

Senescence in breeding success of female Alpine chamois (*Rupicapra rupicapra*): the role of female quality and age

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1 BEHAVIORAL ECOLOGY - ORIGINAL RESEARCH

2 **Senescence in breeding success of female Alpine chamois (*Rupicapra rupicapra*):**
3 **the role of female quality and age**

4

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25 & PB analyzed the data. FT & PB wrote the first draft of the manuscript and all the co-authors commented
26 on the manuscript.

27

28 **ABSTRACT**

29 Although numerous studies have reported reproductive senescence in wild animal populations, we
30 still know very little on inter-individual differences in rates of ageing and on factors accounting for
31 those differences. In a natural population of Alpine chamois (*Rupicapra rupicapra*), we used 15
32 years of data monitoring of individually ear-tagged females to investigate age-related variation in
33 breeding success. Analyses at the population level confirmed the occurrence of a decline in female
34 breeding success, being most noticeable from 9 years of age onward. Using an age-reverse
35 approach, we show that senescence in females' breeding success is age-dependent, as only very old
36 individuals (age at death greater than 16 years) exhibit a decline in breeding success in the years
37 preceding death. Interestingly, we also found evidence that "success comes from success", as
38 females that produced a young in a given year were more likely to give again birth in the
39 subsequent year, and that discrepancies between successful and unsuccessful individuals became
40 more relevant in the very old age classes. There was no evidence of terminal investment. These
41 results emphasized the importance of age-dependent effects and individual quality in shaping
42 reproductive senescence in a wild long-living ungulate.

43

44 **Key words:** ageing; age-dependent; longevity; individual quality; mammal

45

46

47 **INTRODUCTION**

48 Senescence, denoted by a decline in survival and reproductive success at old age, is now
49 well documented to occur not only in humans and domesticated animals but also in wild
50 populations of birds and mammals (e.g. Loison et al. 1999a; Mysterud et al. 2002; van de Pol and
51 Verhulst 2006; Jones et al. 2008; Reed et al. 2008; Berman et al. 2009; Froy et al. 2013; Nussey et
52 al. 2013). Interestingly, whatever the species (humans, domesticated or wild species), there is often
53 large inter-individual variation in the rates of senescence within species (Nussey et al. 2013).
54 Because the study of senescence is always performed on a group of individuals (*i.e.* population; see
55 Loison et al. 1999a for an example), a first essential step is to disentangle age-related variation in
56 reproductive performances driven by demographic effects (*i.e.* population effects) from those
57 occurring at the individual level (*i.e.* senescence *per se*). For example, if individuals with a lower
58 than average reproductive success also tend to live longer, they will be overrepresented in older age
59 categories (Vaupel et al. 1979). As a consequence, the finding of an age-related decline in
60 reproduction might be wrongly interpreted as senescence rather than as selective disappearance of
61 individuals with a higher than average reproductive success (van de Pol and Verhulst 2006). A
62 second and complementary step is then to investigate the importance of individual quality in
63 modeling heterogeneity in the rates of ageing (Weladji et al. 2008).

64 A central tenet of life-history theories is that allocation in reproduction are traded off against
65 allocation in somatic maintenance, and thus that reproduction comes at a cost of longevity (Stearns
66 1989). Despite experimental evidence demonstrating the occurrence of a longevity cost of
67 reproduction at the within-individual level (Clutton-Brock et al. 1989; Daan et al. 1996; Robinson et
68 al. 2012; Santos and Nakagawa 2012), among-individual studies are often reporting a positive
69 association between reproduction and survival, with the longer lived individuals being also better at
70 raising offspring (Weladji et al. 2006; Hamel and Côté 2009). This positive association is thought to
71 be rooted in inter-individual variation in their capacity, for instance, to monopolize, store or acquire
72 resources, with high quality individuals having more resources to allocate in both reproduction and

73 maintenance (Reznick et al. 2000). As ‘reproductive costs’ or ‘individual quality’ are the primary
74 factors driving the co-variance between reproduction and longevity, Weladji and colleagues (2008)
75 have proposed two ‘extreme’ scenarios: the ‘individual cost-only’ and the ‘individual quality-only’.
76 In the ‘cost-only’ scenario, one prediction is that females that successfully produced an offspring
77 should have a lower reproductive success at their following reproductive attempt compared to
78 unsuccessful females, whereas the ‘individual quality-only’ scenario predicts that females being
79 able to produce offspring should be more able to produce again offspring in the following breeding
80 event compared to unsuccessful females. Life-history theories are also postulating that individuals
81 should increase their allocation into reproduction as their future reproductive prospects decline
82 (Stearns 1992), thus leading to a maximal allocation in reproduction in the last reproductive attempt
83 (also referred to as ‘terminal investment’; Froy et al. 2013). Of note, all these processes can further
84 interact, if for example only the high quality individuals might have enough remaining resources to
85 allocate in their terminal investments. To adequately address and decomposed these different
86 hypotheses, long-term data on the reproduction of the same individuals are required coupled with
87 state-of-the-art statistical models that allow separating between-individual effects (i.e. selection,
88 quality) from within-individual effects (i.e. senescence *per se*, cost; van de Pol and Verhulst 2006).

89 In this study we considered breeding success data of female Alpine chamois (*Rupicapra*
90 *rupicapra*) living in a protected areas where human disturbance and hunting were forbidden. The
91 Alpine chamois is a polygynous ungulate native to European mountains that shows moderate sexual
92 dimorphism (Rughetti and Festa-Bianchet 2010). The mating period takes place from November to
93 early December. In female chamois, age at first reproduction is approximately at 2 years of age
94 (Loison et al. 1999b). Following a gestation period of ca. 170 days, females give birth to a single
95 calf, more rarely twin, in May or early June (Ruckstuhl and Ingold 1999; Pioz et al. 2008). Kids
96 start following their mothers almost immediately after birth (Ruckstuhl and Ingold 1994). Only
97 females give parental care, establishing a strong and close association with its kid(s) using
98 following strategy (Lent 1974) to reduce predation risk (Ruckstuhl and Ingold 1994). Weaning

99 occurs at *ca.* six months after birth (i.e. November to early December; Ruckstuhl and Ingold 1999),
100 but it is not rare to still observe suckling behaviours until January. Our aim was to investigate the
101 importance of individual quality, reproduction success and terminal investment in shaping the rates
102 of senescence in breeding success of female Alpine chamois.

103

104 **MATERIALS AND METHODS**

105 *Study site and data collection*

106 Data were collected in the Swiss National Park, an area of integral protection covering 172.4 km² ,
107 located in south eastern Switzerland. Habitats of the Park are dominated by forests of Arolla pine
108 (*Pinus cembra*) and larch (*Larix decidua*) below the tree line (2200m altitude) and by alpine
109 grasslands and bare rocks above it. Annual precipitations amount to 700-1200 mm of rain, and the
110 growing period above tree line is *ca.* 80 days per year. The Swiss National Park was created in 1914
111 and chamois hunting ceased in 1920. Their only predator is the golden eagle (*Aquila chrysaetos*)
112 that can prey upon small kids. Population census shows that the number of chamois within the
113 protected area is naturally fluctuating over the years of this study from a maximum of 1677
114 individuals (9.7 individuals per Km²; 791 females, 442 males and 444 individuals younger than two
115 years) to a minimum of 1163 individuals (6.7 individuals per Km²; 544 females, 332 males and 287
116 individuals younger than two years; official data of the Swiss National Park).

117 Each year since 1995 one to nineteen female chamois were live-trapped and individually
118 identified with numbered ear tags. In total, 102 females were ear tagged between 1995 and 2010,
119 with 72% of those individuals having being tagged before 2001. At capture, the exact year of birth
120 by counting the number of annual incremental growth rings on the horns was determined (Schröder
121 and von Elsner-Schack 1985). Ear-tagged females have been the subject of an individual-based
122 study on reproductive success since 1995. Each year the rangers of the Swiss National Park devoted
123 a large effort to monitor ear-tagged females, and in particular to observe if these females were
124 followed by kid or not. Most of the sightings of chamois were made during the birth period (May-

125 June). Reproductive performances of each ear-tagged female were monitored from the year of
126 tagging to the year of their last appearance in population, with an annual rate of re sightings of 1 for
127 each female in between these two events. Annual breeding success of ear-tagged females was
128 scored using a binomial score, with an individual being attributed a score of 1 from the moment it
129 was observed followed by a kid during May-June or a score of 0 if not observed with a kid. Thus,
130 this measure of annual breeding success takes into account both the probability of a female to give
131 birth and the early survival of its offspring. The history of breeding success of each ear-tagged
132 female is fully known from its year of tagging to its last appearance in the population.

133

134 ***Ethical note***

135 Female Alpine chamois were tagged by rangers of the Swiss National Park under the legal
136 authorization of the Swiss Veterinary Office.

137

138 ***Data analyses***

139 Age-related variations in female annual breeding success (BS) were analyzed using generalized
140 linear mixed effects models (GLMMs) using restricted maximum-likelihood method in the R
141 package *lme4* (Bates et al. 2014). To account for the binomial distribution of our response variable
142 BS the error distribution of our models was set to ‘binomial’ and we used a ‘logit-link’ function. All
143 the models included as random effects the individual identity (ID) that allowed accounting for the
144 non-independence of repeated measures on the same individuals, and the year of observation that
145 allowed accounting for annual variation in breeding success. We ran two different sets of analyses,
146 exploring initially age-related variations in female breeding success at the population level, and then
147 decomposing the patterns observed at the population level in between-individual and within-
148 individual effects.

149

150 ***Variation in female breeding success at the population level***

151 We investigated age-related variation in female BS at the population level using the full dataset (i.e.
152 654 observations from the 102 ear-tagged females). We used different GLMMs to test whether the
153 shape of the relationship with BS was best explained by linear, quadratic and/or logarithmic age
154 functions; the null model considered year and individual as random terms, but no age as fixed effect
155 (see Table 1). We also ran threshold models to identify breakpoints (inflection points) in age-related
156 variation in female BS using the R cran package “*segmented*” (Muggeo 2008; Berman et al. 2009;
157 Froy et al. 2013; Table 1). Breakpoints are useful to quantify an abrupt change of the response
158 variable. The different models were compared based on Akaike Information Criterion (AIC). The
159 model with the lowest BIC was retained as the best model (Table 1).

160

161 *Between-individual and within-individual variation in breeding success*

162 The population level approach indicated a bell shape relationship of female BS in relation to age
163 (see the Results section), and hereafter we used a data centering approach to tease apart the between
164 and within individual contribution to the decline in breeding success at older age (van de Pol and
165 Verhulst 2006). We did not investigate the increase in female BS over the first years of life because
166 most of the individuals were tagged after they had already reproduced most likely one or more
167 times (mean tagging age was 6.13 years), thus preventing a careful examination of age-related
168 reproductive improvement over the first reproductive attempts. To ensure taking into account in our
169 analyses only females possibly showing ageing effects, we restricted our analyses to observations
170 fulfilling the three following conditions:

- 171 (i) We only kept records of individuals that appeared for the last time in our records in 2010 or
172 earlier. It follows that those individuals have not been re-sighted for at least two years and
173 were considered dead. We have no cases of female disappeared for one or more years that
174 were subsequently re-sighted inside the study area. Regular finding by park rangers of
175 marked chamois carcasses supported this approach. Thus, hereafter we refer to the age at
176 last appearance as age at death (ADH);

- 177 (ii) At the population level, female BS was reaching a plateau between 5 and 13 years of age
178 followed by a marked decline after 13 years of age (Fig. 1). To include information on pre-
179 senescent females in the analyses, we kept observations of individuals aged 9 years or older
180 and of an ADH 11 years of more. We used 9 years of age as a cut-of-point since this is
181 halfway between 5 and 13 years of age; in other words it is the age with the highest
182 estimated productivity. We considered ADH of 11 years of more because individuals should
183 have been observed over at least three consecutive years before ADH to be included in the
184 analyses (see also point (iii));
- 185 (iii) To investigate within-individual changes in reproductive performances, we only kept
186 individuals observed consecutively at least during their three last years of life. Furthermore,
187 to strictly focus on the last years of life (*i.e.* senescence *per se*), we restricted our dataset to
188 observations collected in the last five (maximum) or three (minimum) years of life.

189 In total, we trimmed our dataset to 206 observations from 44 females (see the Results section), and
190 to study senescence *per se*, we used an age-reverse approach by centering our data on ADH (for
191 similar approach see Reed et al. 2008; Martin and Festa-Bianchet 2011; Froy et al. 2013). This
192 means that we are expressing the age term as years before death (YBDH), with age 0 denoting the
193 final year of life, which is a powerful approach to compare senescence in breeding success of
194 individuals with contrasting life expectancies. In the starting statistical model of factors influencing
195 variation in BS, we entered ADH as a continuous variable to test for selective disappearance (*i.e.*
196 between-individual effect), YBDH as a continuous variable to investigate senescence *per se* (*i.e.*
197 within-individual effect), a one-level factor for female breeding success in the past attempt (BS_{t-1})
198 to test whether BS in year t was influenced by carry over costs associated with a successful
199 reproduction in year $t-1$ (Clutton-Brock et al. 1983; but see Festa-Bianchet 1989), and (iii) a two-
200 level factor for final breeding attempt (FBA) to test for terminal investment, comparing the final
201 breeding attempt (value 1) with the previous one (value 0; Bouwhuis et al. 2009 and Froy et al.
202 2013). Our starting statistical model included thus the following fixed terms:

203
$$BS = ADH + YBDH + BS_{t-1} + FBA + ADH^2 + YBDH^2 + ADH*YBDH + ADH*BS_{t-1} +$$

204
$$ADH*FBA.$$

205 The terms ADH^2 and $YBDH^2$ allowed testing for quadratic effects of ADH or YBDH on BS, and
206 the interactions $ADH*YBDH$, $ADH*BS_{t-1}$ and $ADH*FBA$ for differences in the rate of senescence,
207 in costs of reproduction and in terminal investment of individuals that disappeared early or late
208 from the population. The minimal adequate model was obtained by backwards model selection
209 based on Akaike Information Criterion (AIC) and least significant p -values (starting with
210 interactions), to retain the best fitting model with the lowest AIC. All statistical analyses were
211 performed using the R.2.15.1 statistical software (R Development Core Team 2012).

212

213 **RESULTS**

214 On the entire data set ($n = 654$, $N = 102$) mean (\pm SE) age at tagging of females was 6.13 ± 0.15
215 years of age (minimum – maximum: 6 months to 17 years) and mean (\pm SE) age at death was 13.63
216 ± 0.17 years of age (minimum – maximum: 1 to 21 years). In the trimmed dataset used to analyze
217 the reproductive senescence ($n = 206$, $N = 44$) the mean (\pm SE) age at death of females was $15.44 \pm$
218 0.18 years of age (minimum – maximum: 11 to 20 years).

219

220 ***Variation in female breeding success at the population level***

221 The model fitting a quadratic effect of age best explained variation in female breeding success at the
222 population level (Table 1A, Fig. 1). Additional analyses using breakpoints show that this bell
223 shaped variation in female breeding success was best described using two breakpoints, and in turn
224 three segments (Table 1B). Female breeding success significantly increased until 5 years of age (*i.e.*
225 first break point) before reaching a plateau between 5 and 13 years of age (*i.e.* second break point),
226 followed by a significant decline from 13 years of age onward (Fig. 1).

227

228 ***Between-individual and within-individual variation in breeding success***

229 The decrease in breeding success at older ages was best explained by a model retaining as
230 explanatory variables age at death (ADH), years before death (YBDH), breeding reproductive
231 success of the previous year (BS_{t-1}), and the interactions between ADH and YBDH and between
232 ADH and BS_{t-1} (Tab. 2). The significant ADH by YBDH interaction revealed that intra-individual
233 decline in breeding success (*i.e.* measured by YBDH) was becoming foremost apparent in females
234 that reached an old age at death (*i.e.* measured by ADH) (see Fig. 2). The ADH by BS_{t-1} interaction
235 was explained by the fact that females who successfully produced a kid the year before (year $t-1$)
236 were more likely to be successful again at their following reproductive attempt (year t) (*i.e.*
237 measured by BS_{t-1}), and those differences between successful and unsuccessful breeding success
238 were more apparent in long-lived than short-lived females (*i.e.* measured by ADH; Fig. 3).
239 Inspection of the random terms shows strong effect of the year, but not of individual identity, on the
240 variance in annual breeding success. Effects of final breeding attempt (FBA), alone or in interaction
241 with other terms, were not retained in the best model.

242

243 **DISCUSSION**

244 Our analyses in a natural population of Alpine chamois show that the probably for females
245 to give birth follows a classical bell-shape in relation to age (Fig. 1). Individuals were less likely to
246 reproduce in either young- or old-age classes. The underlying mechanisms explaining the lower
247 reproductive success in young- and old-age classes are however most likely to differ. Because in the
248 present study females chamois were tagged on average at 6.13 years and most of the increase in
249 breeding performance was observed before 6 years of age, our data do not allow addressing the
250 mechanisms accounting for an increase in reproductive performance from young- to middle-age
251 classes. However, our data are suitable to disentangle between-individual effects (selection, quality)
252 from within-individual effects (senescence *per se*) in the decline in reproductive success in old age
253 categories. Analyses at the individual level show that senescence in females' breeding success is
254 age-dependent evidencing as reduction in breeding success with increasing age appears in very old

255 individuals only (see also Martin and Festa-Bianchet 2011). Our results also indicate the presence
256 of *successful* and *unsuccessful* females in the population: females observed with a kid were more
257 likely to be observed again with a kid the following year, whereas unsuccessful females were more
258 likely to remain unsuccessful in the following year. This strong dichotomy in breeding success
259 between *successful* and *unsuccessful* females become evident at older ages, which suggests that
260 females were not all ageing at the same rate. *Unsuccessful* females were suffering a stronger decline
261 in breeding success at older ages compared to *successful* females. No support was found for the
262 presence of terminal investment (an increase in reproductive success in the ultimate reproductive
263 attempt).

264 To highlight that in Alpine chamois senescence in breeding success is age-dependent, we
265 used a reverse-age approach where “years before death” (YBDH) is used as an alternative measure
266 to age (e.g. Reed et al. 2008; Martin and Festa-Bianchet 2011; Bize et al. 2014; Froy et al. 2013). In
267 so doing, we quantified senescence *per se*. We proved a decline in breeding success that became
268 apparent only in long-living female chamois (age at death ≥ 16 ; Fig. 2), whereas no decline in
269 breeding success was observed in female chamois dying between 9 and 16 years of age (Fig. 2).
270 Thus, the present results indicate an age-dependent senescence becoming apparent at very old age
271 only, rather than age-independent which would have been denoted by similar patterns of senescence
272 whatever the age at death from maturity onwards (Martin and Festa-Bianchet 2011). Clear evidence
273 of age-dependent senescence in breeding success have been previously reported in common
274 guillemots (*Uria aalge*; Reed et al. 2008), Asian elephants (*Elephas maximus*; Robinson et al.
275 2012) or bighorn sheep (*Ovis canadensis*; Martin and Festa-Bianchet 2011), and evidence of age-
276 independent senescence in reproductive effort have been reported in Black-legged kittiwakes (*Rissa*
277 *tridactyla*; Coulson and Fairweather 2001) or bighorn sheep (*Ovis canadensis*; Martin and Festa-
278 Bianchet 2011). A previous study on the same population of Alpine chamois focusing on adult
279 survival showed that this species has a very high survival (i.e. >0.90), and that survival does not
280 differ between sexes and remains constant between young (2-7 years) and middle-age (8+) classes

281 (Corlatti et al. 2012). From our results, senescence in breeding success occurs in very old age
282 categories (16+ years), and additional data will be helpful to address the occurrence of a similar
283 decline in survival in very old individuals.

284 The inclusion of breeding success in the preceding year (BS_{t-1}) in the analyses of breeding
285 success in the year t revealed an important effect of individual quality in the Alpine chamois, with
286 the presence of two possible extreme kinds of females (*sensu* Weladji et al. 2008): *successful*
287 females that can successfully breed offspring over several consecutive years without reduction in
288 reproductive performances, and *unsuccessful* females that keep being unsuccessful breeders over
289 the years. Positive links between past reproductive success on current reproductive success have
290 been previously reported in male fallow dears (*Dama dama*; McElligott et al. 2002), in female
291 reindeers (*Rangifer tarandus*; Weladji et al. 2006 and Weladji et al. 2008) and in female
292 subantarctic fur seals (*Arctocephalus tropicalis*; Beauplet et al. 2006). The amount of energy that a
293 female can allocate to reproduction depends on one hand on the amount of resources available in
294 the environment (shaped by environment productivity and variability; Hirshfield and Tinkle 1975)
295 and on the other hand on its ability to gather, process and store resources from their environment
296 (Festa-Bianchet 1989). The strong effect of past reproductive success on future reproductive
297 success suggests that the *successful* females were consistently better than the *unsuccessful* ones at
298 extracting resources from their environment and investing them in reproduction.

299 We also tested for the occurrence of terminal investment when analyzing individual
300 reproductive strategies, but we found no evidence that female Alpine chamois had an increase in
301 breeding success in their last reproductive attempt. Alternatively, in male Alpine chamois patterns
302 of reproductive allocation may be a continuum from downturns in reproduction efforts at old age to
303 terminal investment (Mason et al. 2011). In general, this study highlights that long-term individual
304 follow-up are essential to study lifelong variation in animal reproductive performances, and in so
305 doing (*i*) to tease apart processes taking place at the population level from those taking place at the
306 individual level, (*ii*) to discriminate between processes that are age-dependent and age-

307 independent, (iii) to test the importance of ‘reproductive costs’ or ‘individual quality’ as the primary
308 factors driving the co-variance between reproduction and longevity, and to (iv) determine the
309 occurrence of terminal investment. It supports the existence of strong heterogeneity in individual
310 quality and the needs to take into account this heterogeneity when addressing evolutionary
311 processes such as ageing or in population dynamics studies.

312

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333 **REFERENCES**

- 334 Bates D, Maechler M, Bolker B, Walker S (2014) lme4: Linear mixed-effects models using Eigen
335 and S4. R package version 1.0-6. <http://CRAN.R-project.org/package=lme4>
- 336 Beauplet G, Barbraud C, Dabin W, Küssener C, Guinet C (2006) Age-specific survival and
337 reproductive performances in fur seals: evidence of senescence and individual quality. *Oikos*
338 112:430-441
- 339 Berman M, Gaillard JM, Weimerskirch H (2009) Contrasted patterns of age-specific reproduction
340 in long-lived seabirds. *Proceedings of the Royal Society B: Biological Sciences* 276:375-
341 382
- 342 Bize P, Cotting S, Devevez G, van Roozen J, Lalubin F, Glaizot O, Christe P (2014) Senescence in
343 cell oxidative status in two bird species with contrasting life expectancy. *Oecologia*
344 174:1097-1105
- 345 Bouwhuis S, Sheldon BC, Verhulst S, Charmantier A (2009) Great tits growing old: selective
346 disappearance and the partitioning of senescence to stages within the breeding cycle.
347 *Proceedings of the Royal Society B: Biological Sciences* 276:2769-2777
- 348 Clutton-Brock TH, Albon SD, Guinness FE (1989) Fitness costs of gestation and lactation in wild
349 mammals. *Nature* 337:260-262
- 350 Clutton-Brock TH, Guinness FE, Albon SD (1983) The costs of reproduction to red deer hinds.
351 *Journal of Animal Ecology* 52:367-383
- 352 Corlatti L, Lebl K, Filli F, Ruf T (2012) Unbiased sex-specific survival in Alpine chamois.
353 *Mammalian Biology* 77:135-139
- 354 Coulson JC, Fairweather JA (2001) Reduced reproductive performance prior to death in the black-
355 legged kittiwake: senescence or terminal illness? *Journal of avian biology* 32:146-152
- 356 Daan S, Deerenberg C, Dijkstra C (1996) Increased daily work precipitates natural death in the
357 kestrel. *Journal of Animal Ecology* 65:539-544

358 Festa-Bianchet M (1989) Individual differences, parasites, and the costs of reproduction for bighorn
359 ewes (*Ovis canadensis*). *The Journal of Animal Ecology*:785-795

360 Froy H, Phillips RA, Wood AG, Nussey DH, Lewis S (2013) Age-related variation in reproductive
361 traits in the wandering albatross: evidence for terminal improvement following senescence.
362 *Ecology Letters* 16:642-649

363 Hamel S, Côté SD (2009) Foraging decisions in a capital breeder: trade-offs between mass gain and
364 lactation. *Oecologia* 161:421-432

365 Hirshfield MF, Tinkle DW (1975) Natural selection and the evolution of reproductive effort.
366 *Proceedings of the National Academy of Sciences* 72:2227-2231

367 Jones OR et al. (2008) Senescence rates are determined by ranking on the fast-slow life-history
368 continuum. *Ecology Letters* 11:664-673

369 Lent PC (1974) Mother-infant relationships in ungulates. In: Geist V, Walther F (ed) *The behaviour*
370 *of ungulates and its relation to management*. IUCN, Morges, pp 14-55

371 Loison A, Festa-Bianchet M, Gaillard J-M, Jorgenson JT, Jullien J-M (1999a) Age-specific survival
372 in five populations of ungulates: evidence of senescence. *Ecology* 80:2539-2554

373 Loison A, Jullien J-M, Menaut P (1999b) Subpopulation structure and dispersal in two populations
374 of chamois. *Journal of Mammalogy* 80:620-632

375 Martin JGA, Festa-Bianchet M (2011) Age-independent and age-dependent decreases in
376 reproduction of females. *Ecology letters* 14:576-581

377 Mason THE, Chirichella R, Richards SA, Stephens PA, Willis SG, Apollonio M (2011) Contrasting
378 life histories in neighbouring populations of a large mammal. *PloS one* 6:e28002-e28002

379 McElligott AG, Altwegg R, Hayden TJ (2002) Age-specific survival and reproductive probabilities:
380 evidence for senescence in male fallow deer (*Dama dama*). *Proceedings of the Royal*
381 *Society of London. Series B: Biological Sciences* 269:1129-1137

382 Muggeo VMR (2008) *Segmented*: an R package to fit regression models with broken-line
383 relationships. *R news* 8:20-25

- 384 Mysterud A, Steinheim G, Yoccoz NG, Holand Åy, Stenseth NC (2002) Early onset of reproductive
385 senescence in domestic sheep *Ovis aries*. *Oikos* 97:177-183
- 386 Nussey DH, Froy H, Lemaitre J-Fo, Gaillard J-M, Austad SN (2013) Senescence in natural
387 populations of animals: widespread evidence and its implications for bio-gerontology.
388 *Ageing research reviews* 12:214-225
- 389 Pioz M et al. (2008) Diseases and reproductive success in a wild mammal: example in the alpine
390 chamois. *Oecologia* 155:691-704
- 391 R Development Core Team (2012) R: A language and environment for statistical computing. In. R
392 Foundation for Statistical Computing, Vienna, Austria
- 393 Reed TE, Kruuk LEB, Wanless S, Frederiksen M, Cunningham EJA, Harris MP (2008)
394 Reproductive senescence in a long-lived seabird: rates of decline in late-life performance are
395 associated with varying costs of early reproduction. *The American Naturalist* 171:E89-E101
- 396 Reznick D, Nunney L, Tessier A (2000) Big houses, big cars, superfleas and the costs of
397 reproduction. *Trends in Ecology & Evolution* 15:421-425
- 398 Robinson MR, Mar KU, Lummaa V (2012) Senescence and age-specific trade-offs between
399 reproduction and survival in female Asian elephants. *Ecology Letters* 15:260-266
- 400 Ruckstuhl K, Ingold P (1994) On the suckling behaviour of Alpine chamois *Rupicapra rupicapra*
401 *rupicapra*. *Zeitschrift für Säugetierkunde* 59:230-235
- 402 Ruckstuhl KE, Ingold P (1999) Aspects of mother-kid behavior in Alpine chamois, *Rupicapra*
403 *rupicapra rupicapra*. *Zeitschrift für Säugetierkunde* 64:76-84
- 404 Rughetti M, Festa-Bianchet M (2010) Compensatory Growth Limits Opportunities for Artificial
405 Selection in Alpine Chamois. *Journal of Wildlife Management* 74:1024-1029
- 406 Santos ESA, Nakagawa S (2012) The costs of parental care: a meta-analysis of the trade-off
407 between parental effort and survival in birds. *Journal of Evolutionary Biology* 25:1911-1917
- 408 Schröder W, von Elsner-Schack I (1985) Correct age determination in chamois. In: Lovari S (ed)
409 *The Biology and Management of Mountain Ungulates*. Croom Helm, London, pp 67-70

410 Stearns S (1992) *The Evolution of Life Histories*. Oxford University Press, Oxford, New York.

411 Stearns SC (1989) Trade-Offs in Life-History Evolution. *Functional Ecology* 3:259-268

412 van de Pol M, Verhulst S (2006) Age-dependent traits: a new statistical model to separate within-
413 and between- individual effects. *The American Naturalist* 167:766-773

414 Vaupel JW, Manton KG, Stallard E (1979) The impact of heterogeneity in individual frailty on the
415 dynamics of mortality. *Demography* 16:439-454

416 Weladji RB et al. (2006) Good reindeer mothers live longer and become better in raising offspring.
417 *Proceedings of the Royal Society B: Biological Sciences* 273:1239-1244

418 Weladji RB et al. (2008) Heterogeneity in individual quality overrides costs of reproduction in
419 female reindeer. *Oecologia* 156:237-247

420

421

422 **TABLES**

423 **Table 1.** Null, linear, quadratic, logarithmic and threshold models used to explain the effect of age
 424 on breeding success (BS) of chamois females in the Swiss National Park (A). The best model,
 425 selected using AIC values, is reported in bold. (B) shows results of the best threshold model
 426 predicting two breakpoints, and in turn three segments. Slopes of each the three segments are
 427 reported.

428

(A) Model *AGE*

		AIC	Δ AIC
BS ~ 1	No effect of age on breeding	670.85	46.82
BS ~ age	Effect of age	672.19	48.16
BS ~ age + age²	Quadratic effect of age	624.03	0
BS ~ log (age + 1)	Logarithmic effect of age	668.92	44.89
BS ~ I st	Existence of one segment	I st :0-21	657.12
BS ~ I st + II st	Existence of two segments	I st :0-5; II st :6-21	656.38
BS ~ I st + II st + III st	Existence of three segments	I st :0-5; II st :5-13; III st :13-21	644.91

429

(B) *Slope* of each segments before and after the breakpoints

	Estimate	SE
slope before the first breakpoint (5 years)	0.1721	0.0401
slope between the breakpoints (5 and 13 years)	- 0.0111	0.0116
slope after the second breakpoint (13 years)	-0.0621	0.0181

430

431 **Table 2.** GLMM models on breeding success (BS) during the last 5 years before death in function
 432 of age at death (ADH), years before death (YBDH), breeding success at year $t-1$ (BS_{t-1}) and final
 433 breeding attempt (FBA) (A). Female identity and year of observation were fitted as random effects.
 434 * stands for an interactions. The best model, selected using AIC values, is reported in bold. (B)
 435 provides the estimates of the fixed and random terms of the best model.
 436

(A) Model <i>breeding success</i>		
	AIC	Δ AIC
BS ~ 1	209.65	25
BS ~ ADH + YBDH + BS_{t-1} + FBA + ADH ² + YBDH ² + ADH*YBDH + ADH* BS_{t-1} + ADH*FBA	188.22	3.57
BS ~ ADH + YBDH + BS_{t-1} + FBA + ADH ² + YBDH ² + ADH*YBDH + ADH* BS_{t-1}	186.78	2.13
BS ~ ADH + YBDH + BS_{t-1} + FBA + ADH ² + ADH*YBDH + ADH* BS_{t-1}	185.89	1.24
BS ~ ADH + YBDH + BS_{t-1} + FBA + ADH*YBDH + ADH* BS_{t-1}	185.12	0.47
BS ~ ADH + YBDH + BS_{t-1} + ADH*YBDH + ADH*BS_{t-1}	184.65	0

437

438

(B) Results best model <i>breeding success</i>				
Factor	Effect size	SE	z-value	P-value
ADH	-0.891	0.214	-4.166	<0.001
YBDH	-2.992	1.157	-2.587	0.009
BS_{t-1}	-6.367	2.956	-2.154	0.031
ADH*YBDH	0.189	0.189	2.535	0.011
ADH* BS_{t-1}	0.491	0.491	2.508	0.012

439

Random effects	Variance	SD
Female identity	<0.001	0.0002
Year of observation	1.49	1.222

440

441 **FIGURE CAPTIONS**

442 **Fig. 1.** Mean breeding success (BS) of chamois female in relation to age in Swiss National Park.
443 The dashed curve shows the quadratic fit of BS in relation to age, and the solid regression lines are
444 fitted for each break points, obtained using the R package *segmented*. Regression lines are shown
445 with the 95% confidence intervals and the slope of each regression line is reported in Table 2. Data
446 are on 654 observations from 102 female Alpine chamois. The number of females observed for each
447 age is reported above the X-axis.

448

449 **Fig. 2.** Mean breeding success in relation to years before death (YBDH) of chamois female in Swiss
450 National Park. For illustrative purpose, individuals were divided into three age at death (ADH)
451 classes (n : number of observations; N : number of individuals): $ADH < 12$ ($n = 15$; $N = 4$); $13 <$
452 $ADH < 16$ ($n = 100$, $N = 22$); $ADH > 16$ ($n = 74$, $N = 18$). Each dot represents a mean breeding
453 success values per YBDH per ADH class. Fitted lines are shown with 95% confidence intervals. R^2
454 and the slope of each of the three segments are reported in the panels.

455

456 **Fig. 3.** Mean breeding success at year t in relation to age at death (ADH) and breeding success at
457 year $t-1$ of chamois females in Swiss National Park. Left panel: 81 observations from 29 female that
458 successfully produced a kid at year t ; right panel: 84 observations from 34 females that failed to
459 produce a kid at year $t-1$. Regression lines are shown with 95% confidence intervals. R^2 of each
460 regression line are reported in the panels.

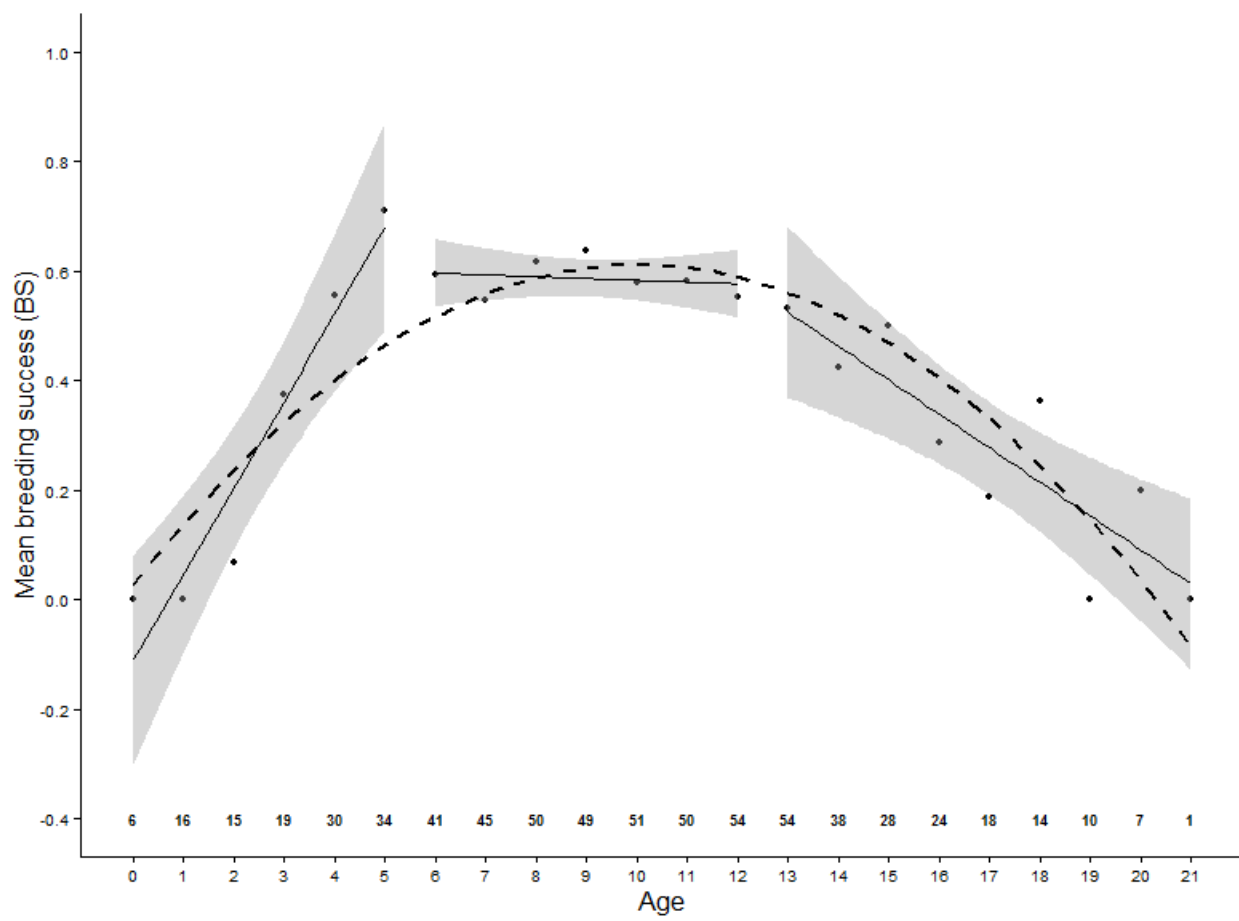
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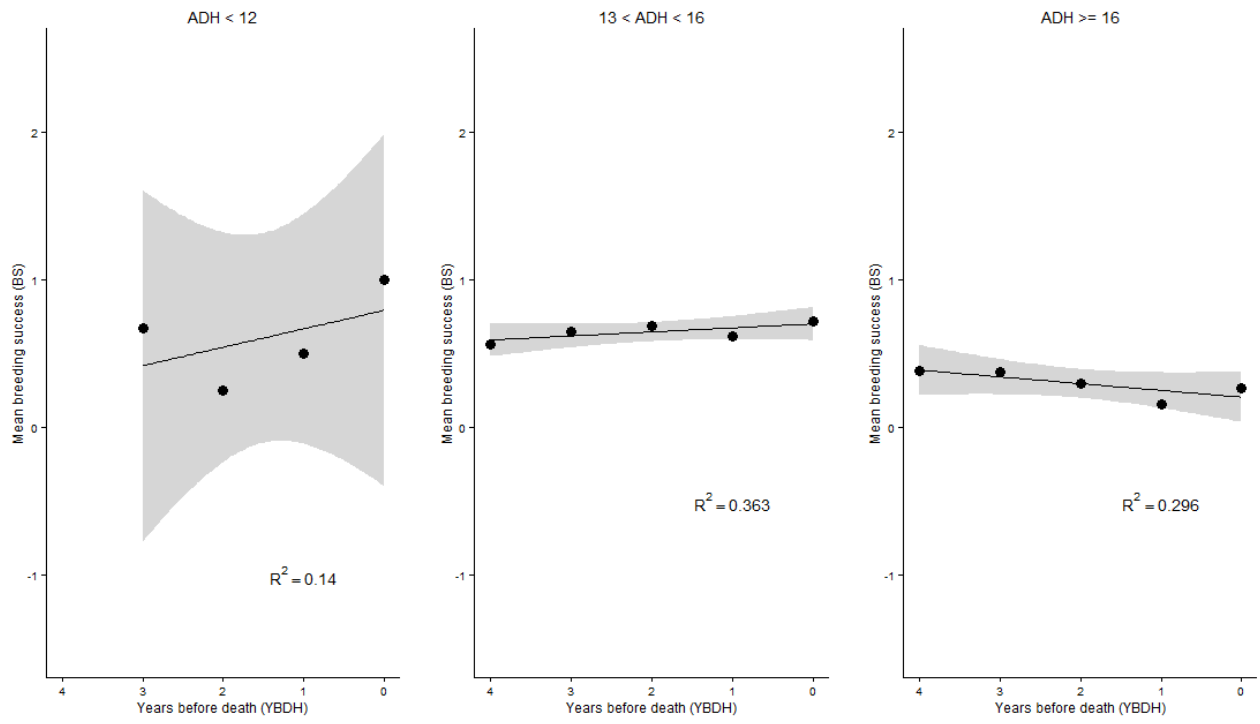


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467 **Figure 1**

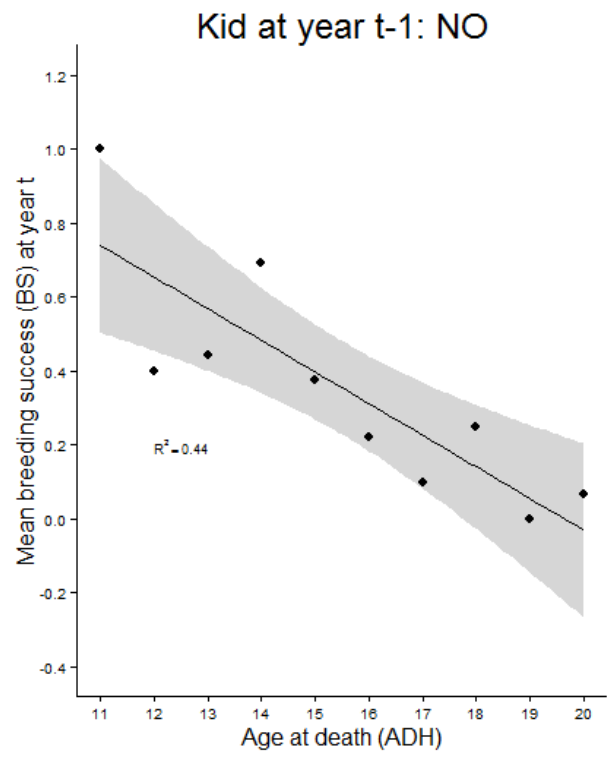
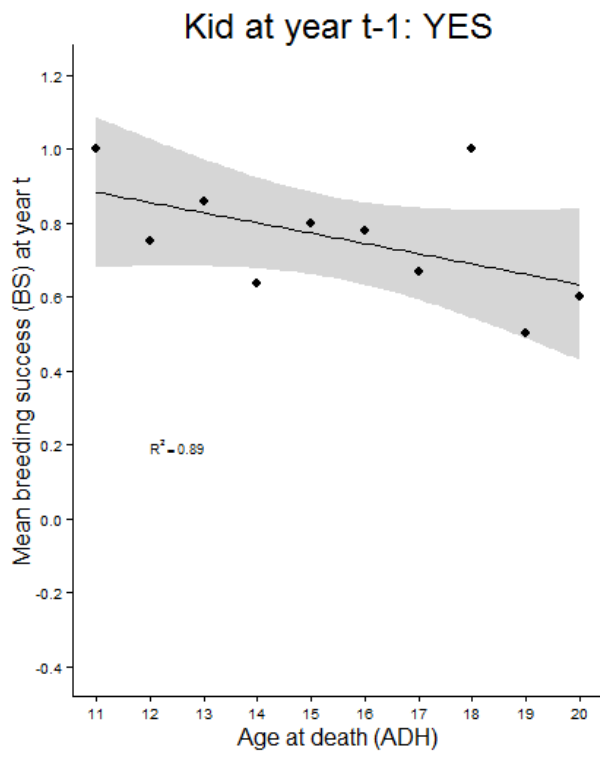
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470

471 **Figure 2**



472

473 **Figure 3**