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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

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¹ 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.

17

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

19 *Rupicapra rupicapra, senescence.*

20

INTRODUCTION

21

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.

69

70

71

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°C , mean annual rainfall = 1361.8 ± 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 ΔAICc 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, ΔAICc to other models ≥ 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 ($P_{\text{max}} (\text{Bauges}) = 0.4238$ vs. $P_{\text{max}} (\text{SNP}) = 0.3297$). 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 (SD and P_{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 $P_{\text{max}} < 0.155$).

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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240 SUMMARY STATEMENT

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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 | 12 | 1669.71¹ | 12 | 1040.17 |
| M5 | Age-class | | 1 / 0-1 | 2-7 | 8-12 | >12 | 4/4 | 13 | 1671.73 | 12 | 1032.91² |
| 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 | 1030.97³ |
| M10 | Linear trend | | | | | 0 | -- | -- | -- | 10 | 1054.41 |
| M11 | Quadratic trend | | | | | 0 | -- | -- | -- | 11 | 1047.93 |
| M12 | (Age class +) linear trend | 0 | | | | 1 | --/1 | 11 | 1660.43⁴ | 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 | 1662.16⁵ | 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 | 1031.05⁶ |

* 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).

¹ deviance = 1645.42 ; ² deviance = 1008.46 ; ³ deviance = 1008.59 ; ⁴ deviance = 1638.18 ; ⁵ deviance = 1637.86 ; ⁶ 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 | Δ AICc |
|---|-----------|----------------|----------------|---------------|
| 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 |

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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