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BEHAVIORAL ECOLOGY - ORIGINAL RESEARCH

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

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**ABSTRACT**

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

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

## INTRODUCTION

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

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

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

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

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

## MATERIALS AND METHODS

### *Study site and data collection*

Data were collected in the Swiss National Park, an area of integral protection covering 172.4 $km^2$ , located in south eastern Switzerland. Habitats of the Park are dominated by forests of Arolla pine (*Pinus cembra*) and larch (*Larix decidua*) below the tree line (2200m altitude) and by alpine grasslands and bare rocks above it. Annual precipitations amount to 700-1200 mm of rain, and the growing period above tree line is ca. 80 days per year. The Swiss National Park was created in 1914 and chamois hunting ceased in 1920. Their only predator is the golden eagle (*Aquila chrysäetos*) that can prey upon small kids. Population census shows that the number of chamois within the protected area is naturally fluctuating over the years of this study from a maximum of 1677 individuals (9.7 individuals per $Km^2$; 791 females, 442 males and 444 individuals younger than two years) to a minimum of 1163 individuals (6.7 individuals per $Km^2$; 544 females, 332 males and 287 individuals younger than two years; official data of the Swiss National Park).

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

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

***Ethical note***

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

***Data analyses***

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

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

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

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

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

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

*(ii)* At the population level, female BS was reaching a plateau between 5 and 13 years of age followed by a marked decline after 13 years of age (Fig. 1). To include information on pre-senescent females in the analyses, we kept observations of individuals aged 9 years or older and of an ADH 11 years of more. We used 9 years of age as a cut-of-point since this is halfway between 5 and 13 years of age; in other words it is the age with the highest estimated productivity. We considered ADH of 11 years of more because individuals should have been observed over at least three consecutive years before ADH to be included in the analyses (see also point (*iii*));

*(iii)* To investigate within-individual changes in reproductive performances, we only kept individuals observed consecutively at least during their three last years of life. Furthermore, to strictly focus on the last years of life (*i.e.* senescence *per se*), we restricted our dataset to observations collected in the last five (maximum) or three (minimum) years of life.

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

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

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

## RESULTS

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

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

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

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

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

## DISCUSSION

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

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

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

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

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

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

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

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## TABLES

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

(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 + age$^2$** | **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 | 33.09 |
| BS ~ I$^{st}$ + II$^{st}$ | Existence of two segments | I$^{st}$:0-5; II$^{st}$:6-21 | 656.38 | 32.35 |
| 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 | 20.88 |

(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 |

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

(A) Model ***breeding success***

| | AIC | ΔAIC |
|---|---|---|
| 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** |

(B) Results best model ***breeding success***

| **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 |

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

## FIGURE CAPTIONS

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

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

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

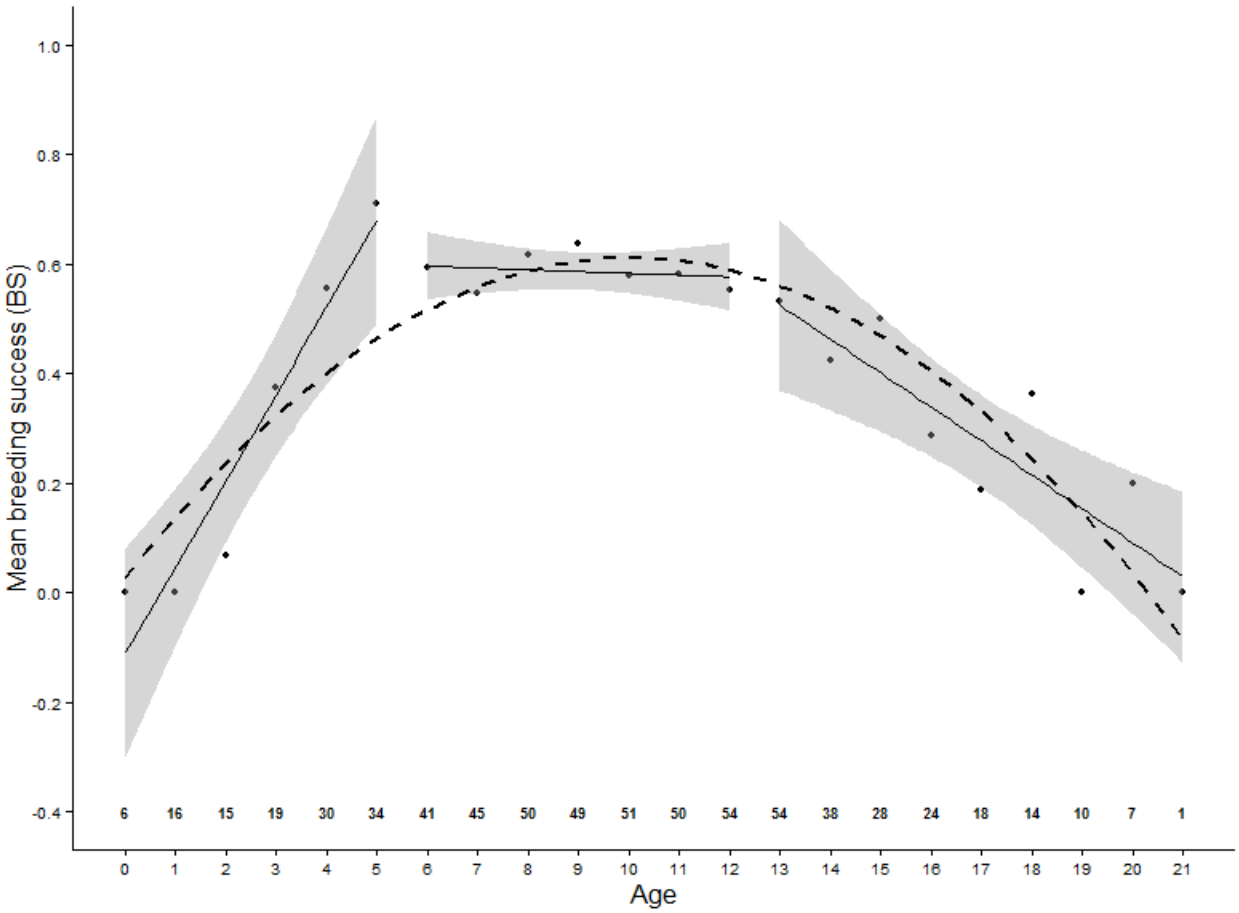
Mean breeding success (BS)
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
6 16 15 19 30 34 41 45 50 49 51 50 54 54 38 28 24 18 14 10 7 1
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21
Age

**Figure 1**

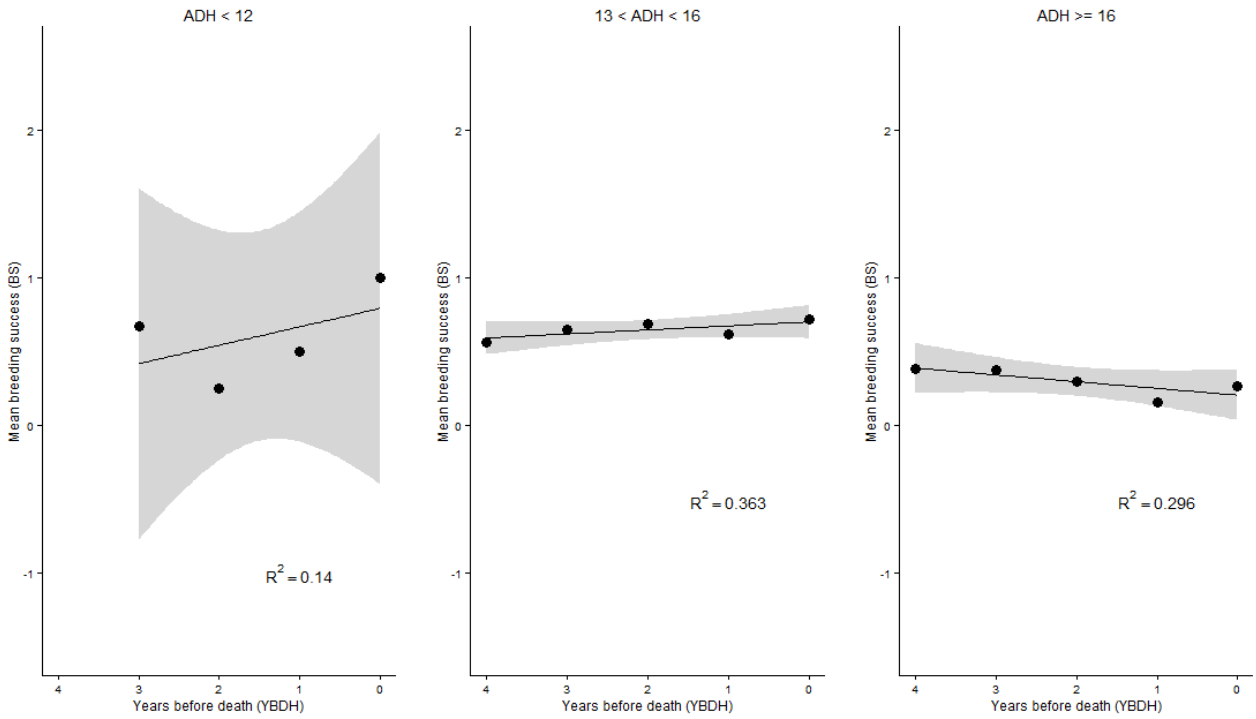
ADH < 12
13 < ADH < 16
ADH >= 16
Mean breeding success (BS)
Years before death (YBDH)
R2 = 0.14
R2 = 0.363
R2 = 0.296

**Figure 2**

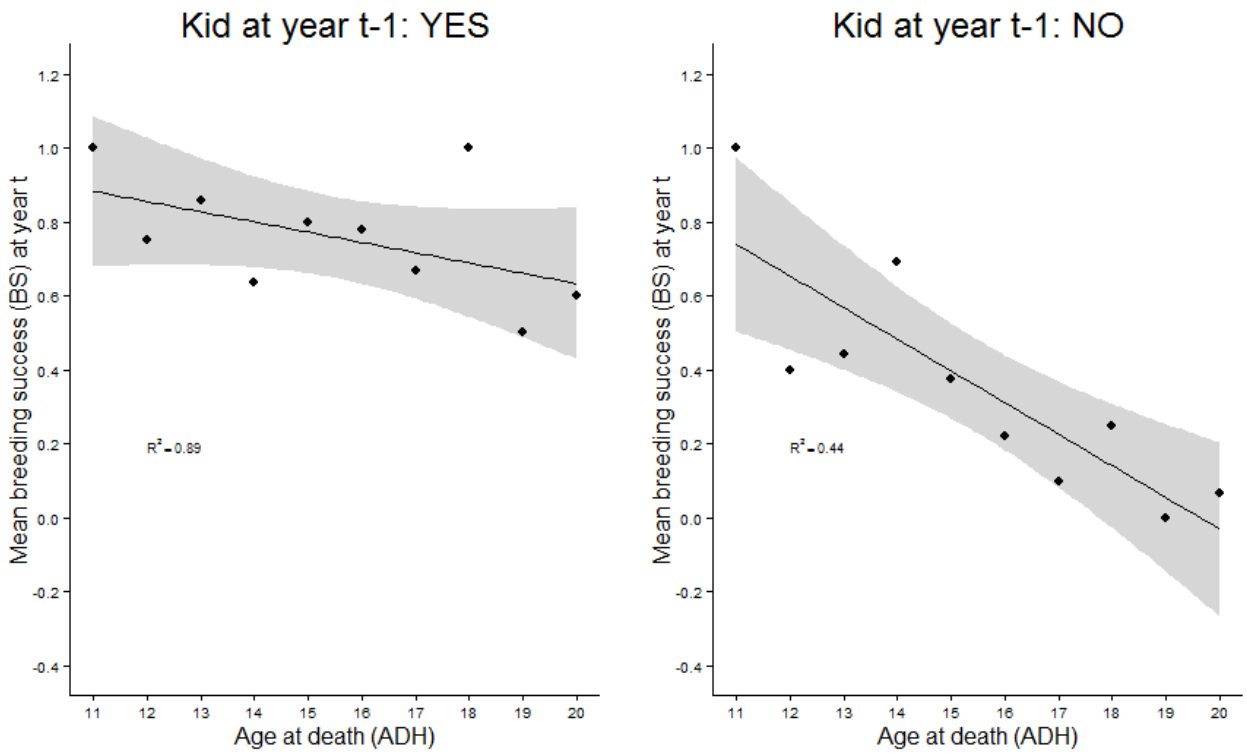
Kid at year t-1: YES
Kid at year t-1: NO
Mean breeding success (BS) at year t
Age at death (ADH)
R² = 0.89
R² = 0.44
1.2
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
11
12
13
14
15
16
17
18
19
20

**Figure 3**