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**Running Head:** age-specific survival of female chamois

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

Josefa Bleu<sup>1\*</sup>, Ivar Herfindal<sup>1</sup>, Anne Loison<sup>2,3</sup>, Anne M.G. Kwak<sup>1,4</sup>, Mathieu Garel<sup>5</sup>, Carole Toïgo<sup>5</sup>, Thomas Rempfler<sup>6</sup>, Flurin Filli<sup>6</sup>, Bernt-Erik Sæther<sup>1</sup>

<sup>1</sup>Department of Biology, Centre for Biodiversity Dynamics, Norwegian University of Sciences and Technology, N-7491 Trondheim, Norway

<sup>2</sup> Université de Savoie ; CNRS ; UMR 5553 Laboratoire d'Écologie Alpine, 73376 Le Bourget du Lac, France

<sup>3</sup> LTER "Zone Atelier Alpes", 38000 Grenoble, France

<sup>4</sup> Radboud University, Institute for Water and Wetland Research, Department of Animal Ecology and Ecophysiology, PO Box 9100, 6500 GL, Nijmegen, Netherlands

<sup>5</sup> Office National de la Chasse et de la Faune Sauvage (ONCFS), ZI Mayencin, 38610 Gières, France

<sup>6</sup> Swiss National Park, Chastè Planta-Wildenberg, CH-7530 Zernez, Switzerland

\* Corresponding author: [josefa.bleu@gmail.com](mailto:josefa.bleu@gmail.com)

Current 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

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<sup>1</sup> Declaration of authorship: 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.

1 *Abstract.* In many species, population dynamics are shaped by age-structured demographic  
2 parameters, such as survival, which can cause age-specific sensitivity to environmental  
3 conditions. Accordingly, we can expect populations with different age-specific survival to be  
4 differently affected by environmental variation. However, this hypothesis is rarely tested at  
5 the intra-specific level. Using capture-mark-recapture models, we quantified age-specific  
6 survival and the extent of annual variations in survival of females of alpine chamois in two  
7 sites. In one population survival was very high ( $> 0.94$  ; Bauges, France) until the onset of  
8 senescence at approximately 7 years old whereas the two other populations (Swiss National  
9 Park, SNP) had a later onset (12 years old) and a lower rate of senescence. Senescence  
10 patterns are therefore not fixed within species. Annual variation in survival was higher in the  
11 Bauges ( $SD = 0.26$ ) compared to the SNP populations ( $SD = 0.20$ ). Also, in each population,  
12 the age classes with the lowest survival also experienced the largest temporal variation, in  
13 accordance with inter-specific comparisons showing a greater impact of environmental  
14 variation on these age classes. The large difference between the populations in age-specific  
15 survival and variation suggests that environmental variation and climate change will affect  
16 these populations differently.

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18 *Key words: age-specific survival, capture-mark-recapture, environmental variability,*

19 *Rupicapra rupicapra, senescence.*

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## INTRODUCTION

22 Demographic parameters of many long-lived species are strongly structured by age (e.g.  
23 Gaillard et al. 2000). This has important implications for population dynamics (Benton et al.  
24 2006; Sæther et al. 2013) through age-specific contribution to the population growth rate  
25 (Coulson et al. 2005). Age-structure has been shown to influence how the population is  
26 affected by harvesting (e.g. Milner et al. 2007) and its response to environmental variation.  
27 For example, the effects of weather on dynamics of wild soay sheep (*Ovis aries*) were  
28 different between populations of equal size but differing in age- and sex-structures (Coulson  
29 et al. 2001). The importance of age-structure in shaping the responses to environmental  
30 changes can be explained by age-specific sensitivity to environmental conditions among age-  
31 classes, resulting in differences in the variation in survival among age-classes. Understanding  
32 these mechanisms is essential in order to predict how climate change will affect populations,  
33 particularly in populations experiencing rapid environmental changes (Hansen et al. 2011;  
34 Engler et al. 2011).

35 In ungulates, prime-aged females have a high survival with low variance (Gaillard et  
36 al. 2000). However, individuals belonging to age-classes with lower survival (young and  
37 senescent individuals) may be more sensitive to environmental variation with a corresponding  
38 higher temporal variation in survival suggesting high environmental stochasticity in these age-  
39 classes. Accordingly, the age at which individuals are in the more vulnerable age classes (i.e.  
40 young or senescent stages) may affect how environmental variation affect population  
41 dynamics (Pfister 1998; Sæther and Bakke 2000; Gaillard and Yoccoz 2003). As the  
42 senescent stage normally is considerably longer than juvenile stage, and senescent individuals  
43 also contribute by reproduction, variation in the characteristics of senescence is of particular  
44 importance for population dynamics: we can expect that the later the onset of senescence (and  
45 hence the longer the prime-age stage) and/or the smaller the rate of senescence, the lower the

46 impact of environmental variation on population dynamics. Senescence has been described in  
47 many wild animals from very diverse taxa (Nussey et al. 2013, but see also Jones et al. 2014).  
48 A large part of the inter-specific variation in senescent rates can be explained by life history  
49 variation along a slow-fast continuum (Jones et al. 2008). However, variations at the intra-  
50 specific level also exist (see below). The evolutionary theories of senescence (antagonistic  
51 pleiotropy theory, disposable soma theory) rely on the fact that selection is weak at late ages  
52 and converge on the idea that there is a trade-off between early performance/somatic  
53 maintenance and late survival (Kirkwood and Austad 2000). In accordance with these  
54 theories, it has been shown that early environmental conditions or investment in reproduction  
55 affected senescence both within populations (Nussey et al. 2007; Péron et al. 2010) and, in a  
56 handful of studies, between populations of the same species (Austad 1993; Bronikowski et al.  
57 2002; Bryant and Reznick 2004). At the intra-specific level, studies comparing survival  
58 patterns and also age-specific variation in this vital rate between populations are rare. The  
59 difficulty is that such studies require long-term studies of marked individuals of known age in  
60 several wild populations of the same species, a requirement which is rarely met.

61         Based on long-term longitudinal datasets and capture-mark-recapture methods in three  
62 populations of the same species, we could estimate age-specific survival patterns and age-  
63 specific inter-annual variation in survival rates in females in three contrasted populations of  
64 an alpine ungulate, the chamois (*Rupicapra rupicapra*). We assessed the among-populations  
65 differences in (1) average survival rates per age-classes, and more specifically senescence  
66 patterns; (2) inter-annual variation in survival rates. This allowed us to examine at the intra-  
67 specific level, whether temporal variation in survival rates may be used as a proxy of the age-  
68 specific sensitivity to environmental stochasticity.

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## MATERIAL AND METHODS

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

### 75 *French study site*

76 Chamois were monitored since the early 1980s in the Game and Wildlife Reserve of the  
77 Bauges massif (45°40'N 6°13'E), in the northern French Alps (e.g. Loison et al. 1994). We  
78 studied the chamois from the Armenaz site (227.4 ha, Table S1), which has a continental  
79 climate with oceanic influence (weather station at 595 m: mean annual temperature =  $9.22 \pm$   
80  $0.46^\circ\text{C}$ , mean annual rainfall =  $1361.8 \pm 210.6$  mm). The area is characterized by sub-alpine  
81 meadows (e.g., *Carex* sp. and *Sesleria caerulea*) with shrublands (e.g. *Rhododendron*  
82 *ferrugineum* and *Vaccinium* sp.), mountain hay meadows, and screes (Duparc et al. 2013). In  
83 this site, chamois have no natural predators and are not in sympatry with other wild ungulates  
84 (Darmon et al. 2014). Chamois are trapped below falling nets baited with salt (May to  
85 September) and are marked with a collar. Between 1991 and 2012, 238 females, aged 1 to 12  
86 years old, were captured (see detailed sample sizes in Table S2). The mean estimated  
87 probability of observation of an individual is 0.70 (SE=0.27) (estimates from model M4).  
88 Individuals that died from non-natural causes (e.g. hunting) were right-censored to estimate  
89 natural survival probabilities (Lebreton et al. 1992) (Table S2).

### 90 *Swiss study sites*

91 In the Swiss national park (SNP, 46°40'N 10°12'E), two populations of chamois are  
92 monitored, one in Val Trupchun (ca. 2 000 ha in the SNP and 4 000 ha in Italy) and one in Il  
93 Fuorn (ca. 5 025 ha in the SNP) (Filli and Suter 2006, Table S1). The SNP has a continental  
94 climate with low annual precipitation (weather station at 1800 m: mean annual temperature =  
95  $0.98 \pm 0.48^\circ\text{C}$ , mean annual rainfall =  $882.5 \text{ mm} \pm 213.2$  mm). Hunting is prohibited and visitors

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

#### 110 *Statistical analyses*

111 We kept the observations between May and December, in order to have similar periods  
112 between the sites and to estimate winter survival (the period of highest mortality for chamois ;  
113 Jonas et al. 2008). We first analyzed the Bauges population and the SNP populations  
114 separately (pooling Il Fuorn and Val Trupchun). Survival estimates were obtained  
115 independently of re-sighting probabilities using capture-mark-recapture (CMR) modeling  
116 based on the open population model of Cormack-Jolly-Seber (Clobert et al. 1987). This model  
117 produces apparent survival estimates resulting from mortality and emigration. We used the  
118 program E-surge (version 1.9.0) to fit models (Choquet et al. 2009). For all populations we  
119 found no transience in the data but a strong trap-happiness (details in ESM). The best model  
120 to account for trap-happiness was a two-state mixture model with transitions between the

121 states (see details in Table S3). From this model, we selected the best model describing the  
122 effect of the year in re-sighting probabilities (Table S4). Finally, we fitted models on the  
123 survival probabilities. We compared models with different age class and/or with a continuous  
124 effect of age (see Table 1 for candidate models). The different models were built from typical  
125 age-classes already described in ungulates: juveniles, yearlings, prime-aged adults (2-7 years  
126 old), old adults (8-12 years old) and senescent individuals (after 12 years old) (Gaillard et al.  
127 2000; Gaillard et al. 2004). We also tested models with a continuous effect of age as  
128 senescence can also be realistically described by a linear decrease of survival with age on a  
129 log scale (Gompertz models) (e.g. Loison et al. 1999; Gaillard et al. 2004). Models were  
130 implemented with a logit link, which has been shown to be a good approximation of the  
131 Gompertz model (Loison et al. 1999; Viallefont 2011). In those models, the rate of senescence  
132 was the slope from the linear function between survival rates and age with a logistic link. For  
133 the SNP populations, we also tested the effect of site on the initial state, transition, re-sighting  
134 and survival probabilities.

135 In a next step, we examined differences between the Bauges and SNP populations by  
136 analyzing all the data together, using the best model structure selected in the separate  
137 analyses. Finally, we examined the variation of survival between years by allowing survival to  
138 vary among years and calculated the age- and population-specific standard deviation (SD) in  
139 survival from the annual survival rates. However, concern have been raised regarding the  
140 comparison of variances from estimates that are limited between 0 and 1 (Morris and Doak  
141 2004). We therefore also calculated scaled variances,  $P_{\max}$ , following Morris and Doak  
142 (2004). Results did not differ qualitatively between estimates of SD and  $P_{\max}$  (Table 3).

143 Model selection was based on AICc (Akaike Information Criterion corrected for small  
144 sample size ; Burnham and Anderson 2002). In the results we report the estimates of survival



145 from the models (back-transformed from the logit scale) and the parametric 95% confidence  
146 interval (CI), unless otherwise noted.

## 147 RESULTS

148 The age-specific survival of the Bauges population was best described with a linear decrease  
149 of survival with age (logit-scale) from 1 years onwards (model M12 in Table 1, AICc =  
150 1660.43, estimates in Table S5). Survival was relatively stable and high until 7 years of age,  
151 when a more pronounced decrease in survival occurred (Figure 1a). In the second best model  
152 ( $\Delta\text{AICc} = 1.73$ ), the linear decrease starts at 2 years old (model M14, Tables 1 and S5). The  
153 best model where age was grouped in classes included the following age-classes: 1-7, 8-12  
154 and > 12 years old ( $\Delta\text{AICc} = 9.28$ , model M4 in Tables 1 and S5, Figure 1a) and was  
155 consistent in term of pattern with the model with a linear trend. The estimates of a classic 4  
156 age-classes model (model M5 in Table 1) are given in Table S5 ( $\Delta\text{AICc} = 11.30$ ).

157 In the SNP populations, two models had almost similar AICc-value and both  
158 supported a senescence starting after age 12. The best model with age grouped to classes had  
159 three age-classes: 0-1 years old, 2-12 years old and > 12 years old (model M9, AICc =  
160 1030.97, Tables 1 and S5, Figure 1b). A model with equal support ( $\Delta\text{AICc} = 0.08$ ) had similar  
161 survival as the previous model for 0-1 and 2-12 years old, but a linear decrease in survival  
162 after age 12 (model M20 in Tables 1 and S5, Figure 1b). Model M5, the second best model  
163 with age-classes ( $\Delta\text{AICc} = 1.94$ , Table 1), considered two distinct age-classes for prime-aged  
164 females (2-7 and 8-12 years old) (Table S5). All the highest ranked models grouped 0 and 1  
165 years old females together, as supported from the similar survival estimates shown in Figure  
166 1B (and model M6 in Table S5).

167 The two populations in the SNP were similar in terms of survival probabilities (Table  
168 S6 and Figure S1). Indeed, while the model with lowest AICc included an additive effect of  
169 site, suggesting overall higher survival in Il Fuorn, the  $\Delta\text{AICc}$  with the model with no effect

170 of site was only 1.21 (Table S6). We therefore pooled these two populations in further  
171 analyses.

172 We then examined further the differences in survival pattern and corresponding  
173 variation between the Bauges and SNP populations. As a base model, we used the four age-  
174 classes model (model M5 in Table 1) which was the most parsimonious model when  
175 considering both study areas simultaneously. Age-specific survival differed between the SNP  
176 and Bauges populations (Table 2,  $\Delta\text{AICc}$  to other models  $\geq 3.88$ ). The survival estimates  
177 from this model confirmed the differences observed on Figure 1 A and B: survival is lower in  
178 the Bauges population than in the SNP populations except for the first age-class (Figure 1c).  
179 In adults, the difference is largest for the 8-12 years old females (Figure 1c).

180 Finally, we compared the annual variation in age-specific survival in each population  
181 by including temporal (i.e. annual) variation in the CMR models. We allowed survival to vary  
182 with year differently for each population and each age-class (Figures S2 and S3). Overall,  
183 survival is more variable in the Bauges population than in the SNP population ( $\text{SD (Bauges)} =$   
184  $0.2638$  vs.  $\text{SD (SNP)} = 0.2017$ ), even if we account for the overall lower survival in the  
185 Bauges population ( $\text{P}_{\text{max}} (\text{Bauges}) = 0.4238$  vs.  $\text{P}_{\text{max}} (\text{SNP}) = 0.3297$ ). In both populations, the  
186 females from the age-class with the lowest survival (young and senescent females) showed  
187 also the highest variation of their survival ( $\text{SD}$  and  $\text{P}_{\text{max}}$ , Table 3), with an effect more  
188 pronounced for old females in the Bauges and for young females in SNP. Conversely, the  
189 variation of survival of females with the highest survival ( $> 0.94$ : age-class 2-7 in Bauges and  
190 2-7 and 8-12 in SNP) is low ( $\text{SD} < 0.093$  and  $\text{P}_{\text{max}} < 0.155$ ).

## 191 DISCUSSION

192 Thanks to similar monitoring of individuals of known age for  $>16$  years in 3  
193 populations of the same species, we found evidence of clear differences in age at occurrence  
194 and rate of senescence at the intra-specific level, along with differences in age-specific annual

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

212         Since age-specific survival patterns differed between the two study sites, we expected  
213 differences in annual variation in survival. This can occur because environmental variability  
214 (e.g. changes in weather conditions, habitat quality, population density) have a larger impact  
215 on individuals of lower quality, i.e. that have a lower survival (e.g. for climate effects,  
216 Willisch et al. 2013). Moreover, it has been suggested that in prime-aged female ungulates  
217 survival is partly buffered against environmental variations through an adjustment of the  
218 reproductive effort (Gaillard et al. 2000; Gaillard and Yoccoz 2003). In agreement with the  
219 interspecific comparisons of Gaillard and Yoccoz (2003), we supported, at the intra-specific

220 level, that the lower the overall survival (in the Bauges vs the SNP population) during prime-  
221 age, the higher annual variation in survival. This can again reflect a faster life-history strategy  
222 (Sæther et al. 2004) and/or more variable environmental conditions in the Bauges. A shorter  
223 length of the prime-age stage and longer senescence stage in the Bauges population suggest  
224 that this population may be more vulnerable to environmental variation such as climate  
225 change, compared to the SNP population where females spend more years in a stage with high  
226 survival and low variation.

227 This study exemplifies that age, a factor already known to affect demographic rates,  
228 also relates to the variability in survival, and thus is an important factor to understand the  
229 sensitivity to environmental changes (Pardo et al. 2013). Further studies on differences in age-  
230 specific survival and variation in survival between populations of the same species could be  
231 important to understand population-specific impact of environmental changes (e.g. Grøtan et  
232 al. 2008).

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242 **Conflict of interest:** The authors declare that they have no conflict of interest

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

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

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**Table 1.** Models describing age-specific survival of female chamois in Les Bauges and the Swiss National Park (SNP). The age pattern was modeled either with age grouped in classes, as a continuous relationship (linear and quadratic functions), or as a combination of classes and continuous relationships.

ID	Model types	Juvenile*	Young	Adult1	Adult2	old†	# age classes Bauges / SNP	Bauges		SNP	
								# parameters	AICc	# 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	<b>12</b>	<b>1669.71<sup>1</sup></b>	12	1040.17
M5	Age-class		1 / 0-1	2-7	8-12	>12	4/4	13	1671.73	<b>12</b>	<b>1032.91<sup>2</sup></b>
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	<b>11</b>	<b>1030.97<sup>3</sup></b>
M10	Linear trend					0	--	--	--	10	1054.41
M11	Quadratic trend					0	--	--	--	11	1047.93
M12	(Age class +) linear trend	0				1	--/1	<b>11</b>	<b>1660.43<sup>4</sup></b>	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	<b>12</b>	<b>1662.16<sup>5</sup></b>	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	<b>12</b>	<b>1031.05<sup>6</sup></b>

\* this age class is only relevant for the Swiss populations, because we did not have captures at 0 years old in the French population.

† the old age class or the age of the onset of the continuous negative effect of age for continuous models (linear or quadratic trends).

<sup>1</sup> deviance = 1645.42 ; <sup>2</sup> deviance = 1008.46 ; <sup>3</sup> deviance = 1008.59 ; <sup>4</sup> deviance = 1638.18 ; <sup>5</sup> deviance = 1637.86 ; <sup>6</sup> deviance = 1006.60

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

Model	k	Deviance	AICc	$\Delta$ AICc
<b>Step 1</b>				
<b>Effect of site on transition</b>	<b>19</b>	<b>2681.64</b>	<b>2720.07</b>	<b>0</b>
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
<b>Step 2</b>				
<b>Different effect of site in each age-class</b>	<b>23</b>	<b>2655.87</b>	<b>2702.49</b>	<b>0</b>
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

**Table 3.** Temporal variance in survival in the different sites and age-classes. The table shows estimated mean and standard deviation (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  $SD^2/[mean*(1-mean)]$  (Morris and Doak 2004; Altwegg et al. 2007).

Site	Age-class	Mean	SD	$P_{\max}$
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

370 **Figure legends**

371

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

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