

Age-specific survival and annual variation in survival of female chamois differ between populations

Josefa Bleu^{1,7}  · Ivar Herfindal¹ · Anne Loison^{2,3} · Anne M. G. Kwak^{1,4} · Mathieu Garel⁵ · Carole Toïgo⁵ · Thomas Rempfler⁶ · Flurin Filli⁶ · Bernt-Erik Sæther¹

Received: 12 March 2015 / Accepted: 5 August 2015
© Springer-Verlag Berlin Heidelberg 2015

Abstract In many species, population dynamics are shaped by age-structured demographic parameters, such as survival, which can cause age-specific sensitivity to environmental conditions. Accordingly, we can expect populations with different age-specific survival to be differently affected by environmental variation. However, this hypothesis is rarely tested at the intra-specific level. Using capture–mark–recapture models, we quantified age-specific survival and the extent of annual variations in survival of females of alpine chamois in two sites. In one

population, survival was very high (>0.94; Bauges, France) until the onset of senescence at approximately 7 years old, whereas the two other populations (Swiss National Park, SNP) had a later onset (12 years old) and a lower rate of senescence. Senescence patterns are therefore not fixed within species. Annual variation in survival was higher in the Bauges (SD = 0.26) compared to the SNP populations (SD = 0.20). Also, in each population, the age classes with the lowest survival also experienced the largest temporal variation, in accordance with inter-specific comparisons showing a greater impact of environmental variation on these age classes. The large difference between the populations in age-specific survival and variation suggests that environmental variation and climate change will affect these populations differently.

Communicated by Janne Sundell.

Electronic supplementary material The online version of this article (doi:[10.1007/s00442-015-3420-5](https://doi.org/10.1007/s00442-015-3420-5)) contains supplementary material, which is available to authorized users.

✉ Josefa Bleu
josefa.bleu@gmail.com

- ¹ Department of Biology, Centre for Biodiversity Dynamics, Norwegian University of Sciences and Technology, 7491 Trondheim, Norway
- ² Université de Savoie, CNRS, UMR 5553 Laboratoire d'Écologie Alpine, 73376 Le Bourget du Lac, France
- ³ LTER "Zone Atelier Alpes", 38000 Grenoble, France
- ⁴ Institute for Water and Wetland Research, Department of Animal Ecology and Ecophysiology, Radboud University, PO Box 9100, 6500 GL Nijmegen, The Netherlands
- ⁵ Office National de la Chasse et de la Faune Sauvage (ONCFS), ZI Mayencin, 38610 Gières, France
- ⁶ Swiss National Park, Chastè Planta-Wildenberg, 7530 Zernez, Switzerland
- ⁷ Present Address: Université Pierre et Marie Curie, Institut d'écologie et des sciences de l'environnement, Bat A, 7ème étage, case courrier 237, 7 quai Saint Bernard, 75252 Paris Cedex 05, France

Keywords Age-specific survival · Capture–mark–recapture · Environmental variability · *Rupicapra rupicapra* · Senescence

Introduction

Demographic parameters of many long-lived species are strongly structured by age (e.g. Gaillard et al. 2000). This has important implications for population dynamics (Benton et al. 2006; Sæther et al. 2013) through age-specific contribution to the population growth rate (Coulson et al. 2005). Age structure has been shown to influence how the population is affected by harvesting (e.g. Milner et al. 2007) and its response to environmental variation. For example, the effects of weather on dynamics of wild soay sheep (*Ovis aries*) were different between populations of equal size but differing in age- and sex-structures (Coulson et al. 2001). The importance of age structure in shaping the

responses to environmental changes can be explained by age-specific sensitivity to environmental conditions among age classes, resulting in differences in the variation in survival among age classes. Understanding these mechanisms is essential in order to predict how climate change will affect populations, particularly in populations experiencing rapid environmental changes (Hansen et al. 2011; Engler et al. 2011).

In ungulates, prime-aged females have a high survival with low variance (Gaillard et al. 2000). However, individuals belonging to age classes with lower survival (young and senescent individuals) may be more sensitive to environmental variation with a corresponding higher temporal variation in survival, suggesting high environmental stochasticity in these age classes. Accordingly, the age at which individuals are in the more vulnerable age classes (i.e. young or senescent stages) may affect how environmental variation affects population dynamics (Pfister 1998; Sæther and Bakke 2000; Gaillard and Yoccoz 2003). As the senescent stage is normally considerably longer than the juvenile stage, and senescent individuals also contribute by reproduction, variation in the characteristics of senescence is of particular importance for population dynamics. We can expect that the later the onset of senescence (and hence the longer the prime-age stage) and/or the smaller the rate of senescence, the lower the impact of environmental variation on population dynamics. Senescence has been described in many wild animals from very diverse taxa (Nussey et al. 2013; but see also Jones et al. 2014). A large part of the inter-specific variation in senescent rates can be explained by life-history variation along a slow–fast continuum (Jones et al. 2008). However, variations at the intra-specific level also exist (see below). The evolutionary theories of senescence (antagonistic pleiotropy theory, disposable soma theory) rely on the fact that selection is weak at late ages and converge on the idea that there is a trade-off between early performance/somatic maintenance and late survival (Kirkwood and Austad 2000). In accordance with these theories, it has been shown that early environmental conditions or investment in reproduction affected senescence both within populations (Nussey et al. 2007; Péron et al. 2010) and, in a handful of studies, between populations of the same species (Austad 1993; Bronikowski et al. 2002; Bryant and Reznick 2004). At the intra-specific level, studies comparing survival patterns and also age-specific variation in this vital rate between populations are rare. The difficulty is that such studies require long-term studies of marked individuals of known age in several wild populations of the same species, a requirement which is rarely met.

Based on long-term longitudinal datasets and capture–mark–recapture methods in three populations of the same species, we could estimate age-specific survival patterns

and age-specific inter-annual variation in survival rates in females in three contrasted populations of an alpine ungulate, the chamois (*Rupicapra rupicapra*). We assessed the among-populations differences in (1) average survival rates per age classes, and more specifically senescence patterns, and (2) inter-annual variation in survival rates. This allowed us to examine at the intra-specific level whether temporal variation in survival rates may be used as a proxy of the age-specific sensitivity to environmental stochasticity.

Materials and methods

We used longitudinal data from long-term monitoring of female chamois from three populations. Chamois were trapped annually, marked and then visually monitored. Age at capture was determined by counting horn annuli (Schröder and von Elsner-Schack 1985).

French study site

Chamois have been monitored since the early 1980s in the Game and Wildlife Reserve of the Bauges massif (45°40'N, 6°13'E), in the northern French Alps (e.g. Loison et al. 1994). We studied the chamois from the Armenaz site (227.4 ha; Table S1), which has a continental climate with oceanic influence (weather station at 595 m: mean annual temperature = 9.22 ± 0.46 °C, mean annual rainfall = 1361.8 ± 210.6 mm). The area is characterized by sub-alpine meadows (e.g., *Carex* sp. and *Sesleria caerulea*) with shrublands (e.g. *Rhododendron ferrugineum* and *Vaccinium* sp.), mountain hay meadows, and screes (Duparc et al. 2013). In this site, chamois have no natural predators and are not in sympatry with other wild ungulates (Darmion et al. 2014). Chamois are trapped below falling nets baited with salt (May–September) and marked with a collar. Between 1991 and 2012, 238 females, aged 1–12 years old, were captured (see detailed sample sizes in Table S2). The mean estimated probability of observation of an individual is 0.70 (SE = 0.27) (estimates from model M4). Individuals that died from non-natural causes (e.g. hunting) were right-censored to estimate natural survival probabilities (Lebreton et al. 1992) (Table S2).

Swiss study sites

In the Swiss national park (SNP; 46°40'N, 10°12'E), two populations of chamois are monitored, one in Val Trupchun (ca. 2000 ha in the SNP and 4000 ha in Italy) and one in Il Fuorn (ca. 5025 ha in the SNP) (Filli and Suter 2006; Table S1). The SNP has a continental climate with low annual precipitation (weather station at 1800 m: mean annual temperature = 0.98 ± 0.48 °C, mean annual

rainfall = 882.5 mm \pm 213.2 mm). Hunting is prohibited and visitors must stay on designated footpaths. Val Trupchun is dominated by screes, sub-alpine meadows (nutrient-poor *Elyno-Seslerietea* and nutrient-rich *Poion alpinae* grasslands), whereas Il Fuorn is dominated by screes, sub-alpine meadows (nutrient-poor *Seslerio-Sempervirentum* meadows and *Carex firma* turfs) and mountain pine *Pinus mugo*. In both sites, predation is very rare but golden eagle (*Aquila chrysaetos*) may attack kids. Interspecific competition may occur from red deer (*Cervus elaphus*) and ibex (*Capra ibex*) (more pronounced in Val Trupchun). Chamois are captured all year round using box or sling traps and are marked with ear tags (Filli and Suter 2006). Between 1995 and 2012, 89 females were captured in Il Fuorn and 40 in Val Trupchun. Age at capture ranged from 0 to 23 years old (see detailed sample sizes in Table S2). The mean estimated probability of observation of an individual is 0.58 (SE = 0.39) (estimates from model M9). Some females were captured between January and April, but were considered as if they had been captured in the following May (and thus belonged to the following age class). The results were qualitatively similar if these individuals were considered as captured the preceding December (analyses not shown).

Statistical analyses

We kept the observations between May and December in order to have similar periods between the sites and to estimate winter survival (the period of highest mortality for chamois; Jonas et al. 2008). We first analysed the Bauges population and the SNP populations separately (pooling Il Fuorn and Val Trupchun). Survival estimates were obtained independently of re-sighting probabilities using capture-mark-recapture (CMR) modelling based on the open population model of Cormack–Jolly–Seber (Clobert et al. 1987). This model produces apparent survival estimates resulting from mortality and emigration. We used the program E-surge (v.1.9.0) to fit models (Choquet et al. 2009). For all populations, we found no transience in the data but a strong trap-happiness (details in ESM). The best model to account for trap-happiness was a two-state mixture model with transitions between the states (see details in Table S3). From this model, we selected the best model describing the effect of the year in re-sighting probabilities (Table S4). Finally, we fitted models on the survival probabilities. We compared models with different age class and/or with a continuous effect of age (see Table 1 for candidate models). The different models were built from typical age classes already described in ungulates: juveniles, yearlings, prime-aged adults (2–7 years old), old adults (8–12 years old) and senescent individuals (more than 12 years old) (Gaillard et al. 2000, 2004). We also tested models with a continuous effect of age as senescence can also be realistically

described by a linear decrease of survival with age on a log scale (Gompertz models) (e.g. Loison et al. 1999; Gaillard et al. 2004). Models were implemented with a logit link, which has been shown to be a good approximation of the Gompertz model (Loison et al. 1999; Viallefont 2011). In those models, the rate of senescence was the slope from the linear function between survival rates and age with a logistic link. For the SNP populations, we also tested the effect of site on the initial state, transition, re-sighting and survival probabilities.

In a next step, we examined differences between the Bauges and SNP populations by analysing all the data together, using the best model structure selected in the separate analyses. Finally, we examined the variation of survival between years by allowing survival to vary among years and calculated the age- and population-specific standard deviation (SD) in survival from the annual survival rates. However, concerns have been raised regarding the comparison of variances from estimates that are limited between 0 and 1 (Morris and Doak 2004). We therefore also calculated scaled variances, P_{\max} , following Morris and Doak (2004). Results did not differ qualitatively between estimates of SD and P_{\max} (Table 3).

Model selection was based on AICc (Akaike information criterion corrected for small sample size; Burnham and Anderson 2002). In the “Results” we report the estimates of survival from the models (back-transformed from the logit scale) and the parametric 95 % confidence interval (CI), unless otherwise noted.

Results

The age-specific survival of the Bauges population was best described with a linear decrease of survival with age (logit-scale) from 1 year onwards (model M12 in Table 1, AICc = 1660.43, estimates in Table S5). Survival was relatively stable and high until 7 years of age, when a more pronounced decrease in survival occurred (Fig. 1a). In the second best model (Δ AICc = 1.73), the linear decrease starts at 2 years old (model M14, Tables 1 and S5). The best model where age was grouped in classes included the following age classes: 1–7, 8–12 and >12 years old (Δ AICc = 9.28, model M4 in Tables 1 and S5; Fig. 1a) and was consistent in term of pattern with the model with a linear trend. The estimates of a classic 4 age classes model (model M5 in Table 1) are given in Table S5 (Δ AICc = 11.30).

In the SNP populations, two models had almost similar AICc-value and both supported a senescence starting after age 12. The best model with age grouped to classes had three age classes: 0–1 years old, 2–12 years old and >12 years old (model M9, AICc = 1030.97, Tables 1 and

Table 1 Models describing age-specific survival of female chamois in Les Bauges and the Swiss National Park (SNP)

ID	Model types	Juvenile ^a	Young	Adult1	Adult2	Old ^b	No. age classes Bauges/SNP	Bauges		SNP		
								No. parameters	AICc	No. parameters	AICc	
M1	No effect of age on survival	–					–	10	1726.58	9	1072.58	
M2	Full age model	We estimate a survival probability for each age						20/27	29	1676.37	35	1053.35
M3	Age class	1/0–1	2–7			>7	3/3	12	1681.58	11	1059.86	
M4	Age class	0	1–7	8–12		>12	3/4	12	1669.71^c	12	1040.17	
M5	Age class	1/0–1	2–7	8–12		>12	4/4	13	1671.73	12	1032.91^d	
M6	Age class	0	1	2–7	8–12	>12	5	–	–	13	1034.97	
M7	Age class	0	1–7			>7	2/3	11	1679.54	11	1068.10	
M8	Age class	0	1–12			>12	2/3	11	1685.59	11	1039.66	
M9	Age class	1/0–1	2–12			>12	3/3	12	1686.39	11	1030.97^e	
M10	Linear trend					0	–	–	–	10	1054.41	
M11	Quadratic trend					0	–	–	–	11	1047.93	
M12	(Age class +) linear trend	0				1	–/1	11	1660.43^f	11	1048.95	
M13	(Age class +) quadratic trend	0				1	–/1	12	1662.44	12	1047.63	
M14	Age class + linear trend	1/0–1				2	1/1	12	1662.16^g	11	1035.77	
M15	Age class + linear trend	1/0–1	2–7			>7	2/2	13	1665.61	12	1036.06	
M16	Age class + linear trend	0	1–7	8–12		>12	2/3	13	1668.69	13	1040.28	
M17	Age class + linear trend	1/0–1	2–7	8–12		>12	3/3	14	1670.72	13	1033.05	
M18	Age class + linear trend	0	1–7			>7	1/2	12	1663.61	12	1043.44	
M19	Age class + linear trend	0	1–12			>12	1/2	12	1686.19	12	1039.53	
M20	Age class + linear trend	1/0–1	2–12			>12	2/2	13	1686.90	12	1031.05^h	

The age pattern was modelled either with age grouped in classes, as a continuous relationship (linear and quadratic functions), or as a combination of classes and continuous relationships. Best models are in bold

^a This age class is only relevant for the Swiss populations, because we did not have captures at 0 years old in the French population

^b The old age class or the age of the onset of the continuous negative effect of age for continuous models (linear or quadratic trends)

^c Deviance = 1645.42

^d Deviance = 1008.46

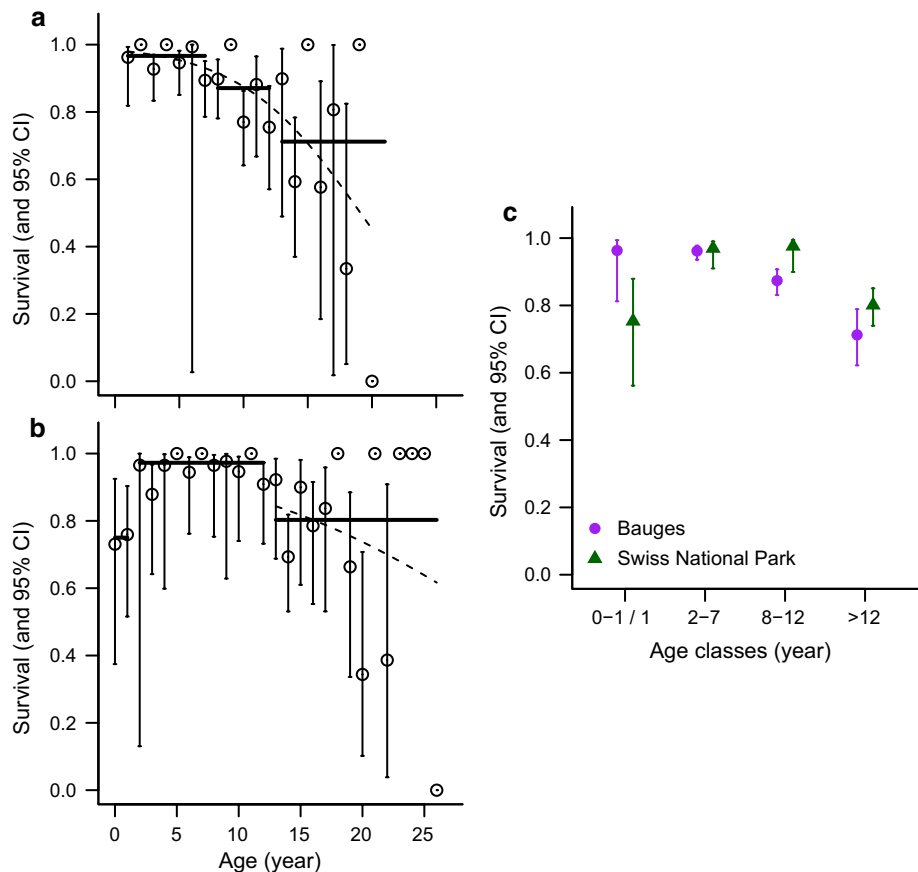
^e Deviance = 1008.59

^f Deviance = 1638.18

^g Deviance = 1637.86

^h Deviance = 1006.60

Fig. 1 Age-specific survival of female chamois in **a** Les Bauges (France), **b** the Swiss National Park (SNP), and **c** both sites. *Open circles* show estimates from the full age model with confidence intervals (model M2 in Table 1). *Dotted lines* are the estimates from the best linear models (models M12 and M20 in Table 1 in **a** and **b**, respectively), and *solid lines* are estimates from the best age class models (models M4 and M9 in Table 1 in **a** and **b**, respectively). **c** The estimates of a direct comparison between the two sites based on a model with 4 age classes (Table 2). Juveniles (0 years old) are only in the SNP dataset



S5; Fig. 1b). A model with equal support ($\Delta\text{AICc} = 0.08$) had similar survival as the previous model for 0–1 and 2–12 years old, but a linear decrease in survival after age 12 (model M20 in Tables 1 and S5; Fig. 1b). Model M5, the second best model with age classes ($\Delta\text{AICc} = 1.94$, Table 1), considered two distinct age classes for prime-aged females (2–7 and 8–12 years old) (Table S5). All the highest ranked models grouped 0 and 1 years old females together, as supported from the similar survival estimates shown in Fig. 1b (and model M6 in Table S5).

The two populations in the SNP were similar in terms of survival probabilities (Table S6 and Fig. S1). Indeed, while the model with lowest AICc included an additive effect of site, suggesting overall higher survival in Il Fuorn, the ΔAICc with the model with no effect of site was only 1.21 (Table S6). We therefore pooled these two populations in further analyses.

We then further examined the differences in survival pattern and corresponding variation between the Bauges and SNP populations. As a base model, we used the four age classes model (model M5 in Table 1) which was the most parsimonious model when considering both study areas simultaneously. Age-specific survival differed between the SNP and Bauges populations (Table 2, ΔAICc to other models ≥ 3.88). The survival estimates from this model confirmed the differences observed on Fig. 1a and b: survival is

lower in the Bauges population than in the SNP populations except for the first age class (Fig. 1c). In adults, the difference is largest for the 8- to 12-year-old females (Fig. 1c).

Finally, we compared the annual variation in age-specific survival in each population by including temporal (i.e. annual) variation in the CMR models. We allowed survival to vary with year differently for each population and each age class (Figs. S2, S3). Overall, survival is more variable in the Bauges population than in the SNP population [SD (Bauges) = 0.2638 vs. SD (SNP) = 0.2017], even if we account for the overall lower survival in the Bauges population [P_{max} (Bauges) = 0.4238 vs. P_{max} (SNP) = 0.3297]. In both populations, the females from the age class with the lowest survival (young and senescent females) showed also the highest variation of their survival (SD and P_{max} ; Table 3), with an effect more pronounced for old females in the Bauges and for young females in SNP. Conversely, the variation of survival of females with the highest survival (>0.94 : age class 2–7 in Bauges and 2–7 and 8–12 in SNP) is low ($\text{SD} < 0.093$ and $P_{\text{max}} < 0.155$).

Discussion

Thanks to similar monitoring of individuals of known age for >16 years in 3 populations of the same species, we

Table 2 Ranking of models explaining age-specific survival of female chamois in Les Bauges and the Swiss National Park (SNP)

Model	<i>K</i>	Deviance	AICc	ΔAICc
Step 1				
Effect of site on transition	19	2681.64	2720.07	0
Effect of site on transition and initial state	20	2681.08	2721.56	1.49
No effect of site (model M5 from Table 1)	18	2687.04	2723.43	3.36
Effect of site on initial state	19	2685.31	2723.74	3.67
Step 2				
Different effect of site in each age class	23	2655.87	2702.49	0
Effect of site in age class 8–12	20	2665.90	2706.37	3.88
Same effect of site in all age classes	20	2672.64	2713.11	10.62
Effect of site in age class 0–1	20	2674.28	2714.76	12.27
Effect of site in age class >12	20	2677.16	2717.64	15.15
No effect of site in survival	19	2681.64	2720.07	17.58
Effect of site in age class 2–7	20	2681.53	2722.00	19.51

All models included four age classes (0–1, 2–7, 8–12 and >12 years old) and site-specific resighting probabilities (Table S4). We proceeded in 2 steps: first, we tested the additive effect of site on the transition and initial state probabilities (which are properties of mixture models see Supplementary methods); second, we tested the effect of site on the survival probabilities from the best model selected in the first step. Best models according to AICc for each step are in bold. The number of parameters of each model is *k*

Table 3 Temporal variance in survival in the different sites and age classes

Site	Age class	Mean	SD	<i>P</i> _{max}
Bauges	1	0.8271	0.1781	0.2218
Bauges	2–7	0.9408	0.0929	0.1550
Bauges	8–12	0.8513	0.1621	0.2076
Bauges	>12	0.5523	0.3651	0.5391
SNP	0–1	0.7114	0.3058	0.4555
SNP	2–7	0.9473	0.0758	0.1151
SNP	8–12	0.9447	0.0812	0.1262
SNP	>12	0.8197	0.1530	0.1584

Estimated means and standard deviations (SD) from a model with annual variation in survival. To compare the variation in survival [measured on the (0, 1) scale], we computed the proportion of the maximum possible variance *P*_{max} as $SD^2/[mean \times (1 - mean)]$ (Morris and Doak 2004; Altwegg et al. 2007)

found evidence of clear differences in age at occurrence and rate of senescence at the intra-specific level, along with differences in age-specific annual variation in survival. In most large herbivores comparable to chamois, the senescent stage is expected after approximately 7 years of age

(Gaillard et al. 2003; Péron et al. 2010). Accordingly, the onset of senescence at 7 years old in the Bauges population is typical whereas the onset at 12 years old in the SNP populations is later than expected. Our evidence for inter-population differences in senescence supports the idea that senescence patterns are not fixed within species and can be influenced by, for instance, environmental conditions (Loison et al. 1999; Ricklefs and Scheuerlein 2001; Lemaître et al. 2013). The difference in senescence between the Bauges population and the SNP populations could be caused by contrasting environmental conditions resulting in a faster life-history strategy in the Bauges population compared to the SNP populations. A faster life-history strategy could be selected by hunting (which is permitted in the Bauges but not in the SNP populations) (e.g. Hutchings and Baum 2005) or by harsher environmental conditions (Promislow and Harvey 1990). However, we have no evidence that climatic or general environmental conditions are harsher in the low-altitude population of the Bauges compared to SNP (Table S1). Future studies need to compare age at maturity and reproductive effort of females in each population to address the hypothesis that different survival rates and senescent patterns correspond to different life-history strategies (Nussey et al. 2013).

Since age-specific survival patterns differed between the two study sites, we expected differences in annual variation in survival. This can occur because environmental variability (e.g. changes in weather conditions, habitat quality, population density) have a larger impact on individuals of lower quality, i.e. that have a lower survival (e.g. for climate effects; Willis et al. 2013). Moreover, it has been suggested that, in prime-aged female ungulates, survival is partly buffered against environmental variations through an adjustment of the reproductive effort (Gaillard et al. 2000; Gaillard and Yoccoz 2003). In agreement with the interspecific comparisons of Gaillard and Yoccoz (2003), we confirmed, at the intra-specific level, that the lower the overall survival (in the Bauges vs. the SNP population) during prime-age, the higher the annual variation in survival. This can again reflect a faster life-history strategy (Sæther et al. 2004) and/or more variable environmental conditions in the Bauges. A shorter length of the prime-age stage and longer senescence stage in the Bauges population suggest that this population may be more vulnerable to environmental variation such as climate change, compared to the SNP population where females spend more years in a stage with high survival and low variation.

This study exemplifies that age, a factor already known to affect demographic rates, also relates to the variability in survival, and thus is an important factor to understand the sensitivity to environmental changes (Pardo et al. 2013). Further studies on differences in age-specific survival and

variation in survival between populations of the same species could be important to understand population-specific impact of environmental changes (e.g. Grøtan et al. 2008).

Acknowledgments We thank the Office National de la Chasse et de la Faune Sauvage (ONCFS), and in particular Jean-Michel Jullien and Thibaut Amblard, and the Swiss National Park for collecting and managing data with the help of many volunteers. This research was conducted on the Long-Term Ecosystem Research (LTER) site Zone Atelier Alpes, a member of the ILTER-Europe network. The study received support from the European Research Council (STOCHPOP research grant to B.-E.S.).

Author contribution statement JB, IH, AL, B-ES formulated the idea. FF, MG, AL, TR, CT conducted field work and supervised the projects of long-term monitoring of chamois populations. JB, AMGK performed statistical analyses. JB wrote the manuscript with the help of the other authors.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical statement All applicable national guidelines for the care and use of animals were followed.

Funding European Research Council (STOCHPOP research grant to B.-E.S.).

References

- Altwegg R, Schaub M, Roulin A (2007) Age-specific fitness components and their temporal variation in the barn owl. *Am Nat* 169:47–61. doi:10.1086/510215
- Austad SN (1993) Retarded senescence in an insular population of Virginia opossums (*Didelphis virginiana*). *J Zool* 229:695–708. doi:10.1111/j.1469-7998.1993.tb02665.x
- Benton TG, Plaistow SJ, Coulson TN (2006) Complex population dynamics and complex causation: devils, details and demography. *Proc R Soc Lond B* 273:1173–1181. doi:10.1098/rspb.2006.3495
- Bronikowski AM, Alberts SC, Altmann J et al (2002) The aging baboon: comparative demography in a non-human primate. *Proc Natl Acad Sci USA* 99:9591–9595. doi:10.1073/pnas.142675599
- Bryant MJ, Reznick D (2004) Comparative studies of senescence in natural populations of guppies. *Am Nat* 163:55–68. doi:10.1086/380650
- Burnham KP, Anderson DR (2002) Model selection and multi-model inference: a practical information-theoretic approach, 2nd edn. Springer, New York
- Choquet R, Rouan L, Pradel R (2009) Program E-Surge: a software application for fitting multievent models. In: Thomson DL, Cooch EG, Conroy MJ (eds) Modeling demographic processes in marked populations. Springer, New York, pp 845–865
- Clobert J, Lebreton J-D, Allainé D (1987) A general approach to survival rate estimation by recaptures or resightings of marked birds. *Ardea* 75:133–142
- Coulson T, Catchpole EA, Albon SD et al (2001) Age, sex, density, winter weather, and population crashes in soay sheep. *Science* 292:1528–1531. doi:10.1126/science.292.5521.1528
- Coulson T, Gaillard J-M, Festa-Bianchet M (2005) Decomposing the variation in population growth into contributions from multiple demographic rates. *J Anim Ecol* 74:789–801. doi:10.1111/j.1365-2656.2005.00975.x
- Darmon G, Bourgoin G, Marchand P et al (2014) Do ecologically close species shift their daily activities when in sympatry? A test on chamois in the presence of mouflon. *Biol J Linn Soc* 111:621–626. doi:10.1111/bj.12228
- Duparc A, Redjadj C, Viard-Crétat F et al (2013) Co-variation between plant above-ground biomass and phenology in sub-alpine grasslands. *Appl Veg Sci* 16:305–316. doi:10.1111/j.1654-109X.2012.01225.x
- Engler R, Randin CF, Thuiller W et al (2011) 21st century climate change threatens mountain flora unequally across Europe. *Glob Change Biol* 17:2330–2341. doi:10.1111/j.1365-2486.2010.02393.x
- Filli F, Suter W (eds) (2006) Ungulate research in the Swiss National Park. Schweizerischer Nationalpark, Zerne
- Gaillard J-M, Yoccoz NG (2003) Temporal variation in survival of mammals: a case of environmental canalization? *Ecology* 84:3294–3306. doi:10.1890/02-0409
- Gaillard J-M, Festa-Bianchet M, Yoccoz NG et al (2000) Temporal variation in fitness components and population dynamics of large herbivores. *Annu Rev Ecol Syst* 31:367–393. doi:10.1146/annurev.ecolsys.31.1.367
- Gaillard J-M, Loison A, Festa-Bianchet M et al (2003) Ecological correlates of life span in populations of large herbivorous mammals. *Popul Dev Rev* 29:39–56
- Gaillard J-M, Viallefont A, Loison A, Festa-Bianchet M (2004) Assessing senescence patterns in populations of large mammals. *Anim Biodivers Conserv* 27:47–58
- Grøtan V, Sæther B-E, Filli F, Engen S (2008) Effects of climate on population fluctuations of ibex. *Glob Change Biol* 14:218–228. doi:10.1111/j.1365-2486.2007.01484.x
- Hansen BB, Aanes R, Herfindal I et al (2011) Climate, icing, and wild arctic reindeer: past relationships and future prospects. *Ecology* 92:1917–1923. doi:10.1890/11-0095.1
- Hutchings JA, Baum JK (2005) Measuring marine fish biodiversity: temporal changes in abundance, life history and demography. *Philos Trans R Soc Lond B* 360:315–338. doi:10.1098/rstb.2004.1586
- Jonas T, Geiger F, Jenny H (2008) Mortality pattern of the Alpine chamois: the influence of snow-meteorological factors. *Ann Glaciol* 49:56–62. doi:10.3189/172756408787814735
- Jones OR, Gaillard J-M, Tuljapurkar S et al (2008) Senescence rates are determined by ranking on the fast-slow life-history continuum. *Ecol Lett* 11:664–673. doi:10.1111/j.1461-0248.2008.01187.x
- Jones OR, Scheuerlein A, Salguero-Gómez R et al (2014) Diversity of ageing across the tree of life. *Nature* 505:169–173. doi:10.1038/nature12789
- Kirkwood TBL, Austad SN (2000) Why do we age? *Nature* 408:233–238. doi:10.1038/35041682
- Lebreton J-D, Burnham KP, Clobert J, Anderson DR (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol Monogr* 62:67–118. doi:10.2307/2937171
- Lemaître J-F, Gaillard J-M, Lackey LB et al (2013) Comparing free-ranging and captive populations reveals intra-specific variation in aging rates in large herbivores. *Exp Gerontol* 48:162–167. doi:10.1016/j.exger.2012.12.004
- Loison A, Gaillard J-M, Houssin H (1994) New insight on survivorship of female chamois (*Rupicapra rupicapra*) from observation of marked animals. *Can J Zool* 72:591–597. doi:10.1139/z94-081
- Loison A, Festa-Bianchet M, Gaillard J-M et al (1999) Age-specific survival in five populations of ungulates: evidence of senescence. *Ecology* 80:2539–2554. doi:10.1890/0012-9658(1999)080[2539:ASSI FP]2.0.CO;2
- Milner JM, Nilsen EB, Andreassen HP (2007) Demographic side effects of selective hunting in ungulates and carnivores. *Conserv Biol* 21:36–47. doi:10.1111/j.1523-1739.2006.00591.x

- Morris WF, Doak DF (2004) Buffering of life histories against environmental stochasticity: accounting for a spurious correlation between the variabilities of vital rates and their contributions to fitness. *Am Nat* 163:579–590. doi:[10.1086/382550](https://doi.org/10.1086/382550)
- Nussey DH, Kruuk LEB, Morris A, Clutton-Brock TH (2007) Environmental conditions in early life influence ageing rates in a wild population of red deer. *Curr Biol* 17:R1000–R1001. doi:[10.1016/j.cub.2007.10.005](https://doi.org/10.1016/j.cub.2007.10.005)
- Nussey DH, Froy H, Lemaître J-F et al (2013) Senescence in natural populations of animals: widespread evidence and its implications for bio-gerontology. *Ageing Res Rev* 12:214–225. doi:[10.1016/j.arr.2012.07.004](https://doi.org/10.1016/j.arr.2012.07.004)
- Pardo D, Barbraud C, Authier M, Weimerskirch H (2013) Evidence for an age-dependent influence of environmental variations on a long-lived seabird's life-history traits. *Ecology* 94:208–220. doi:[10.1890/12-0215.1](https://doi.org/10.1890/12-0215.1)
- Péron G, Gimenez O, Charmantier A et al (2010) Age at the onset of senescence in birds and mammals is predicted by early-life performance. *Proc R Soc Lond B* 277:2849–2856. doi:[10.1098/rspb.2010.0530](https://doi.org/10.1098/rspb.2010.0530)
- Pfister CA (1998) Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. *Proc Natl Acad Sci USA* 95:213–218
- Promislow DEL, Harvey PH (1990) Living fast and dying young: a comparative analysis of life-history variation among mammals. *J Zool* 220:417–437. doi:[10.1111/j.1469-7998.1990.tb04316.x](https://doi.org/10.1111/j.1469-7998.1990.tb04316.x)
- Ricklefs RE, Scheuerlein A (2001) Comparison of aging-related mortality among birds and mammals. *Exp Gerontol* 36:845–857. doi:[10.1016/S0531-5565\(00\)00245-X](https://doi.org/10.1016/S0531-5565(00)00245-X)
- Sæther B-E, Bakke Ø (2000) Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* 81:642–653. doi:[10.1890/0012-9658\(2000\)081\[0642:ALHVAC\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[0642:ALHVAC]2.0.CO;2)
- Sæther B-E, Engen S, Møller AP et al (2004) Life-history variation predicts the effects of demographic stochasticity on avian population dynamics. *Am Nat* 164:793–802. doi:[10.1086/425371](https://doi.org/10.1086/425371)
- Sæther B-E, Coulson T, Grøtan V et al (2013) How life history influences population dynamics in fluctuating environments. *Am Nat* 182:743–759. doi:[10.1086/673497](https://doi.org/10.1086/673497)
- Schröder W, von Elsner-Schack I (1985) Correct age determination in chamois. In: Lovari S (ed) *The Biology and management of mountain ungulates*. Croom Helm, London, pp 65–70
- Viallefont A (2011) Capture-recapture smooth estimation of age-specific survival probabilities in animal populations. *J Agric Biol Environ Stat* 16:131–141. doi:[10.1007/s13253-010-0031-9](https://doi.org/10.1007/s13253-010-0031-9)
- Willisch CS, Bieri K, Struch M et al (2013) Climate effects on demographic parameters in an un hunted population of Alpine chamois (*Rupicapra rupicapra*). *J Mammal* 94:173–182. doi:[10.1644/10-MAMM-A-278.1](https://doi.org/10.1644/10-MAMM-A-278.1)