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1 Year-round sexual segregation in the isard, a nearly
2 monomorphic polygynous herbivore

3
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20

1 Year-round sexual segregation in the Pyrenean chamois, a nearly 2 monomorphic polygynous herbivore

3
4 Running head: sexual segregation in the Pyrenean chamois

5
6 ABSTRACT: Adult females and males live apart outside the mating period in many social vertebrates, but the
7 causes of this phenomenon remain a matter of debate. Current prevailing hypotheses predict no sexual
8 segregation outside the early period of maternal care in nearly monomorphic species such as the Pyrenean
9 chamois (*Rupicapra pyrenaica*). We examined sexual segregation in a population of the species, using data
10 collected over 143 consecutive months on groups' location and composition, and extending statistical procedures
11 introduced by Conrath (1998b) and Bonenfant et al. (2007). In addition, we analysed the social interactions
12 recorded between group members. As expected, habitat segregation was low throughout the year, with a
13 maximum during the early lactation period. However, social and spatial segregation was consistently high,
14 contradicting the predictions of the current prevailing hypotheses, while suggesting social causes were
15 predominant. The scarcity of social interactions outside the mating season makes unlikely the hypothesis that
16 males segregate to improve their reproductive success. We rather suspect that higher social affinities within than
17 between the two sexes are at work. However, this hypothesis alone is probably insufficient to account for spatial
18 segregation. Our results should revive the debate regarding the causes of sexual segregation.

19
20 Keywords

21 Caprini; Grouping patterns; Habitat use; Mountain ungulates; Spatial distribution

22 23 **1. Introduction**

24
25 'I am not convinced that the answers to the underlying reasons for sexual segregation will
26 be achieved by focusing on mechanisms of forage intake and digestion. By definition this
27 approach will fail to explain sexual segregation in species that are not strongly dimorphic...
28 and cannot, therefore, increase our understanding of a more universal explanation' (Main,

29 1998: 1414). Indeed, sexual segregation has been studied mainly in sexually dimorphic
30 species, and most explanations suggest that it results from sexual differences in habitat use
31 due to difference in body size. As coined by the above citation, when sexual segregation
32 occurs in monomorphic species, it challenges the hypotheses that rely on dimorphism in body
33 mass.

34 Sexual segregation is manifested typically when adult males and females live separated in
35 space outside the mating period (Bowyer, 2004). It spans a number of vertebrate taxa (see
36 Bleich et al., 1997; Ruckstuhl and Neuhaus, 2005; Wearmouth and Sims, 2008), particularly
37 in sexually dimorphic ruminants (Main & Coblentz, 1990; Bon & Campan, 1996). Most
38 authors consider that sexual segregation is driven by habitat segregation, i.e., the differential
39 use of ecological resources by the two sexes. It was also proposed that social segregation, i.e.,
40 the propensity for each sex to associate with same-sex conspecifics, may contribute to sexual
41 segregation. Multiple environmental factors are suspected of causing habitat segregation
42 whereas behavioural factors are invoked to explain social segregation (Bon, 1992; Miquelle et
43 al., 1992; Bon and Campan, 1996; Bleich et al., 1997; Conradt, 1999, 2005; Mysterud, 2000;
44 Ruckstuhl, 2007).

45 The main current hypotheses explaining habitat segregation rely on: (1) allometry in
46 metabolic requirement and efficiency of food digestion allowing larger-bodied individuals to
47 feed on less nutritive/more fibrous forage ('gastro-centric hypothesis' GCH, derived from the
48 Jarman-Bell principle; Illius and Gordon, 1987; Gordon and Illius, 1996); (2) allometry in rate
49 of energy intake and body surface, which would lead larger individuals to be more sensitive to
50 microclimatic conditions ('weather sensitivity hypothesis' WSH; Conradt et al., 2000; Loe et
51 al., 2006; Mason et al., 2017; Bourgoïn et al., 2018); (3) exclusive involvement of females in
52 parental care and offspring security ('reproductive strategy-predation risk hypothesis' RSH);
53 (4) higher risk of predation for smaller-bodied individuals, which would use safer habitats

54 independently of their reproductive status ('sexual dimorphism-predation risk hypothesis',
55 also referred to as 'predation hypothesis' PH by Biggerstaff et al., 2017; Main and Coblentz,
56 1990; Miquelle et al., 1992; Bleich et al., 1997; Ruckstuhl and Neuhaus, 2000; Michaud,
57 2005; Croft et al., 2006; Grignolio et al., 2007; Richardson and Weckerly, 2007; Wearmouth
58 and Sims, 2008; Husek et al., 2015).

59 Social segregation might also result from body-size dimorphism. According to the 'activity
60 budget hypothesis' (ABH; Conradt, 1998a; Ruckstuhl, 1998, 2007, see also references in Bon
61 and Campan, 1996: 145), females and males would differ in time spent foraging and moving
62 versus resting and ruminating due to allometry in energy needs. The difference in activity
63 budget and resulting lack in activity synchrony would make mixed-sex groups especially
64 unstable and more unlikely than same-sex groups.

65 However, according to several other hypotheses, social segregation would rather have
66 social causes, either at the ultimate level (Main et al., 1996), at proximate level or both (see
67 MacFarlane and Coulson, 2007, 2009; Ruckstuhl, 2007). Main et al. (1996) suggested that
68 social segregation outside the rut allow males to practice fighting skills important in sexual
69 contest during the rut (Geist and Petocz, 1977; Whiteside et al., 2017) and females to learn the
70 location of feeding resources and birth areas ('social factors hypothesis' SFH). Other authors
71 hypothesized that social segregation results from (1) sexual differences in social behaviour
72 and affinity for same-sex conspecifics ('social affinity hypothesis' SAH, also referred to as
73 'social preference hypothesis'; Bon, 1991; Bon and Campan, 1996; Cransac et al., 1998;
74 Ruckstuhl and Neuhaus, 2000; Pérez-Barbería et al., 2005; Guilhem et al., 2006; MacFarlane
75 and Coulson, 2009), (2) females avoiding agonistic interactions addressed by males and
76 subsequent agonistic interactions among females ('female avoidance of males hypothesis'
77 FAMH; Nievergelt, 1967; Grubb, 1974; Clutton-Brock et al., 1982: p. 190; Ozoga and
78 Verme, 1985; Hass and Jenni, 1991; Lagory et al., 1991; Le Pendu et al., 2000; Weckerly et

79 al., 2001, 2004; Peterson and Weckerly, 2017), (3) males avoiding females to prevent
80 aggressive male-male interactions linked to the presence of the opposite sex ('male avoidance
81 of females' MAFH; Morgantini and Hudson, 1981; Prins, 1989). In order to reduce male
82 sexual harassment (SHH), it was also hypothesized that females would modify their
83 movement and association with males according to their reproductive status ('sexual
84 harassment hypothesis' SHH; Sundaresan et al., 2007). It is worth noting that sexual
85 dimorphism in body mass is not a prerequisite for sexual segregation to occur under these
86 social hypotheses.

87 The bulk of the studies dedicated to sexual segregation concentrates on large and sexually
88 dimorphic species (Bowyer, 2004; du Toit, 2005; MacFarlane and Coulson, 2005) and the
89 extent to which the degree of sexual dimorphism in body mass/size plays a key role in
90 explaining segregation is seldom addressed (but see Ruckstuhl and Neuhaus, 2002;
91 Ruckstuhl, 2007; Garnick et al., 2014). Mysterud (2000) reported a positive relationship
92 between ecological segregation and body-size dimorphism for browser species but not for
93 intermediate and grazer species. Illius and Gordon (1987) predicted a sexual segregation in
94 grazers when males are at least 20% larger than females, in periods of food restriction (see
95 Ruckstuhl and Neuhaus, 2002).

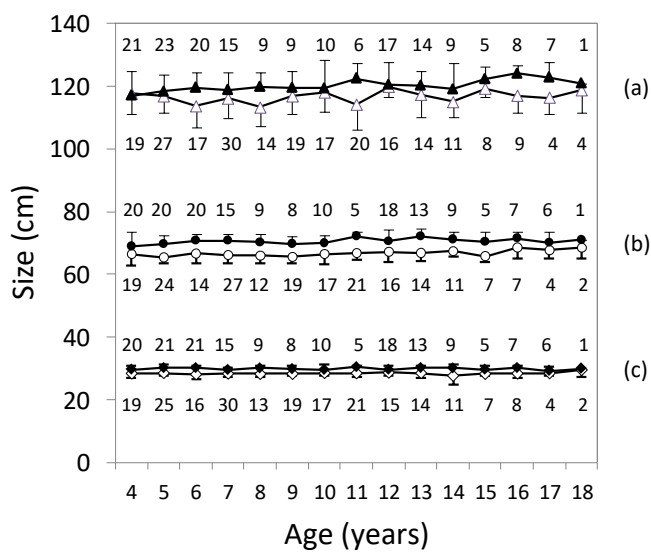
96 Monomorphic species are appropriate models to test existing hypotheses regarding the
97 origin of sexual segregation outside the rut period (Lewis et al., 2002; Ruckstuhl and
98 Neuhaus, 2002; Sims, 2005). According to the RSH, irrespective of sexual dimorphism in
99 body mass and because parental care is exclusive to females in ungulates, habitat segregation
100 would peak when lactating females restrict themselves into areas that limit the risk of
101 predation on their offspring. No ecological and spatial segregation would occur past the
102 weaning period according to the GCH, WSH and PH. The ABH predicts that when both sexes
103 are similar in body mass, outside the lactation period, they should associate freely (Ruckstuhl,

104 1999; Barboza and Bowyer, 2000; Neuhaus and Ruckstuhl, 2002; Ruckstuhl and Neuhaus,
105 2000, 2002, 2009; Lewis et al., 2002; Staniland, 2005; Wearmouth and Sims, 2008: p. 143).
106 The SHH is valid only during the period of sexual activity and then restricted to the period of
107 rut which span a short period of time in temperate latitude and mountain habitat. When
108 species adopt a polygynous mating system, the SFH suggests that males would benefit from
109 sparring interactions in all-male groups outside the rut (Ruckstuhl and Neuhaus, 2000). Such
110 interactions, if any, would occur during spring and summer when resources are plentiful and
111 permit energetically costly activities. The FAMH predicts that when males are dominant and
112 address agonistic acts to females, these latter would avoid males and engage in intra-sex
113 agonistic interactions more frequently than in same-sex groups.

114 The two species of the *Rupicapra* genus, the Alpine chamois (*R. rupicapra*) and the isard
115 or Pyrenean chamois (*R. pyrenaica*), are polygynous and have well-defined mating and birth
116 seasons (Krämer, 1969; Corlatti et al., 2013). In contrast to what prevails in many other
117 Caprini and despite geographical variation in body size, they are nearly monomorphic in
118 many characters (Pépin et al., 1996; Bocci et al., 2010; Pérez-Barbería et al., 2010; Ferreti et
119 al., 2014; Fig. 1) with both sexes similar in mass, except in summer-early autumn when males
120 are heavier than females (Fig. 2; Crampe et al., 1997; Loison et al., 1999; Pérez-Barbería and
121 Gordon, 2000; Bassano et al., 2003; Garel et al., 2009; Pérez-Barbería et al., 2010; Rughetti
122 and Festa-Bianchet, 2011). *Rupicapra* sp. are thus a valuable model to work out the origin of
123 sexual segregation (Ruckstuhl and Neuhaus, 2002).

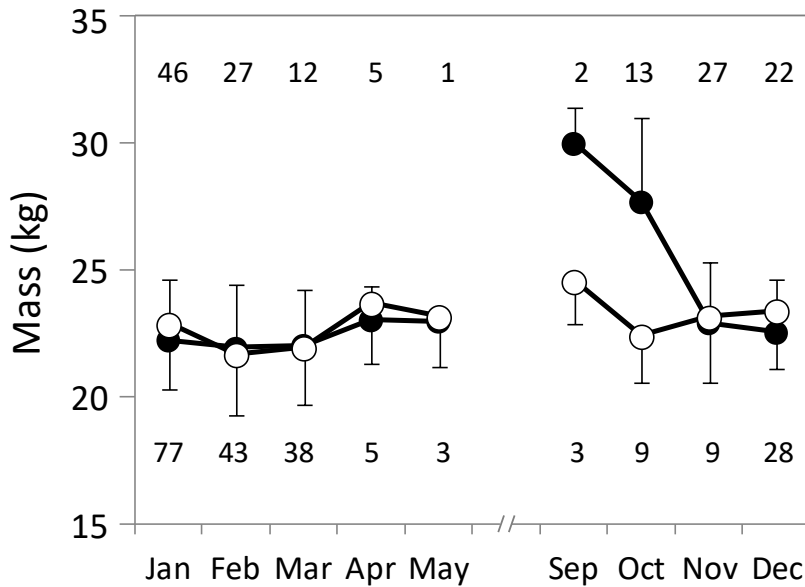
124 Like many other Caprini, chamois are mountain-dwelling intermediate feeders (Hofmann,
125 1989; Garcia-Gonzalez and Cuartas, 1996) that live in open-membership groups (Pépin and
126 Gerard, 2008). Sexual segregation is known to occur (Berducou and Bousses, 1985; Gerard
127 and Richard-Hansen, 1992; Bonenfant et al., 2007), peaking in spring and summer (Shank,
128 1985) and relaxed in early winter (Gerard and Richard-Hansen, 1992; Pérez-Barbería and

129 Nores, 1994; Herrero et al., 2002; Bonenfant et al., 2007), coinciding with the period of
 130 parental care and rut, respectively. However, its intensity may also vary according to
 131 populations. Over the whole annual cycle, mixed-sex groups have been reported to form 20-
 132 25% of the observed groups (lone animals included) in some Pyrenean chamois populations
 133 (Pérez-Barbería and Nores, 1994: Table 2; Herrero et al., 2002: Table 3; Dalmau et al., 2013:
 134 Table 1) but 8-12% in others (Richard-Hansen et al., 1992).
 135



136
 137 **Fig. 1.** Mean body length (a), shoulder height (b) and metatarsus length (c) of Pyrenean
 138 chamois live-trapped in the study area as a function of age and sex (open symbols: females,
 139 filled symbols: males). Error bars represent standard deviation (SD); for the sake of clarity,
 140 only positive and negative SD values have been drawn for males and females, respectively.
 141 Numbers above and below the curves are sample sizes for males and females, respectively.
 142 Grand means: (a) males 119.7 cm, females 116.5 cm; ratio 1.03; (b) males 70.4 cm, females
 143 66.5 cm; ratio 1.06; (c) males 29.9 cm, females 28.4 cm; ratio 1.05.

144



145

146 **Fig. 2.** Mean body mass of Pyrenean chamois females (open symbols) and males (filled
 147 symbols) >3 years old, live-trapped in the study area (Crampe et al., 2007). Only positive and
 148 negative standard deviations (error bars, with sample sizes above and below) are drawn for
 149 males and females respectively for the sake of clarity. Grand means (males vs females); Sep-
 150 Oct: 28.0 vs 23.0 kg (ratio 1.22); Nov-May: 22.4 vs 22.6 kg (ratio 0.99).

151

152 In this paper, we investigate the annual variation of social, spatial and habitat components of
 153 segregation and its inter-annual pattern using a 12 consecutive year survey of a Pyrenean
 154 chamois population. We propose an original statistical method derived from the ‘sexual
 155 segregation and aggregation statistic’ which permits controlling for habitat, spatial and social
 156 components in the degree of segregation. A modified version of the segregation coefficient
 157 (Conradt, 1998b) allows a comparison with former studies. The rates of social interactions
 158 between individuals of the same and of opposite sex were calculated to test social hypotheses.
 159 We were able to test the WSH, RSH, PH, SFH, FAMH, MAFH, SHH. We discuss the GSH,
 160 ABH, and SAH considering the quasi-monomorphism of the studied species and the observed
 161 patterns of the different components of sexual segregation.

162

163 **2. Material and Methods**

164

165 *2.1. Study area and population*

166

167 The study was conducted in ‘Clot-Cayan’, a South-facing slope of 355 hectares situated in
168 the Marcadau valley (42°51' N, 0°10' W) within the Pyrénées National Park (PNP), France.
169 Lower elevation follows the valley bottom, ranging from 1,500 to 1,620 m asl. Higher
170 elevation corresponds to a 3.5 km-long ridge and ranges between 2,150 and 2,428 m asl.
171 Climate is hemiboreal to boreal according to elevation (‘Dfb’ to ‘Dfc’ in Köppen’s
172 classification; Peel et al., 2007), with mean annual snowfall of ca. 6 m at 1,850 m. Below
173 2,000 m in elevation, the area is a mosaic of grassland, coniferous woodland and alpine
174 heathland, interspersed with screes and cliffs. Above 2,000 m, trees and screes become rare
175 and the slope is covered mainly by high-elevation grassland, along with some alpine heaths
176 and cliffs.

177 The Pyrenean chamois population has been free from any harvest since 1956 (Crampe et
178 al., 2007). The individuals are wintering in Clot-Cayan from November to April, as the sun-
179 facing slopes afford snow-free foraging areas during mild periods in winter. At this season,
180 population density can reach 80 animals/km². From May to October, about half of the
181 individuals emigrate from the study area, extending the range occupied by the population to
182 ca. 100 km² (Crampe et al., 2007). Births generally occur mostly from mid-May to early June
183 with a peak during the 3rd week of May (Richard-Hansen and Campan, 1992; Ruckstuhl and
184 Ingold, 1994; Pépin et al., 1997). The rut, as defined by the frequency of courtship behaviour,
185 extends from mid-October to late December. No large predators were present, but golden

186 eagle (*Aquila chrysaetos*) and red fox (*Vulpes vulpes*) occasionally killed neonates or adults
187 hampered by deep snowpack (JPC, personal observation).

188

189 2.2. Data collection

190

191 Data were collected by visual observation by JPC from August 1997 to June 2009 (143
192 consecutive months) along standard transects and at vantage points, using 10 x 40 binoculars
193 and a 30 x 75 binocular spotting scope. Individuals were considered to belong to the same
194 group when at a distance < 50 m apart (Pérez-Barbería and Nores, 1994; Pépin and Gerard,
195 2008). The location of every group sighted (solitary individuals included) was plotted on a
196 square grid of 1,167 cells overlaying a panoramic photograph of the area (Crampe et al.,
197 2007). Following Berducou and Bousses (1985), animals were assigned to four age-sex
198 classes according to morphological criteria, i.e., kids (< 1 year old; small body size, horns
199 absent or very short), yearlings (≥ 1 and < 2 years old; larger body size, horns not higher than
200 ears), adult males and females (≥ 2 years old; horns higher than ears in both sexes, more
201 curved at the extremity and thicker in males than females). Pyrenean chamois groups often
202 fuse and split up in the course of the day (Pépin and Gerard, 2008), and successive field
203 surveys were separated by at least two days. Therefore, the data collected on group size and
204 composition were considered as independent.

205 During the field surveys, the interactions occurring within any sighted group were recorded
206 using an instantaneous recording method. On the basis of the repertoire given by Lovari
207 (1985), these interactions were assigned to four categories: mild aggression (threat, side
208 display), severe aggression (butt, hook, chase), play-like behaviour (short run, hop), and
209 sexual behaviour (courtship, copulation). When a given individual addressed a series of
210 different acts to the same group member, only the first act of the series was taken into

211 account. When the individual interacted with a new member in a short period of time in the
212 same spotted group, the interaction was registered as a novel occurrence.

213

214 2.3. Habitats and patch-based polygons

215

216 The grid used to locate the animals was projected on a digitised vegetation map established by
217 the cartography service of the PNP within the framework of the NATURA 2000 European
218 network. This map was based upon field records and used the CORINE Biotope typology as a
219 reference. We simplified the typology to eleven habitat types for the present study: (1) cliff;
220 (2) scree, mainly found below 2,000 m and generally unconnected with any cliff; (3) alpine
221 heath, dominated by Ericaceae; (4) rocky alpine heath, similar to the previous habitat but
222 interspersed with rocky outcrops; (5) high-elevation grassland found above 2,000 m and
223 composed of various acidophilous grasses and forbs including Pyrenees' fescue (*Festuca*
224 *eskia*) and alpine clover (*Trifolium alpinum*); (6) mid-elevation grassland present below 2,000
225 m and dominated by sheep's fescue (*Festuca ovina*), tor-grass (*Brachypodium pinnatum*) and
226 brome (*Bromus erectus*); (7) rocky mid-elevation grassland, similar to the previous habitat but
227 interspersed with rocky outcrops; (8) low-elevation grassland found below 1,700m and
228 dominated by mat-grass (*Nardus stricta*); (9) wetland located below 1,650 m; (10) mountain
229 pine (*Pinus uncinata*) and (11) scots pine (*Pinus sylvestris*) forests, typically found above and
230 below 1,750 m, respectively.

231 The 11 habitat types made up a set of 98 patches in the study area. In order to assess spatial
232 segregation, six patches covering 12-60 ha in surface area were divided into smaller units (\leq
233 10 ha). Then, we obtained a set of 114 patch-based homogeneous polygons (mean surface
234 area: 3.12 ha; range: 0.18–8.83 ha) as regards habitat type and to which groups and
235 individuals were assigned.

236

237 *2.4. Testing for social segregation*

238

239 We tested for social segregation, extending the procedure proposed by Bonenfant et al.
240 (2007). For a period where the population sex ratio and grouping patterns can be considered
241 as stationary, these authors suggest using the ‘sexual segregation and aggregation statistic’

242
$$SSAS = \chi^2 / N, \quad (1)$$

243

244 where χ^2 is the Pearson’s independence chi-square calculated on the numbers of adult males
245 and females in the groups (including at least, and possibly reduced to, one adult) and N is the
246 total number of adults. The statistic varies from 0 when the sex ratio within each group is
247 identical to the sex ratio in the whole sample, to 1 when mixed-sex groups are never found. If
248 all the groups were large in size, the calculated Pearson’s χ^2 would follow a standard χ^2
249 distribution under the (null) hypothesis that individuals associate independently of their sex.
250 However, as small-sized groups are common, Bonenfant et al. (2007) recommend computing
251 the 95% confidence interval (CI) of SSAS expected under the null hypothesis of sex-
252 independent association, by performing random permutations of the sexes of the sighted
253 adults. An observed value of SSAS above or below the 95% CI then leads either to the
254 conclusion that the sexes socially segregated or that they aggregated more than expected by
255 chance, respectively.

256 In order to check that the null hypothesis was not rejected primarily because the sex ratio
257 differed between the subsample of adults observed isolated (or only with kids and/or
258 yearlings) and the subsample of adults observed with other adults, SSAS was calculated on all
259 the sampled groups including at least (and possibly reduced to) one adult, but also on the
260 groups including at least two adults. Moreover, we expected a seasonal variation of the

261 grouping patterns, and population sex ratio fluctuated over the 12 study years. *SSAS* was thus
 262 computed for each month i of the annual cycle as

$$263 \quad SSAS_i = \frac{\sum_{j=1}^{12} \chi_{ij}^2}{\sum_{j=1}^{12} N_{ij}} \quad (2)$$

264 where χ_{ij}^2 is the Pearson's independence chi-square and N_{ij} the total number of adults
 265 sighted for month i and year j . Furthermore, the CIs of the expected values of $SSAS_i$ were
 266 computed performing 10,000 random permutations of the sexes within each month i and year
 267 i . In order to obtain an overall 95% CI for the 12 months of the year, CI was fixed at $1 -$
 268 $0.05/12 \approx 99.6\%$ for each month (Bonferroni correction).

269 This first procedure tested for sexual segregation on the basis of group composition.
 270 However, it did not test whether social segregation was a mere consequence of sex-related
 271 differences in habitat use (habitat segregation) or space use (spatial segregation). Thus we
 272 computed two additional 95% CI, performing the 10,000 random permutations of the sexes of
 273 month i and year j inside each habitat and inside each patch-based polygon, respectively.

274

275 *2.5. Testing for habitat and spatial segregation*

276

277 Following Ficetola et al. (2013), we also used *SSAS* to test for habitat and spatial
 278 segregation. Accordingly, $SSAS_i$ (Eq. 2) was computed using the numbers of adult males and
 279 females sighted per habitat (instead of their numbers per group), then their numbers per patch-
 280 based polygon. As for social segregation, expected 95% CIs were obtained by permuting
 281 randomly the sexes of the sighted adults ($N = 10,000$ replicates). To investigate whether
 282 spatial segregation was a mere consequence of habitat segregation, the randomization

283 procedure was further performed with permutation of the sexes within each month, year and
 284 habitat.

285

286 2.6. Decomposition of SSAS computed on habitats

287

288 When applied to the number of males and females sighted per habitat, $SSAS_i$ (Eq. 2) is

289 based upon the sum of independence χ^2 , each of which is in turn a sum of terms

290 corresponding to the different habitats. We used this peculiarity to calculate the contribution

291 of each habitat type to the computed values of $SSAS_i$, and thus identify the habitats that

292 primarily contributed to habitat segregation (see Appendix S1).

293

294 2.7. Seasonal variation of the degree of sexual segregation

295

296 Bonenfant et al. (2007) stressed that $SSAS$ is not a measure of sexual segregation or

297 aggregation. Accordingly, we quantified the degree of the social, spatial and habitat

298 segregation using a slightly modified version of the segregation coefficient SC proposed by

299 Conradt (1998b), i.e.,

$$300 \quad SC = 1 - \frac{m + f - 1}{mf} \sum_{k=1}^{K} \frac{m_k f_k}{m_k + f_k - 1} \quad (3)$$

301 where m_k and f_k are the numbers of adult males and females in the k^{th} group (or patch-based

302 polygon, or habitat), and M and F are the total numbers of adult males and females in the K

303 sampled groups (or patch-based polygons or habitats). Because of its definition (Eq. 3), SC

304 must be calculated, discarding the groups (polygons or habitats) that include a single adult. Its

305 expected value is 0 when males and females aggregate (or use space or habitats) randomly

306 (Bonenfant et al., 2007: Appendix B). It takes negative values $\in [-1, 0[$ when males and
307 females aggregate more than expected at random, and positive values in the case of sexual
308 segregation, reaching the maximum of +1 when the sexes never occur in the same groups
309 (polygons or habitats; Conradt, 1998b).

310 SC was computed for each of the 143 study months, on the numbers of adult males and
311 females sighted in the sampled groups (SC_{social}), in the patch-based polygons (SC_{spatial}) and
312 in the different habitats (SC_{habitat}). Because in each case the SC values constituted a time
313 series, the monthly variation of SC in the course of the annual cycle was tested as follows.
314 First, we computed the moving average of SC over the 143 study months, with a symmetric
315 window of 13 months, giving a weight of $\frac{1}{2}$ for the first and 13th month and a weight of one
316 for the others (see Fig. S1). We then subtracted this moving average from the time series to
317 obtain a detrended time series. Finally, we performed an ANOVA to test for the effect of the
318 month on the detrended value of SC , and checked that no temporal autocorrelation remained
319 among residuals by using the Ljung-Box test with a lag of 12 months (the test being
320 considered as not significant for $P > 0.10$). In the event of significant effect of the month, we
321 further checked that the detrended value of SC consistently reached its yearly minimum
322 between October and December (i.e., during the rutting months), performing a one-tailed
323 binomial test with a probability of $3/12 = 0.25$. Similarly, we tested whether the yearly
324 maximum of the detrended value of SC consistently occurred between May and July (birth
325 and early lactation periods) rather than during the six other non-rutting months, performing a
326 one-tailed binomial test with a probability of $3/9 = 0.33$.

327

328 *2.8. Analysis of interactions*

329

330 We estimated the overall initiation rate of interactions between males outside the rutting
331 months, selecting the sighted groups that included at least two males, then fitting the
332 generalised linear model (family: Poisson; link function: log)

333

$$334 I_{mm} \sim \text{offset}(\log(m)) + 1$$

335

336 where I_{mm} is the number of interactions between males recorded in the group, and m the
337 number of males in the group. Because of the offset and the log link, the estimate obtained
338 corresponds to the initiation rate per male. The same procedure of data selection and the same
339 generalised linear model were used for estimating the overall initiation rates of interactions
340 between females, and between males and females.

341 In order to analyse the effects of group size, group composition and month on the initiation
342 rate of mild aggressions between males outside the rut, we selected the sighted groups that
343 included at least two males, then fitted the generalised linear model (family: Poisson; link
344 function: log)

345

$$346 MA_{mm} \sim \text{offset}(\log(m)) + \log(\log(N)) + \log(pm) + \text{female} + \text{month}$$

347

348 where the dependent variable MA_{mm} is the number of mild aggressions between males
349 recorded in the group. In this model, N is group size (kids and yearlings included), a variable
350 that influences the number of immediate neighbours of the mean individual, especially when
351 group size is small, hence the transformation in $\log(\log(N))$. Furthermore, the variable $pm =$
352 $(m-1)/(N-1)$ is the expected proportion of males among the neighbours of any given male in

353 the group. Finally, *female* is a binary variable indicating whether at least one female was
354 present in the group, and *month*, a categorical variable indicating the month of observation.

355 The same procedures of data selection and generalised linear model were used for the
356 initiation rate of severe aggressions between males, and the initiation rates of mild and severe
357 aggressions between females. The models were fitted using maximum likelihood, and the
358 effect of the explanatory variables was tested using the Deviance (χ^2) test.

359 Finally, we used Monte Carlo simulations (Manly, 1997) to test whether males performing
360 severe aggressions in mixed-sex groups were more likely to interact with a male than a
361 female. Each elementary simulation consisted of drawing at random a recipient among the
362 adult members of each mixed-sex group including at least two males and in which a male was
363 observed performing a severe aggression. The result retained was the total number of males
364 among the recipients. The simulation was performed 9,999 times, which gave us 9,999
365 numbers of males under the null hypothesis that none of the two sexes was a preferred
366 recipient. The 9,999 numbers obtained and the number observed were then ranked together in
367 decreasing order, and we finally estimated the probability of obtaining a number of males
368 higher than or equal to that observed under the null hypothesis (one-tailed *P*-value) as $P =$
369 $r/10,000$, where r is the rank of the observed number.

370 Monte Carlo simulations were made using Excel software. All the other statistical
371 analyses, including those described in the previous sections, were performed using R 3.2.1
372 software (R core team, 2015).

373

374 **3. Results**

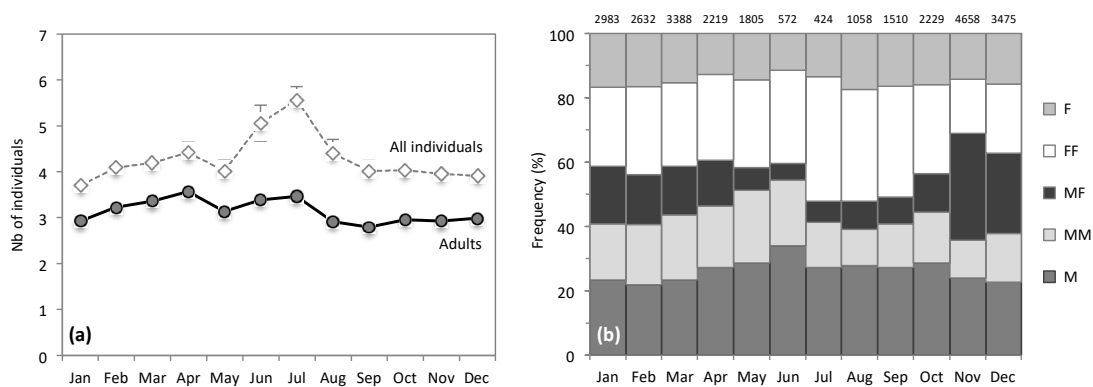
375

376 We observed a total of 27,409 groups over the 12 years of the study (611 – 3131 per year;
377 mean: 2284.1). Group size ranged from 1 to 47 (mean \pm SE: 4.19 ± 0.03). Among the sighted

378 groups, 26,953 (98.3%) included adult(s), whose number ranged from 1 to 35 with a mean (\pm
 379 SE) of 3.17 (\pm 0.02) roughly steady throughout the year (Fig. 3a). Furthermore, 40.3% of the
 380 groups with adult(s) included a single adult that could be a female (15.3%) or a male (25.0%),
 381 41.6% included at least two adults but a single sex among the adults (female groups: 25.1%;
 382 male groups: 16.5%), and 18.1% included adults of both sexes. Unsurprisingly, relative
 383 frequency of the mixed-sex groups peaked during the rut (33.3% in November), while it
 384 dropped to a minimum during the parturition-lactation period (5.2% in June; Fig. 3b).

385 Overall, males represented only 39.2% of the sighted adults ($N = 85,537$), 35.9% in the
 386 groups containing \geq two adults ($N = 74,680$), but 62.1% among the adults seen isolated or
 387 only with kids and/or yearlings ($N = 10,857$).

388



389

390 **Fig. 3.** (a) Average size (\pm SE) of the sighted Pyrenean chamois groups (lone animals
 391 included) considering all individuals or only adults. (b) Relative observation frequency of five
 392 group types. F: lone female or with kid(s) or yearling(s); FF: groups including at least two
 393 adult females but no adult male; MF: groups including adults of both sexes; MM: groups
 394 including at least two adult males but no adult female; M: lone male or with kid(s) or
 395 yearling(s). Values above columns are the numbers of sighted groups (solitary individuals
 396 included).

397

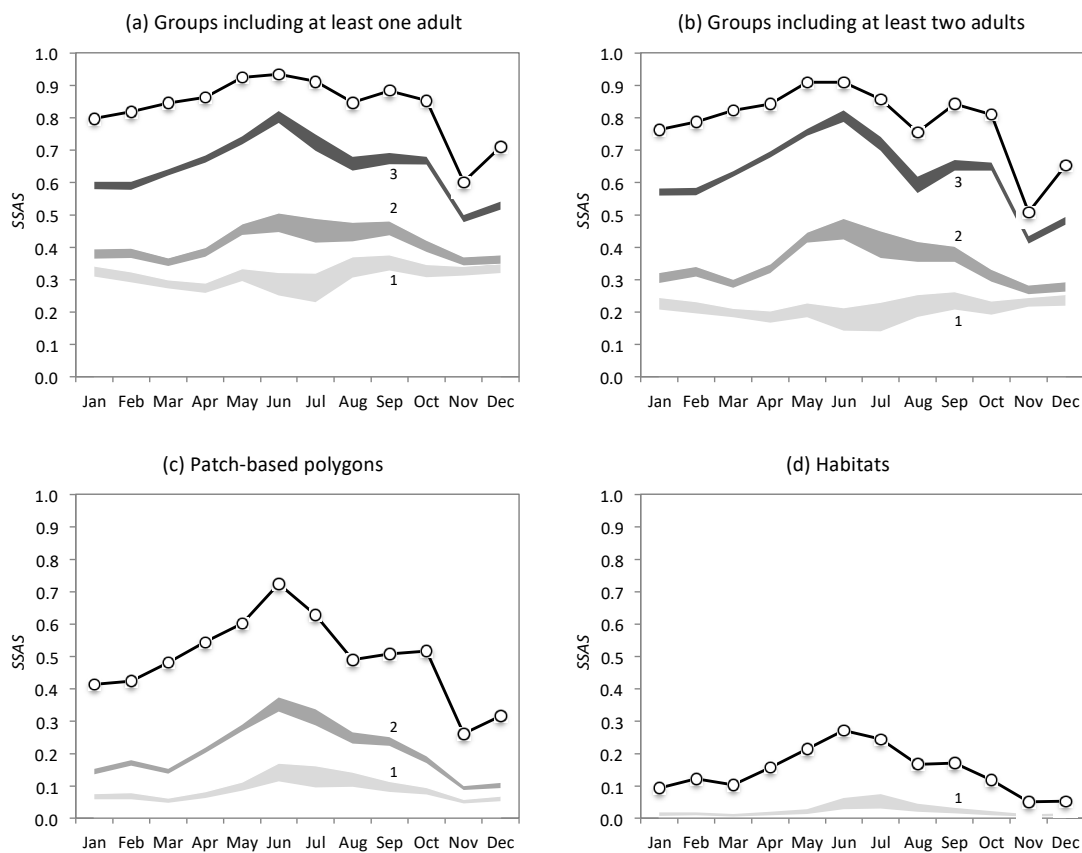
398

399 *3.1. Test of social, spatial and habitat segregation*

400

401 Social segregation was significant throughout the annual cycle, whether or not the groups
402 with a single adult (and the solitary adults) were taken into account. In both cases, indeed, all
403 the monthly values of SSAS computed on the numbers of adult males and females per group
404 were higher than expected under the hypothesis of random association of sexes within each
405 month and year (Fig. 4a, b; CI 1). The same was true when permutations were performed
406 within each month, year and habitat (Fig. 4a, b; CI 2), and within each month, year and patch-
407 based polygon (Fig. 4a, b; CI 3), showing that social segregation was not merely a
408 consequence of sex-related differences in habitat and space use.

409



410

411 **Fig. 4.** Monthly values of SSAS computed on the numbers of adult males and females sighted
412 (a) isolated and in the groups including at least one adult, (b) in the groups including at least
413 two adults, (c) in the patch-based polygons, and (d) in the eleven habitat types. Greyish areas:
414 95% confidence interval (CI) obtained by random permutation of sexes, with permutations (N
415 = 10,000) performed (1) within each month and year, (2) within each month, year and habitat,
416 and (3) within each month, year and patch-based polygon. Observed SSAS value above or
417 below CI indicates either sexual segregation or aggregation.

418

419 Spatial and habitat segregation was also significant throughout the year. All the monthly
420 SSAS values computed on the numbers of males and females in the patch-based polygons
421 were higher than predicted, whether permutations were performed within each month and
422 year (Fig. 4c, CI 1) or within each month, year and habitat (Fig. 4c, CI 2). Similarly, all the
423 monthly SSAS values computed on the numbers of males and females in the 11 habitats were
424 significantly higher than predicted by random permutation of sexes within each month and
425 year (Fig. 4d).

426

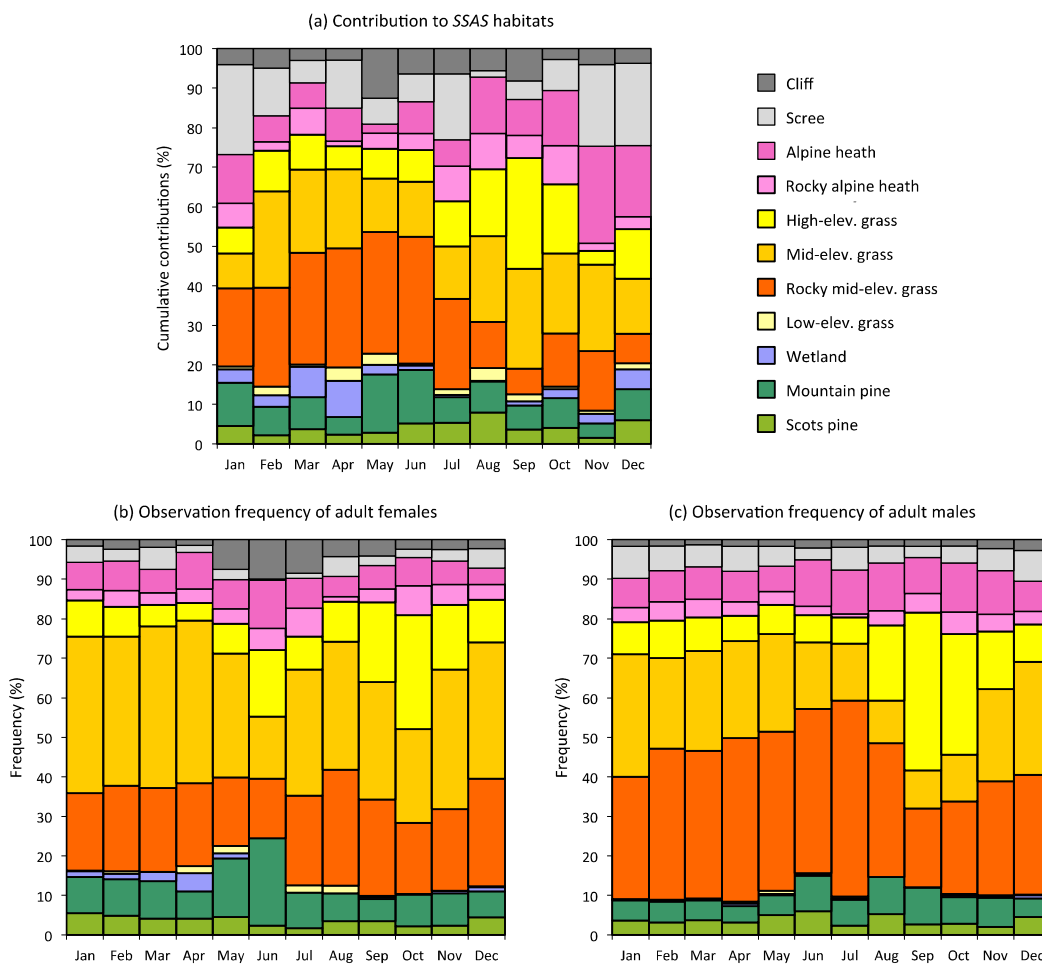
427 *3.2. Contribution of the habitats*

428

429 Five of the 11 habitats contributed to 60.6 – 85.6% (mean: 72.2%) of the monthly values of
430 SSAS computed on the numbers of males and females per habitat (Fig. 5a). Three were
431 grassland types: (1) the rocky mid-elevation grassland, proportionately more used by males
432 than females from January to July (monthly mean: 39.9 vs 19.8%; Fig. 5b, c), (2) the (non-
433 rocky) mid-elevation grassland, with relatively more females than males during most of the
434 year (32.8 vs 20.3%), and (3) the high-elevation grassland with a higher proportion of females
435 than males in June (16.8 vs 6.9%) but the opposite in September–October (15.2 vs 29.5%).

436 The fourth and fifth habitats primarily involved in habitat segregation were alpine heath,
 437 proportionally more used by males than females from August to December (10.4 vs 5.7%),
 438 and screes, more used by males during most of the year (5.4 vs 3.0%). Mountain pine forest
 439 and cliffs also contributed to habitat segregation in May-July (Fig. 5a), i.e., during the birth
 440 and early lactation periods, with females being more often observed than males in both
 441 habitats (mountain pine: 15.3 vs 6.9%; cliffs: 8.6 vs 1.8%; Fig. 5b, c).

442



443

444 **Fig. 5.** (a) Contribution of each habitat to SSAS values computed for testing habitat
 445 segregation (see Fig. 4d), and observation frequency of adult females (b) and adult males (c)
 446 in the eleven habitats.

447

448 3.3. Inter-annual and monthly variation of the social, spatial and habitat segregation

449

450 Over the 143 study months, SC_{social} gave high values (mean \pm SE: 0.70 ± 0.02), SC_{habitat}

451 low (positive) values (mean \pm SE: 0.15 ± 0.01), and SC_{spatial} intermediate values ($0.45 \pm$

452 0.01), indicating habitat segregation was low despite the high degree of sexual segregation

453 revealed by group composition. SC_{habitat} and SC_{spatial} remained steady across the 12 years

454 whereas SC_{social} tended to decrease in 2006-2009 (Fig. S1a). Degree of social, spatial and

455 habitat segregation varied significantly in the course of the annual cycle (Figs. 6 and S1b, c,

456 d; detrended SC_{social} ; $F_{11,119} = 11.525$, $P < 0.0001$; Ljung-Box test: $\chi^2_{12} = 15.632$, $P = 0.21$;

457 detrended SC_{spatial} ; $F_{11,119} = 13.646$, $P < 0.0001$; Ljung-Box test: $\chi^2_{12} = 13.080$, $P = 0.36$;

458 detrended SC_{habitat} ; $F_{11,119} = 4.276$, $P < 0.0001$; Ljung-Box test: $\chi^2_{12} = 17.345$, $P = 0.14$). The

459 minimum of the detrended values of the three coefficients generally occurred between

460 October and December: 8/11 years for SC_{social} , 7/11 for SC_{spatial} and SC_{habitat} (one-tailed

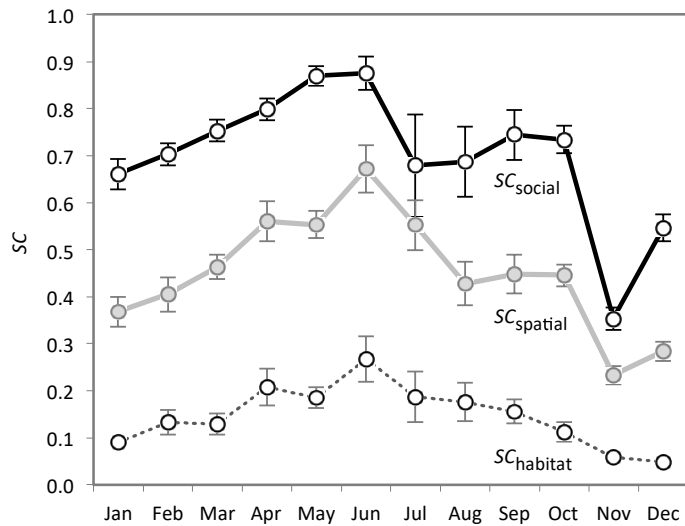
461 binomial test: $P = 0.0012$ et $P = 0.008$, respectively). Furthermore, the maximum of the

462 detrended values of the three coefficients occurred more frequently in May-July than chance

463 alone would suggest: 9/11 years for SC_{social} , 10/11 for SC_{spatial} and 7/11 for SC_{habitat} (one-

464 tailed binomial test: $P = 0.0014$, $P = 0.0001$ and $P = 0.039$, respectively).

465



466

467 **Fig. 6.** Monthly average of the values of SC_{social} , SC_{spatial} and SC_{habitat} computed for each
 468 of the 143 months of the study period. Error bars are standard errors. By construction (see Eq.
 469 3), SC_{social} , SC_{spatial} and SC_{habitat} are calculated discarding the groups, polygons or habitats
 470 that include a single adult.

471

472

473 3.4. Interactions between adults outside the rut

474

475 We observed 574 interactions between adults outside the rutting months, i.e., 0.0591
 476 interaction per group including \geq two adults ($N = 9,712$), and 0.0123 interactions per adult
 477 sighted in such groups ($N = 46,780$). Though males composed 38.4% of the sighted adults,
 478 they initiated 72.5% of the interactions, thus much more than chance might suggest ($\chi_1^2 =$
 479 277.6, $P < 0.0001$).

480 A total of 321 interactions were recorded between males, i.e., an initiation rate of 0.0196
 481 interactions per male sighted in groups including \geq two males ($N = 16,277$). These
 482 interactions included 72.0% mild aggressions, 22.1% severe aggressions and 5.9% play-like

483 interactions. Surprisingly, initiation rates of mild and severe aggressions decreased as group
484 size and the proportion of males in the group increased (Deviance tests, $P < 0.005$).
485 Furthermore, these two rates did not depend on the presence of females in the group
486 (Deviance tests, $P \geq 0.30$), but both varied between months (Deviance tests, $P < 0.0001$) with
487 a peak in May-June.

488 A total of 154 interactions were recorded between females, i.e., an initiation rate of 0.0054
489 interactions per female sighted in groups including \geq two females ($N = 28,263$). These
490 interactions included 72.7% mild aggressions, 16.9% severe aggressions, 9.7% play-like
491 interactions, and 0.6% sexual interactions. Initiation rates of mild and severe aggressions
492 tended to decrease as group size increased (Deviance tests, $P < 0.06$), but increased or tended
493 to increase with the proportion of females in the group (Deviance test: mild aggressions $\chi_1^2 =$
494 6.321, $P = 0.012$; severe aggressions: $\chi_1^2 = 3.387$, $P = 0.066$). The presence of males in the
495 group had no significant effect on the initiation rate of mild aggressions ($\chi_1^2 = 0.521$, $P =$
496 0.47), but increased the initiation rate of severe aggressions ($\chi_1^2 = 10.877$, $P < 0.001$; Fig. S2).
497 Both rates varied between months (Deviance tests, $P < 0.002$), with enhanced values in June
498 and September for mild aggressions, and from July to September for severe aggressions.

499 Finally, 99 of the observed interactions involved one male and one female. Though males
500 composed 25.8% of the adults sighted in mixed-sex groups ($N = 12,041$), they initiated many
501 more male-female interactions than chance alone would predict ($\chi_1^2 = 248.3$, $P < 0.0001$).
502 Indeed, females initiated only four mild aggressions, i.e., 0.0004 interactions per sighted
503 female ($N = 8,929$), whereas males initiated the other interactions, i.e., 0.0305 interactions per
504 sighted male ($N = 3,112$). The interactions initiated by males included 46 sexual interactions,
505 37 severe aggressions, 11 mild aggressions, and one play-like interaction. Most of the sexual
506 interactions (89.1%) were recorded in winter, with a decreasing frequency from January
507 (54.3%) to March (13.0%). In contrast, most male-female aggressions were observed from

508 February to April (severe aggressions: 70.3%; mild: 60.0%). The severe aggressions
509 performed by males in mixed-sex groups including \geq two males ($N = 19$) tended to be more
510 preferentially addressed to males than females (observed frequency of male-male severe
511 aggression: 7; expected frequency: 4.25; Monte Carlo test: $P = 0.0859$).

512

513 **4. Discussion**

514

515 Given the theoretical background that underpins the current hypotheses focusing on
516 ecological factors, sexual segregation should be reduced in the nearly monomorphic Pyrenean
517 chamois, except during the parturition-early lactation period. Our data collected during 12
518 years and the analyses performed in the present paper show that habitat segregation was low
519 outside the parturition-lactation period, but also that social and spatial segregations
520 consistently occurred throughout the year. Takada et al. (2019) also found no sexual
521 differences in habitat use in the nearly monomorphic Japanese serow (*Capricornis crispus*).
522 In this species, however, both females and males are solitary, except when females are
523 accompanied by dependent offspring, and inhabit closed habitat, which perhaps explains the
524 lack of habitat segregation. By contrast, chamois live in open-membership groups and use
525 both forested and open habitats all around the year during daytime.

526

527 *4.1. Habitat segregation*

528

529 Habitat segregation peaked during the parturition and early lactation period as predicted by
530 the ‘reproductive strategy hypothesis’ (RSH). Females occurred in mountain pine forests and
531 cliffs more often than males and more often than during the rest of the year, as also reported
532 in other Pyrenean chamois populations (Pérez-Barbería and Nores, 1994). Moving to steep

533 slopes (Karsch et al., 2016) or where trees provide concealment (Hamr, 1988; Scornavacca et
534 al., 2018) offer protection for offspring against terrestrial carnivores and raptors, as found in
535 sexually dimorphic mountain-dwelling herbivores (Hutchins and Geist, 1987; Kohlmann et
536 al., 1996; Corti and Shackleton, 2002; Grignolio et al., 2007; Karsch et al., 2016; Baruzzi et
537 al., 2017). Females with neonates may also avoid tourists walking on valley bottom and
538 summit trails (Cederna and Lovari, 1985; Bon et al., 1995; Ciuti and Apollonio, 2008).

539 It should further be noted that habitat segregation around parturition may also be explained
540 by a change in females' gregariousness. Females become less social and isolate themselves
541 from conspecifics as in wild sheep (*Ovis* spp.), moose (*Alces alces*), Nubian ibex (*Capra ibex*
542 *nubiana*) and roe deer (*Capreolus capreolus*) (Festa-Bianchet, 1988; Miquelle et al., 1992;
543 Bon et al., 1995; Habibi, 1997; Cransac et al., 1998; Langbein et al., 1998; Maublanc et al.,
544 2012). By using habitat neglected by non-lactating females and males, females in late
545 gestation and during few days post-partum space away from conspecifics, facilitating mutual
546 recognition, the formation of an exclusive bond and exclusive maternal care to their own
547 offspring (Bon et al., 1995; Ciuti et al., 2009; Karsch et al., 2016).

548 Soon after post-partum isolation, lactating females group together (Vaucher, 1988; Karsch
549 et al., 2016), venturing farther from escape terrain. In early summer, isard females in our
550 study area occupied the habitats they used before parturition, predominantly (non-rocky) mid-
551 elevated grassland. At the same time, males kept on using the rocky mid-elevated grassland,
552 and slightly increase their frequentation of alpine heath, which however remains a rather
553 minor habitat for them. Males were reported to use more forested areas and less often alpine
554 meadows than females in Alpine and Apennine chamois (*R. p. ornata*) (Shank, 1985; Lovari
555 and Cosentino, 1986; Untherthiner et al., 2012), shrub and bush areas more than females in
556 Pyrenean and Cantabrian chamois (*R. p. parva*) (Pérez-Barbería et al., 1997; Dalmau et al.,
557 2013). By contrast, Ferretti et al. (2014) found no sexual differences in summer habitat use.

558 In late summer, isard of both sexes increasingly used high-elevated grasslands as found in
559 other *Rupicapra* populations (Hamr, 1984a, 1984b; Crampe et al., 2007; Nesti et al., 2010;
560 Papaioannou et al., 2014) and other mountain ruminants (Mysterud et al., 2001; Parker et al.,
561 2009). This habitat would support more nutritive protein-rich forage due the delayed green-up
562 of vegetation in September-October (Nesti et al., 2010). This change in habitat use was
563 steeper in males. This may reflect lower sensitivity to predation risks than in females.
564 Nevertheless, whether a higher sensitivity of females to predation risks is related to maternal
565 care as predicted by the ‘reproductive strategy-predation risk hypothesis’ (RSH) is unclear
566 because offspring are weaned or nearly in September-October. Female-biased sensitivity to
567 risks, human disturbance or interference due to wild or domestic herbivores (Hamr, 1988;
568 Ciuti and Appolonio, 2008) may be a response of sex per se, as indicated by a higher
569 responsiveness of female black rhinoceros (*Diceros bicornis*) to predators (Berger and
570 Cunningham, 1995) and as also found in domestic sheep (*Ovis aries*) and humans (Wojniusz
571 et al., 2011). Alternatively, a more intense use of high-elevation terrain by males may reflect a
572 higher sensitivity of males than females to heat stress, when they attain their highest body
573 mass, i.e., in the period of highest body mass dimorphism, in accordance with the ‘weather
574 sensitivity hypothesis’ (WSH).

575 Ecological differences between the sexes may occur at a finer spatial scale than the habitat
576 patches considered in the present paper. Ferretti et al. (2014) did not detect any sexual
577 difference in the microhabitats used by Apennine chamois in summer. However, a sex-related
578 difference in diet remains possible. Males feed more on fibrous and less digestible/nutritive
579 food than females in the monomorphic black rhinoceros (Du Toit, 2005), whereas no sexual
580 differences in diet and selection of forage were found in feral horses (*Equus caballus*), males
581 and females white-tailed deer (*Odocoileus virginianus*) of similar body mass, and scimitar-
582 horned oryx (*Oryx dammah*) (Lenarz, 1985; Lagory et al., 1991; Robinson and Weckerly,

583 2010). Pérez-Barbería et al. (1997) found that females have a less fibrous and more
584 digestible/nutritive diet than males outside winter in the Cantabrian chamois. However,
585 summer increase in body mass is higher in males than females in the Pyrenean chamois (Fig.
586 2), and in late summer Pérez-Barbería et al. (1998) found a higher kidney fat index in males
587 than females in the Cantabrian chamois. Though moderate in *Rupicapra* species (Morin et al.,
588 2016), the energy expenditure incurred to face offspring care may limit the capacity for
589 females to store body reserves despite their more nutritive diet. Besides, males may be more
590 efficient than females at allocating energy to fat and/or muscle growth when resources are
591 plentiful and contain relevant nutrients (Rughetti and Festa-Bianchet, 2011; Kernaléguen et
592 al., 2016) and whether this also apply to sexually dimorphic species is not reported to our
593 knowledge.

594

595 4.2. Social segregation

596

597 Outside summer and the rut period, the persistent social and spatial segregation in
598 Pyrenean chamois when food resources become limiting and when body mass of both sexes is
599 comparable cannot be accounted for by ‘reproductive strategy’, ‘gastro-centric’, ‘weather-
600 sensitivity’ and ‘predation risk hypotheses’, and considered as a by-product of habitat
601 segregation (Bowyer et al., 2002; Bowyer, 2004; Main, 2008). The SSAS and SC indicate that
602 social segregation is prominent even when controlling for habitat and spatial segregation, with
603 and without isolated adults (Fig. 4). Whatever the level of sexual dimorphism, almost all
604 Caprini are characterized by social segregation (Shackleton, 1997). Despite intra-specific
605 variation, social segregation is salient in *Rupicapra* spp. (Richard-Hansen et al., 1992; Levet
606 and Pépin, 1994; Bonenfant et al., 2007), reminiscent of what is found in highly sexually
607 dimorphic herbivores (Conradt, 1999; Bon et al., 2001; Bonenfant et al., 2004; Calhim et al.,

608 2006; Loe et al., 2006; Villerette et al., 2006). This strongly suggests that social mechanisms
609 contribute to drive sexual segregation as already advocated for a number of large mammals
610 (e.g. Alpine ibex *Capra ibex ibex*, wild, feral and domestic sheep, red deer *Cervus elaphus*,
611 sea lion *Zalophus californianus wollebaeki*, white-tailed deer, feral goat, and African elephant
612 *Loxodonta africana*; Bon and Campan, 1989; Villaret and Bon, 1995; Cransac et al., 1998;
613 Conradt, 1999; Le Pendu et al., 2000; Bon et al., 2001; Wolf et al., 2005; Pérez-Barbería et
614 al., 2005; Calhim et al., 2006; Shannon et al., 2008; Singh et al., 2010; Alves et al., 2013;
615 Biggerstaff et al., 2017; Bourgoïn et al., 2018).

616 The ‘social factors hypothesis’ (SFH) postulates that in polygynous species, sexual
617 selection should have retained males practicing sparring interactions to develop social skills
618 that ultimately increase access to receptive females (Main et al., 1996; Pérez-Barbería and
619 Yearsley, 2010). The Pyrenean chamois is a polygynous species but our data are poorly
620 consistent with this prediction: males interacted with conspecifics more often than females, as
621 reported in Apennine chamois by Locati and Lovari (1990), but social interactions were
622 seldom observed in the present study. In addition, play-like interactions among males were
623 especially rare and much less frequent than agonistic interactions, which were short lasting.
624 Boschi and Nievergelt (2003) pointed out that hook-shaped horns are dangerous, leading
625 sparring to be scarce. *Rupicapra* spp. avoid clashing and rather perform agonistic display,
626 anti-parallel fight, and chase (Locati and Lovari, 1990; Ruggetti & Festa-Bianchet, 2011;
627 Corlatti et al., 2013).

628 Sexual interactions (46 events in 12 years) were rarely observed past December, as could
629 be expected since the rut is seasonal in chamois as in all mountain-dwelling species. In
630 addition, we did not find that the rate of aggression between males increased in the presence
631 of females. Accordingly, the ‘sexual harassment hypothesis’ (SHH) and the ‘male avoidance
632 of females hypothesis’ (MAFH) do not apply. Inter-sex agonistic interactions were also rare

633 (56 events), as reported in Apennine chamois by Lovari (1985), and mainly observed in
634 winter, perhaps in relation to the scarcity of resources and thus to competition for food. Males
635 were almost always the initiators of such interactions, and the rate of severe conflicts among
636 females increased in the presence of males, which is compatible with the FAMH (Weckerly,
637 2001; Biggerstaff et al., 2017). However, we have to be cautious with this result because
638 chase interactions among females in mixed-sex groups were noticed only on 11 occasions in
639 12 years. The instantaneous recording method used in the study is perhaps a limit to test this
640 hypothesis. Whether co-occurring within the same groups affects foraging efficiency or
641 vigilance level for each sex as reported in white-tailed deer (Biggerstaff et al., 2017) cannot
642 be checked with our data. But assessing social interference between the sexes requires
643 controlling for familiarity, which plays a role in attraction (Pérez-Barbería et al., 2005),
644 whereas males and females seldom group together. The lack of familiarity had previously
645 been mentioned as source of conflict among females themselves (Festa-Bianchet, 1998).

646 Alternatively, as postulated by the ‘social affinity hypothesis’ (SAH) proposed by Bon and
647 Campan (1996), prevalence of same-sex groups may reflect intra-sex attraction or affinity
648 (Gerard and Richard-Hansen, 1992) and maintenance of spatial proximity (Wolf et al., 2005)
649 without overt affiliative interactions (MacFarlane & Coulson, 2009). Coe and Rosenblum
650 (1974) found higher intra-sex than inter-sex spatial proximity in penned squirrel monkey
651 (*Saimiri sciurus*), mirroring the social segregation described in field studies of this species.
652 Higher intra-sex spatial proximity is also documented in mixed-sex groups of wild and
653 domestic sheep, and in feral goat (Le Pendu et al., 1996; Michelena et al., 2004, Calhim et al.,
654 2006). Higher social attraction for same-sex peers was experimentally found in domestic
655 sheep (Michelena et al., 2005; Pérez-Barbería et al., 2005) together with a spatial separation
656 of groups of females and males (Pérez-Barbería et al., 2007). More recently, Griffith et al.
657 (2014) found that wild male and female minnows (*Phoxinus phoxinus*), which are similar in

658 morphology, tend to segregate socially and spatially when introduced in artificial channels.
659 Villerette et al. (2006) found a strong tendency of fallow deer (*Dama dama*) mixed-sex
660 groups to split up into single-sex groups, without group asynchrony being a major cause of
661 fission. MacFarlane and Coulson (2009) reported no avoidance of one sex by another in
662 western grey kangaroo (*Macropus fuliginosus*) but a higher intra-sex attraction particularly in
663 males. Wolf et al. (2005) concluded that segregation probably reflects a social preference for
664 same-sex conspecifics outside the rut. Although our present data cannot disentangle the
665 respective role of avoidance from attraction, these studies and our own give support to the
666 hypotheses relying on social mechanisms.

667 We suspect that cryptic mechanisms linked to sex per se, i.e., sexualisation of behaviour,
668 totally or partially decoupled from sexual mass dimorphism, may partly drive the sexual
669 segregation found in adults. Group living outside the rut is based on non-sexual social
670 attraction and interactions. Sexual differences in behaviour may be dependent on sex-limited
671 gene expression, perinatal action of steroid and corticosteroid hormones (Meaney, 1988;
672 Beery et al., 2009; William and Carroll, 2009). Interestingly, Soay sheep lambs castrated
673 within three days after birth segregate socially and spatially from both females and non-
674 castrated males (Jewell, 1986) despite no segregation in habitat (Ruckstuhl et al., 2006). The
675 ‘social factor hypothesis’ (SFH) hardly accounts for such a segregation. The Soay sheep
676 experiment illustrates how physiological mechanisms may influence the development of
677 social behaviour, social affinity at the individual level and also aggregation and spatial
678 patterns at a population-wide level. In the case of Soay sheep, however, it is difficult to
679 disentangle the relevancy of the ‘activity budget hypothesis’ (ABH) and of hypotheses
680 implying social mechanisms as castrated males outweigh entire males, increasing the sexual
681 dimorphism. On the other hand, non-social behaviour such as response to environmental

682 stressor (Carter, 2003) and social behaviour may be differently regulated by neuropeptides
683 such as oxytocin and vasotocin in females and males (Beery et al., 2009; Goodson, 2013).

684 We did not investigate the activity budget of adult males and females in the present study.
685 Contrasting results have been found in *Rupicapra* species outside winter. Pérez-Barbería and
686 Nores (1994) and Pérez-Barbería et al. (1998) found that females Pyrenean chamois spent
687 more time foraging than males, perhaps reflecting higher selectivity. Ferretti et al. (2014) did
688 not detect any sexual differences in this respect, but Puorger et al. (2018) found that males
689 display higher bite rate and less step rate than females. In winter, snow cover restricts
690 available space, food abundance and quality are low, and the short diurnal time is mostly
691 dedicated to food acquisition and processing, enforcing similar activity budgets as in
692 Cantabrian chamois and feral goat (*Capra hircus*) (Pérez-Barbería et al., 1998; Dunbar and
693 Shi, 2008). Although the ‘activity budget hypothesis’ (ABH) as stated does not account for
694 the intense social segregation observed, we cannot preclude that despite the monomorphism
695 in body mass during more than 6-7 months, sexual differences of metabolic rate or other
696 physiological mechanisms induce different feeding patterns (Lewis et al., 2002), which could
697 make both sexes less synchronous in their activities and thus mixed-sex groups more labile
698 (Alves et al., 2013; Griffiths et al., 2014). For instance, males may have a greater muscle/fat
699 ratio and thus for the same body mass, greater energetic demands due to higher metabolic
700 activity of muscles (Romey and Wallace, 2007). Data collected in the same environment,
701 excluding the influence of gestation and lactation and controlling for group size would be
702 required to test the hypotheses of diet selectivity and activity budget (Pérez-Barbería et al.,
703 2007).

704

705 *4.3. Spatial segregation*

706

707 Bowyer (2004, p. 1040) stressed that ‘one especially problematical aspect with the concept
708 of social segregation is that it does not explain why sexes spatially segregate... any inclusive
709 hypothesis for sexual segregation should be able to cope with the spatial attributes of this
710 process’ (see also Stewart et al., 2015). Indeed, neither sexual differences in activity budget
711 nor preferences to associate with same-sex conspecifics could alone explain spatial
712 segregation, as they do not theoretically preclude both sexes from using independently the
713 same areas (Francisci et al., 1985; Jakimchuk et al., 1987). Nonetheless, inter-sex avoidance
714 might certainly promote spatial segregation (Pérez-Barbería et al., 2005), and at least some
715 other mechanisms not involving ecological factors might do the same.

716 In a number of gregarious Antilopini (including nearly monomorphic species), all-male
717 groups would result to a large extent from the exclusion of their members by territorial males
718 (Leuthold, 1977; Dubost and Feer, 1981; Estes, 1991). The same mechanism might be at work
719 in *Rupicapra* spp.: part of the mature males is reported to be territorial during the rut, and
720 territoriality is also suspected or reported in spring (Levet and Pépin, 1994; Unterthiner et al.,
721 2012) and summer (Shank, 1985; Hardenberg et al., 2000). In the present study, a large
722 proportion of the adults observed alone throughout the year were males. However, severe
723 aggressions were seldom observed between males, and we cannot assert that spatial
724 segregation was primarily caused by inter-male aggression. Another mechanism might be
725 involved in spatial segregation. Mother-young bonds break down in *Rupicapra* sp. for both
726 sexes when juveniles enter their second year of life. Males, however, eventually disperse
727 farther from maternal ranges as in pronghorn (Loison et al., 2008; Barnowe-Meyer et al.,
728 2013) – possibly revealing a weaker attachment to natal ranges and/or social bonds with
729 familiar conspecifics, higher attraction for unfamiliar conspecifics –, and although sex-
730 dependent dispersal is not a pre-requisite to social segregation, it may contribute to spatial
731 segregation. Finally, a model developed by Bon et al. (2005) suggests that higher intra-sex

732 than inter-sex attraction could amplify slight differences in habitat or space use, and thus lead
733 to sexual segregation on a large spatial scale. Such a model, however, remains to be tested
734 experimentally.

735

736 **5. Conclusion**

737

738 Our long-term observational data set showed, unexpectedly, high year-round sexual
739 segregation in the Pyrenean chamois, a nearly monomorphic mammalian herbivore.
740 Segregation peaked during and following parturition as expected in species where parental
741 care is exclusive to females. However, past offspring weaning, we found low habitat
742 segregation whereas social segregation remained very high, which is hardly explained by
743 current hypotheses relying on sexual dimorphism in body size. Social mechanisms that could
744 promote social segregation are difficult to test in the wild. However, the fact that social
745 segregation is prevalent in such a nearly-monomorphic species opens avenues regarding
746 possible mechanisms linked to dispersal, social neuroscience, and collective patterns
747 emerging from social and spatial mechanisms, and in our opinion should revive the scientific
748 debate around sexual segregation.

749

750 **Authors' statement.** JPC: collected the data. GG, JPC and JFG: managed the data. JFG and
751 MG: performed the data analyses. RB, JFG, GG, JPC, and CM: wrote the paper.

752

753 **Declaration of competing interest**

754

755

756

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758

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764

765

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1252 APPENDIX A

1253 Contribution of the habitats

1254

1255 For month i and year j , the Pearson's independence chi-square χ^2_{ij} calculated on the
 1256 numbers of adult males and females sighted in the eleven habitats is a sum of terms, each
 1257 corresponding to a given habitat k :

1258
$$\chi^2_{ij} = h^1 + h^2 + \dots + h + \dots + h^{10} + h^{11}. \quad (A1)$$

1259 Moreover, for month i , the χ^2_{ij} computed for the habitats is

1260
$$= \frac{\sum_{k=1}^{12} h_k^2}{\sum_{k=1}^{12} h_k}, \quad (A2)$$

1261 where $\sum_{k=1}^{12} h_k$ is the total number of adults sighted for month i and year j (see Material and
 1262 Methods). Substituting χ^2_{ij} in Eq. (A2) by its expression (Eq. A1), it comes to

1263
$$= \frac{\sum_{k=1}^{12} h_k^1 + \sum_{k=1}^{12} h_k^2 + \dots + \sum_{k=1}^{12} h_k + \dots + \sum_{k=1}^{12} h_k^{10} + \sum_{k=1}^{12} h_k^{11}}{\sum_{k=1}^{12} h_k}.$$

1264 The absolute contribution of habitat k to χ^2_{ij} is therefore

1265
$$= \frac{\sum_{k=1}^{12} h_k}{\sum_{k=1}^{12} h_k},$$

1266 whereas its relative contribution to χ^2_{ij} is

1267
$$= \frac{\sum_{k=1}^{12} h_k}{\sum_{k=1}^{12} h_k^2}.$$

1268