.44
Mountain goat	59	No. offspring born early	0.003	0.025	0.14	0.89
		No. sons born early	0.001	0.025	0.03	0.98
		No. offspring born early × No. sons born early	0.011	0.022	0.52	0.61
Red deer	254	No. offspring born early	0.043	0.013	3.41	<0.001
		No. sons born early	-0.019	0.013	-1.48	0.14
		No. offspring born early × No. sons born early	0.005	0.010	0.54	0.59

551

Table 3

552

Species	N	Effect	Slope	SE	Z	P
Soay sheep	356	No. offspring weaned early	0.036	0.014	2.48	0.01
		No. twins weaned early	-0.029	0.015	-1.96	0.05
		No. sons weaned early	-0.018	0.011	-1.57	0.12
		No. offspring weaned early \times No. sons weaned early	0.024	0.008	3.04	0.002
Bighorn sheep	115	No. offspring weaned early	0.009	0.028	0.32	0.74
		No. sons weaned early	0.058	0.028	2.04	0.04
		No. offspring weaned early \times No. sons weaned early	0.007	0.021	0.35	0.73
Mountain goat	58	No. offspring weaned early	0.010	0.027	0.39	0.70
		No. sons weaned early	-0.004	0.028	-0.14	0.89
		No. offspring weaned early \times No. sons weaned early	0.009	0.023	0.38	0.70
Red deer	254	No. offspring weaned early	0.031	0.013	2.28	0.02
		No. sons weaned early	-0.009	0.014	-0.62	0.53
		No. offspring weaned early \times No. sons weaned early	-0.003	0.010	-0.31	0.76

553

Species	N	Effect	Slope	SE	Z	P
Soay sheep	703	Lifetime no. offspring born	0.546	0.018	29.51	<0.001
		Lifetime no. twins born	-0.107	0.012	-8.98	<0.001
		Lifetime no. sons born	0.128	0.018	7.10	<0.001
		Lifetime no. offspring born × Lifetime no. sons born	-0.134	0.010	-13.11	<0.001
Bighorn sheep	173	Lifetime no. offspring born	0.331	0.022	15	<0.001
		Lifetime no. sons born	0.034	0.025	1.35	0.18
		Lifetime no. offspring born × Lifetime no. sons born	-0.033	0.014	-2.34	0.02
Mountain goat	92	Lifetime no. offspring born	0.263	0.027	9.62	<0.001
		Lifetime no. sons born	0.037	0.031	1.20	0.23
		Lifetime no. offspring born × Lifetime no. sons born	-0.056	0.016	-3.43	<0.001
Red deer	344	Lifetime no. offspring born	0.283	0.014	19.84	<0.001
		Lifetime no. sons born	0.070	0.015	4.60	<0.001
		Lifetime no. offspring born × Lifetime no. sons born	-0.104	0.010	-10.23	<0.001

Species	N	Effect	Slope	SE	Z	P
Soay sheep	608	Lifetime no. offspring weaned	0.407	0.018	22.60	<0.001
		Lifetime no. twins weaned	-0.073	0.013	-5.78	<0.001
		Lifetime no. sons weaned	0.107	0.018	5.94	<0.001
		Lifetime no. offspring weaned × Lifetime no. sons weaned	-0.102	0.010	-10.34	<0.001
Bighorn sheep	165	Lifetime no. offspring weaned	0.253	0.032	7.85	<0.001
		Lifetime no. sons weaned	0.073	0.030	2.41	0.02
		Lifetime no. offspring weaned × Lifetime no. sons weaned	-0.041	0.019	-2.15	0.03
Mountain goat	84	Lifetime no. offspring weaned	0.197	0.032	6.22	<0.001
		Lifetime no. sons weaned	0.064	0.035	1.83	0.07
		Lifetime no. offspring weaned × Lifetime no. sons weaned	-0.047	0.018	-2.67	0.007
Red deer	325	Lifetime no. offspring weaned	0.330	0.015	15.12	<0.001
		Lifetime no. sons weaned	0.059	0.017	3.58	<0.001
		Lifetime no. offspring weaned × Lifetime no. sons weaned	-0.093	0.011	-8.79	<0.001

560 **Figure captions**

561 Figure 1. Predicted effects of the number of sons weaned during early life (1-6 years) on
562 lifespan (in years) for female Soay sheep that lived more than 6 years and a) produced 4 to 7
563 offspring (values within the 10-90 percentile range) during early life, b) weaned 3 to 6
564 offspring (values within the 10-90 percentile range) during early life. Circles are observed
565 lifespan in one of imputed data sets (see Methods). The size of the circle is proportional to the
566 number of females.

567 Figure 2. Predicted changes in longevity (in years) with the lifetime number of sons produced
568 (a, c, e, g) or weaning (b, d, f, h) relative to the lifetime number of offspring produced/weaned
569 according to each species, female Soay sheep (a, b), bighorn sheep (c, d), mountain goats (e,
570 f), and red deer (g, h). Each line represents predicted longevity for females with a different
571 number of offspring indicated at the end of the line. Predictions are shown between the 10th
572 and the 90th percentile of number of offspring. Circles are observed lifespan in one of imputed
573 data sets (see Methods). The size of the circle is proportional to the number of females.

574