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1 **Social behaviour as a predominant driver of sexual, age-dependent**  
2 **and reproductive segregation in Mediterranean mouflon**

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24 Segregation between the sexes or related to age and/or reproductive status is common in many  
25 animal taxa, particularly in dimorphic species. The causes of this segregation remain difficult to  
26 disentangle, despite numerous attempts. This is probably due to the difficulty of obtaining sufficient  
27 data on animal behaviour (e.g. habitat use, activity budgets) and group composition (age/sex and  
28 reproductive status) during the various phases of the species' reproductive cycle. Based on an  
29 intensive long-term monitoring of a Mediterranean mouflon, *Ovis gmelini musimon* x *Ovis* sp.,  
30 population, we concurrently assessed five hypotheses for segregation linked to forage selection  
31 (FSH), reproductive strategy (RSH), social preference (SPH), activity budget (ABH) and weather  
32 sensitivity (WSH). We found marked segregation between most age/sex classes. Age-dependent  
33 segregation among males was increasingly marked as their age difference increased and segregation  
34 between the sexes also increased as males became older and larger. Over the year, segregation  
35 between sex, age and reproductive status classes was lowest during the rut. We also observed the  
36 highest synchrony of activity in groups composed of individuals of similar age/sex class or  
37 reproductive status. Females occurred closer to both secure and high-quality food habitats,

38 especially during the lambing and rearing periods, whereas males used less secure and lower quality  
39 habitats as they aged. Differences in habitat use between age/sex classes provided partial or full  
40 support for the RSH and FSH. Large males were preferentially observed at higher altitude than  
41 females during hot summer days to buffer against heat stress, in agreement with the WSH. A  
42 preference for interacting and grouping with peers that express similar activity patterns (ABH and  
43 SPH) appears to be the main driver of segregation in this population. Our study confirms the strong  
44 multifactorial nature of segregation in ungulates.

45

46 **Keywords:**

47 activity budgets, dimorphic species, habitat and social segregation, mouflon, *Ovis*, reproductive  
48 strategy, SSAS, weather

49

50 Segregation between males and females, or between individuals of different ages and/or  
51 reproductive status, is common across the animal kingdom (Ruckstuhl & Neuhaus, 2005). This is  
52 particularly true in sexually dimorphic herbivores in which sexual segregation is particularly  
53 widespread and pronounced (e.g. red deer, *Cervus elaphus*: Alves, da Silva, Soares, & Fonseca,  
54 2013; fallow deer, *Dama dama*: Ciuti & Apollonio, 2008; bighorn sheep, *Ovis canadensis*: Geist,  
55 1971; Ruckstuhl, 1998; Svalbard reindeer, *Rangifer tarandus platyrhynchus*: Loe et al., 2006;  
56 Tibetan argali, *Ovis ammon hodgsoni*: Singh, Bonenfant, Yoccoz, & Côté, 2010). Segregation is  
57 hypothesized to be the result of differences in habitat use or social behaviour (Bon & Campan,  
58 1996; Conratt, 1999, 2005; Ruckstuhl, 2007; Table 1). However, differences in body size are  
59 considered the main driver of segregation due to the potential links with resource requirements,  
60 reproductive strategies, activity patterns, social preferences and sensitivity when faced with adverse  
61 weather conditions (Ruckstuhl & Neuhaus, 2005).

62 First, differential use of habitats between animals of different age/sex classes (i.e. habitat

63 segregation) may be explained by several nonexclusive mechanisms. The two most often proposed

64 hypotheses rely on different resource requirements ('forage selection hypothesis', FSH) and/or  
65 different strategies to maximize reproductive success ('reproductive strategy hypothesis', RSH;  
66 a.k.a. predator avoidance hypothesis; Bowyer, 1984; Main & Coblentz, 1996; Main, Weckerly, &  
67 Bleich, 1996; Ruckstuhl, 2007) between age/sex classes. The RSH is linked to divergent  
68 reproductive strategies and sensitivity to predation risk among age/sex classes which promote  
69 habitat segregation (Bleich, Bowyer, & Wehausen, 1997; Main et al., 1996). Indeed, in polygynous  
70 species, males should select habitats and forage of high quality, favouring body growth, so as to  
71 maximize access to females and reproductive success, potentially despite higher predation risk in  
72 those areas (Jakimchuk, Ferguson, & Sopuck, 1987; Main & Coblentz, 1990; Main et al., 1996;  
73 Table 1). Conversely, to maximize long-term reproductive success, females should maximize their  
74 own survival and that of their offspring through the use of habitats with low predation risk, but with  
75 enough food to offset their increased energetic needs (Bleich et al., 1997; Main et al., 1996). Hence,  
76 the RSH states that females with offspring should segregate from other classes of animals that are  
77 less vulnerable to predation (i.e. males and females without offspring) early during the lambing  
78 period (Jakimchuk et al., 1987; Main & Coblentz, 1996; Main et al., 1996).

79 The FSH, also known as the sexual dimorphism–body size, gastrocentric and nutritional needs  
80 hypothesis, has often been invoked to explain segregation between age/sex classes that diverge in  
81 their energetic requirements and ability to process food (the Jarman–Bell principle; Bell, 1971;  
82 Jarman, 1974). For example, smaller individuals (e.g. females or young adult males), which are  
83 physiologically less able to digest low-quality forage, should preferentially select habitats of high-  
84 quality food (rather than quantity) compared to larger individuals (Barboza & Bowyer, 2001; Beier,  
85 1987; Table 1). Habitat segregation may also occur between individuals of the same sex with  
86 similar morphology, but that have different nutritional requirements (e.g. between reproductive and  
87 nonreproductive females during the end of the gestation–lactation period; Gittleman & Thompson,  
88 1988; Loudon, 1985; Oftedal, 1985).

89 In addition to these two main hypotheses, which have often been the focus of attention in previous  
90 studies, other factors may drive habitat segregation, in particular the higher sensitivity of larger  
91 individuals to bad weather conditions (e.g. low temperatures and wind during winter, or high  
92 temperatures, without wind, during summer) compared to smaller individuals. These differences  
93 can be explained by a relatively higher absolute heat loss to energy intake ratio under cold weather  
94 conditions (Conradt et al., 2000; Jackes, 1973) and by a higher thermal inertia and lower  
95 conductance under warm weather conditions (Porter & Kearney, 2009) for larger individuals  
96 compared to smaller ones. Under stressful weather conditions, larger individuals are expected to  
97 select habitats that buffer against harsh climatic conditions more intensively than smaller  
98 individuals, even if those habitats have less foraging resources. These differences in weather  
99 sensitivity might thus be a contributing factor in habitat segregation between dimorphic individuals  
100 in areas where animals experience stressful weather conditions ('weather sensitivity hypothesis',  
101 WSH; Alonso, Salgado, & Palacín, 2016; Conradt et al., 2000; Marchand et al., 2015b).

102 Some previous studies have reported that habitat use was not the primary driver of segregation  
103 between the sexes (e.g. Conradt, 1999; Cransac, Gérard, Maublanc, & Pépin, 1998; Singh et al.,  
104 2010), suggesting other factors, such as social constraints, may drive social but not habitat  
105 segregation. From early in life, males and females exhibit different behaviours that may lead to  
106 social segregation (Bon & Campan, 1996; Gaudin et al., 2015; Guilhem, Bideau, Gerard, Maublanc,  
107 & Pépin, 2006). Some hypotheses state that segregation may arise from interactions between males  
108 to develop their fighting skills and establish hierarchical relationships, which may change with age  
109 (Main et al., 1996; Weckerly, 2001), from aggressiveness of females during parturition (Main et al.,  
110 1996), or from the avoidance of male harassment by females (Brask, Croft, Thompson, Dabelsteen,  
111 & Darden, 2011; Sundaresan, Fischhoff, & Rubenstein, 2007). However, these factors may explain  
112 segregation only during specific periods of the year. The observed preference of individuals of the  
113 same age/sex class to interact, and hence to group together with peers rather than with individuals  
114 of other age/sex classes, is the basis of the social-preference hypothesis (SPH; Bon, 1991; Bon &

115 Campan, 1996; Le Pendu, Briedermann, Gerard, & Maublanc, 1995; Pérez-Barbería, Robertson, &  
116 Gordon, 2005). As females tend to avoid agonistic interactions and males tend to interact with peers  
117 of similar age classes, social segregation between sex and age classes should be observed most of  
118 the year, except during the rutting period (Table 1).

119 Alternatively, social segregation could also be explained by differences in activity patterns.  
120 Individuals living within a group must synchronize their activities to maintain group cohesion  
121 (Jarman, 1974). This behavioural synchronization may be costly for the individual as it can lead to  
122 suboptimal activity patterns and to less efficient use of resources (Aivaz & Ruckstuhl, 2011;  
123 Ruckstuhl, 1998, 1999). As a result, individuals should balance the costs and benefits of remaining  
124 in a group with asynchronous activities and are thus expected to segregate from each other when  
125 behaviour is too asynchronous ('activity budget hypothesis', ABH; Conradt, 1998a; Ruckstuhl,  
126 1998, 1999; Table 1). Ruckstuhl & Neuhaus (2002) demonstrated that between-sex differences in  
127 activity patterns increased with increasing sexual size dimorphism. Indeed, the duration of  
128 foraging/ruminating bouts often differs markedly between individuals with sex- or age-related  
129 differences in metabolic requirements and/or digestive abilities (Conradt, 1998a; Ruckstuhl &  
130 Neuhaus, 2002; see also the Jarman–Bell principle above). Similarly, differing activity patterns may  
131 be linked to the reproductive status of females, as lactating females spend more time foraging and  
132 less time resting than nonlactating females to compensate for the high energetic costs of lactation  
133 (e.g. Hamel & Côté, 2008).

134 These different drivers of segregation may have independent effects or may work in tandem and  
135 fluctuate across the year to generate the observed patterns of segregation (e.g. Alves et al., 2013;  
136 Conradt, 1999; Singh et al., 2010). Thus, the relative importance of these drivers should depend on  
137 the physiological status of individuals and on environmental conditions encountered (Alves et al.,  
138 2013; Bonenfant et al., 2004; Ciuti & Apollonio, 2008; Loe et al., 2006). Despite an abundant  
139 literature on segregation in large herbivores, most studies have focused on certain components of  
140 segregation only (i.e. either segregation between individuals of different age/sex classes, or

141 segregation between females with or without offspring) and restricted their analyses to the  
142 corresponding hypotheses (but see e.g. Alves et al., 2013; Bonenfant et al., 2004; Loe et al., 2006).  
143 This may be due to the difficulty of simultaneously collecting (at the same time or in the same study  
144 area) sufficient data on the behaviour (e.g. habitat use, activity budget) of individuals with variable  
145 characteristics (sex, age, reproductive status). In addition, to explain segregation between sex and  
146 age classes, especially in hot environments, the WSH has been largely ignored, despite an  
147 increasing number of studies revealing specific behaviours in animals with contrasting body size,  
148 when facing adverse weather conditions (Alonso et al., 2016; Aublet, Festa-Bianchet, Bergero, &  
149 Bassano, 2009; Conradt et al., 2000; Garnick, Di Stefano, Elgar, & Coulson, 2014; Shrestha et al.,  
150 2014).

151 To tease apart the relative contribution of habitat, social and climatic factors for explaining  
152 segregation, we analysed a large data set composed of more than 7800 spatially explicit  
153 observations of groups of the polygynous, dimorphic Mediterranean mouflon, *Ovis gmelini*  
154 *musimon* x *Ovis* sp., in the south of France, between 1994 and 2014. We combined this data set  
155 with detailed information on the activity states of each individual recorded from almost 3000 scan  
156 observations of these groups, between 1996 and 1997. We first assessed the temporal patterns of  
157 segregation in relation to sex, age and reproductive status of females. We then investigated the  
158 degree to which differential habitat use and weather conditions drive this pattern. We tested the  
159 influence of stressful climatic conditions on segregation during summer, the critical season for  
160 mouflon in our study area (see Bourgoïn et al., 2008, 2011 and Marchand et al. 2015b for details on  
161 adult behavioural responses to hot conditions, and Garel, Loison, Gaillard, Cugnasse, & Maillard,  
162 2004 for consequences for the survival of young and body mass of adults). We thus expected  
163 habitat segregation between the smallest individuals (i.e. females), individuals of intermediate size  
164 (i.e. young adult males) and large males to be more pronounced during summer because of an  
165 increasing use of high altitudes (providing thermal shelter, Marchand et al 2015b) with increasing  
166 body size and hence sensitivity to the hottest conditions. Finally, we assessed whether differences in

167 activity synchrony between individuals could explain segregation. Based on these analyses, we  
168 assessed the support for the above-mentioned hypotheses underlying segregation in large herbivores  
169 (FSH, RSH, WSH, SPH, ABH; Table 1).

## 170 <H1>METHODS

### 171 <H2>Study Area

172 The studied Mediterranean mouflon population inhabits the Caroux-Espinouse massif (43°38'N,  
173 2°58'E, 17 000 ha, 150–1124 m above sea level), in southern France. The confluence of three  
174 climatic influences (Atlantic, Mediterranean and Montane) in this area leads to hot and dry  
175 summers (mean  $\pm$  SD daily temperature =  $16.5 \pm 3.7$  °C and mean  $\pm$  SD cumulative precipitation =  
176  $151.5 \pm 61.1$  mm in June–August 2003–2014), wet autumns (mean  $\pm$  SD cumulative precipitation =  
177  $487.7 \pm 197.3$  mm in September–November 2003–2014), and fairly cold winters (mean  $\pm$  SD daily  
178 temperature =  $1.61 \pm 4.2$  °C in December–February 2004–2014) with a limited period of snow  
179 cover restricted to hill tops and plateaus (Thiebaut, 1971). The massif consists of high plateaus  
180 separated by deep valleys. Plateaus are mainly composed of coniferous forests (*Pinus sylvestris*,  
181 *Pinus nigra*, *Picea abies*), heather (*Erica cinerea* and *Calluna vulgaris*) or blueberry, *Vaccinium*  
182 *myrtillus*, moorlands and grass-rich areas (pastures, meadows and artificial crops devoted to  
183 wildlife, providing abundant and high-quality food for mouflon [*Brachypodium sylvaticum*, *Festuca*  
184 *rubra*, *Festuca paniculata*, *Festuca ovina*, *Carex* sp.]; Baudière, 1970). Lower quality habitats for  
185 mouflon such as encroaching broom (*Cytisus oromediterraneus*, *Cytisus scoparius*) and fern  
186 (*Pteridium aquilinum*) moorlands also occurred on slopes and at lower elevation. Slopes are also  
187 composed of rocky areas. Deciduous trees (mainly beech, *Fagus sylvatica*, chestnut, *Castanea*  
188 *sativa*, and evergreen oak, *Quercus ilex*) mostly occur at the bottom of valleys (see Marchand et al.,  
189 2015a for a detailed description of vegetation characteristics).

190 No large predators were present in the study area during most of the study period, although  
191 evidence of wolf, *Canis lupus*, presence (mouflon killed by wolf, visual/camera trap observations)



192 were recently recorded (since spring–summer 2014), with a maximum of one wolf observed at a  
193 time. Other potential predators for new-born and sick mouflon are free-roaming dogs, golden  
194 eagles, *Aquila chrysaetos*, and red foxes, *Vulpes vulpes*. Stalking and drive hunting were permitted  
195 each year, from 1 September to the end of February, except in a central Wildlife Reserve of 1658 ha  
196 (Garel et al., 2007; Marchand, Garel, Bourgoïn, Dubray, et al., 2014; Marchand et al., 2015a).  
197 Between 200 and 600 mouflon were harvested per year during the study period 2002–2014.  
198 Population monitoring from foot ground counts (Garel, Cugnasse, Loison, et al., 2005) did not  
199 reveal any marked population trends in abundance.

## 200 <H2>Study population and species

201 The population of mouflon in the Caroux-Espinouse massif was founded with the release of 19  
202 Mediterranean mouflon in the Wildlife Reserve between 1956 and 1960 (Cugnasse, 1990; Garel,  
203 Cugnasse, Gaillard, et al., 2005). Of these 19 individuals, eight were native Corsican mouflon, *Ovis*  
204 *gmelini musimon* var *corsicana*, from the French National Reserve of Cadarache, France, while  
205 others (six from the National Domain of Chambord, France, and five from what was then  
206 Czechoslovakia) originated from populations where potential crossbreeding with other wild or  
207 domestic sheep species had occurred (Boussès & Réale, 1998; Cugnasse, 1994; Montgelard,  
208 Nguyen, & Dubray, 1994; Türcke & Schmincke, 1965; Uloth, 1972). During the study period,  
209 relative density increased as indicated by the marked decrease in lamb body mass, suggesting that  
210 population density was high relative to resource availability (Garel et al., 2007). Mouflon was the  
211 only ungulate species introduced into the study site. Roe deer, *Capreolus capreolus*, and wild boar,  
212 *Sus scrofa*, were also naturally present, but at a much lower density.

213 The Mediterranean mouflon is a gregarious, sexually dimorphic species. In this population during  
214 the 2002–2014 period, mean spring body mass  $\pm$  SD was  $22.7 \pm 5.1$  kg for females  $\geq 1$  year old ( $N$   
215 = 626) and  $17.2 \pm 3.8$  kg,  $25.0 \pm 5.4$  kg and  $34.1 \pm 5.5$  for yearlings, 2–3- and  $\geq 4$ -year-old males,  
216 respectively ( $N = 114, 137$  and  $175$ , respectively; sexual size dimorphism of 66.4% between  
217 females and  $\geq 4$ -year-old males; see also Garel et al., 2007 for similar differences in autumn).

218 Rutting activities occur from late October to early January, with the highest activity from November  
219 to mid-December (Bon, Dardaillon, & Estevez, 1993). During this period, fights between males are  
220 common and males roam from one group of females to another. ‘Tending’ is the predominant  
221 reproductive tactic of males (Bon, Gonzalez, Bosch, & Cugnasse, 1992). After 5 months of  
222 gestation, females give birth to one lamb (twinning rate <3%) from late March to late May (Garel,  
223 Cugnasse, Gaillard, et al., 2005). The birth peak occurs in mid-April, with 95% of births occurring  
224 during 10 days around this peak (Bon, Dardaillon, et al., 1993).

## 225 <H2>Observational data

226 A total of 7880 individuals/groups of mouflon were observed over the year during two periods:  
227 1994–1996 (period 1;  $N = 3783$ ; Cransac et al., 1998; Martinetto, Cugnasse, & Gilbert, 1998) and  
228 2002–2014 (period 2;  $N = 4097$ ). Data were collected during repeated foot surveys along predefined  
229 footpaths and from fixed points, covering the study site. Observations were performed during  
230 daytime, from sunrise to sunset, with an observation peak during the 2 h following sunrise and the 2  
231 h before sunset. Mouflon were observed at a distance (50–1000 m) using binoculars and spotting  
232 scopes (x10–60). For each observation, the group size, its composition in terms of age/sex classes  
233 (see below) and its location were recorded. We considered an individual or a group of individuals at  
234 >50 m from other mouflon as separate groups. The geographical positions of observed groups were  
235 recorded on a grid (125×125 m) mapped on a topographical map (see the ‘Habitat map’ section)  
236 historically used for the study site. We pooled females into a single class, as error in age estimation  
237 during observations is especially high for females (Garel, Cugnasse, Hewison, & Maillard, 2006;  
238 Garel, Cugnasse, & Maillard, 2005). We considered five age/sex classes: lambs, females, yearling  
239 males, young adult males (2–3 years) and adult males ( $\geq 4$  years). As twinning is rare in our study  
240 area (Garel, Cugnasse, Gaillard, et al., 2005), we assumed that the number of females with lambs  
241 was equal to the number of lambs in the group, so that the number of females without lambs was  
242 equal to the total number of females minus the number of lambs.

243 We also recorded the activity status (feeding, moving, resting and vigilant) of all individuals in  
244 groups composed of two or more individuals (excluding lambs). A total of 2947 activity scans were  
245 recorded from 2193 different groups from March to November in 1996–1997 (Benoist, Garel,  
246 Cugnasse, & Blanchard, 2013; Martinetto et al., 1998). Activity was mostly recorded once per  
247 group ( $N = 1804$  groups), and at regular time intervals (15 min; scan sampling) for 389 groups  
248 (mean  $\pm$  SD =  $2.9 \pm 1.7$  successive observations per group). In our analyses, we considered groups  
249 composed of males only (adults, young adults and yearling males;  $N = 1033$  scans), of adult males  
250 and females ( $N = 2006$  scans) recorded from March to November and of females during the April–  
251 June period ( $N = 835$  scans). For the latter two types of groups, lambs and yearling males may have  
252 been present, but their activity was not considered when computing activity synchrony for these  
253 groups.

## 254 <H2>Habitat types

255 Mouflon are grazers (sensu Hofmann, 1989) with digestive ability to process a diet dominated by  
256 grass species (Hofmann, 1989; Kamler, 2001). They mainly feed in open habitats such as pastures,  
257 meadows and sown crops devoted to wildlife (i.e. grass-rich areas), consuming a large proportion of  
258 herbaceous species (40–50% grasses in our study population), and, to a lesser extent, in moorland  
259 habitat with abundant ligneous species (broom, heather, fern and blueberry; Cransac, Valet,  
260 Cugnasse, & Rech, 1997; Faliu, Cugnasse, Auvray, Orliac, & Rech, 1990; Marchand et al., 2013).  
261 In our population, previous analyses of vegetation in grass-rich areas have shown higher digestive  
262 and energetic values for plant species present in this habitat than in areas rich in ligneous species  
263 (Cazau, Garel, & Maillard, 2011). Accordingly, mouflon were in better condition when their home  
264 range included a large proportion of grass-rich areas (Marchand, Garel, Bourgoïn, Michel, et al.,  
265 2014). For these reasons, we considered this habitat to be higher quality for mouflon than  
266 moorlands. We used this contrast to investigate the role of resource quality (see also Benoist et al.,  
267 2013) on segregation (FSH hypothesis). Based on a land cover map (derived from the processing of  
268 a SPOT satellite image from July 2005 and field validation; 25 m grid resolution; Tronchot, 2008),

269 we computed two distance maps (distance to grass-rich areas and distance to moorland areas). The  
270 resolution of these maps was four times higher than the resolution of animal observations (125 m).  
271 We thus downgraded them to 125 m to match the grid map historically used for recording locations  
272 of observed animals. We used these maps to compute the proximity to grass-rich and to moorland  
273 areas (distance to habitat<sup>2</sup>×e(log(1/100)/500<sup>2</sup>); adapted from Nekola & White, 1999) for each  
274 animal location. Proximity ranged in a nonlinear manner from 1 (mean estimated location of the  
275 animal (i.e. centre of a 125x125 m pixel; see above ‘Observational data’) in the focal habitat) to  
276 near 0 (beyond a cut-off distance of 500 m). The cut-off distance of 500 m corresponded to the  
277 upper limit within which 95% of the distances travelled by 26 adult GPS-collared mouflon over 2 h  
278 were included (Marchand et al., 2015b). We considered habitat beyond this cut-off distance to have  
279 low or no influence on movements or habitat selection. We also used a digital elevation model (25  
280 m grid resolution downgraded to 125 m resolution; source: BD ALTI data set from the Institut  
281 Géographique National, France) to get elevations and derive a map of proximity to refuge areas (i.e.  
282 proximity to steep slopes (> 30°); see Marchand, Garel, Bourgoïn, Dubray, et al., 2014; Marchand  
283 et al., 2015a). As precise information on habitat-specific climate was not available, we focused on  
284 elevation as a proxy for ambient temperature: as temperature decreases with elevation, selection for  
285 elevation is one of the ways by which mountain ungulates buffer against summer conditions (ibex,  
286 *Capra ibex*: Aublet et al., 2009; mouflon: Marchand et al., 2015b). Maps of elevation and proximity  
287 to refuge areas allowed us to specifically test the WSH and RSH hypotheses, respectively.

## 288 <H2>Weather data

289 We used minimum and maximum daily temperatures recorded by Météo France to test the WSH.  
290 Temperatures were recorded by the Cambon-et-Salvergues weather station (43°37'N, 02°51'E, 900  
291 m above sea level) during the 1994–1996 period (period 1), and the Fraisse-Murat weather station  
292 (43°38'N, 2°49'E; 1022 m above sea level) during the 2002–2014 period (period 2). They are  
293 situated at 8 and 11 km, respectively, northwest of the barycentre of all the observations. We  
294 computed mean daily temperature as the mean of the maximum and minimum daily temperatures.

## 295 <H2>Statistical analyses

### 296 <H3>Variation in patterns of segregation over the study period

297 Patterns of segregation between the different combinations of age, sex and reproductive status  
298 classes were assessed using the sexual segregation and aggregation statistic (SSAS) developed by  
299 Bonenfant et al. (2007). We computed the SSAS using the formula:

$$300 \quad SSAS = 1 - \frac{N}{XY} \sum_{i=1}^k \frac{X_i Y_i}{N_i}$$

301 where  $k$  is the number of groups observed,  $N_i$  is the group size of the  $i$ th group with  $X_i$  and  $Y_i$   
302 individuals of the two studied age, sex and reproductive status classes, respectively, and  $N = X + Y$ ,  
303 with  $X = \sum X_i$  and  $Y = \sum Y_i$ .

304 In contrast to the segregation coefficient of Conrath (1998b), SSAS considers solitary individuals. It  
305 varies between 0 (no segregation) and 1 (complete segregation). We compared the observed and the  
306 expected distributions of SSAS based on 10 000 permutations (i.e. corresponding to SSAS values  
307 under random association of individuals of the age, sex and reproductive status classes), following  
308 the recommendations of Bonenfant et al. (2007), to test the null hypothesis of random association  
309 between each pairwise combination of age, sex and reproductive status classes. SSAS was  
310 computed for seven pairwise combinations of age, sex and reproductive status classes (e.g. females  
311 with lambs versus females without lambs) and for each month to test the predictions related to our  
312 working hypotheses (Table 1). We also performed preliminary analyses which showed that there  
313 was no temporal trend in segregation patterns over the study period (e.g. related to changes in  
314 relative density; Garel et al., 2007) which might have generated spurious effects (see Fig. A1 in the  
315 Appendix).

### 316 <H3>Differences in habitat use as a driver of segregation

317 We used generalized linear models (GLM) with a binomial error distribution to assess differences in  
318 habitat use between the sexes and/or age classes. The response variable was the proportion of

319 individuals belonging to a focal age/sex class in each observed group. Technically, it was  
320 parameterized using a two-vector object formed of successes (e.g. number of females in a group)  
321 and failures (e.g. number of males in the same group). The explanatory variables were the proximity  
322 to meadows (i.e. food-rich, high-quality habitats), to moorland (i.e. lower quality habitat) and to  
323 steep slopes (i.e. refuge areas). We computed the adjusted coefficient of determination for logistic  
324 regression (adjusted  $R^2$ ; Liao & McGee, 2003) to quantify the global role of the habitat variables in  
325 explaining segregation. We compared the monthly adjusted  $R^2$  values between two combinations of  
326 age, sex and reproductive status classes ( $N = 12$  per class) using a paired Mann–Whitney test with  
327 Bonferroni-corrected  $P$  values.

328 We also used GLM models to test the WSH using the observations of mouflon from the different  
329 age and sex classes during the summer months (July–August) of our two study periods. During  
330 period 2, we did not consider years 2003–2010 as only a few groups were observed in July–August  
331 ( $N = 1$  in 2005 and 2009,  $N = 8$  in 2010 and  $N = 0$  in 2003–2004 and 2006–2008). Temperatures  
332 were recorded by two weather stations (Cambon-et-Salvergues and Fraisse-Murat, see above). We  
333 centred the daily temperatures for each period to limit potential biases. We compared models  
334 including only the elevation as explanatory variable to the model with the interaction between  
335 elevation and temperature. We compared both models using Akaike’s information criterion (AICc)  
336 with second-order adjustment to correct for small sample bias. We considered two competing  
337 models as different when their difference in AICc ( $\Delta\text{AICc}$ ) was  $>2$  (Burnham & Anderson, 2002).  
338 We computed predicted values and confidence intervals ( $\pm 1.96 \times \text{SE}$ ) based on the selected model  
339 under hot and cool weather conditions at low and high elevation (i.e. 10 and 90% quantiles of  
340 temperature and elevation from all the observations, respectively).

### 341 *<H3>Differences in activity budget as a driver of segregation*

342 Finally, we computed the synchronization coefficient developed by Conradt (1998a) on our activity  
343 data recorded in 1996–1997. We considered individuals that were eating, moving and vigilant as  
344 active. The synchronization coefficient ranges from 0 (no synchronization of activity within groups)

345 to 1 (complete synchronization). This coefficient was computed with data recorded from March to  
346 November for (1) females only, adult males only and mixed groups; (2) groups of males,  
347 considering all groups composed of males of similar age class (i.e. groups of adults, of young adults  
348 and of yearling males) and groups composed of males of different age classes. We computed  
349 synchrony also for (3) groups of females with lambs (i.e. groups with  $N_{\text{lambs}} \geq N_{\text{females}}$ ), females  
350 without lambs and mixed (i.e. groups with  $N_{\text{females}} > N_{\text{lambs}} > 0$ ) females for each month around  
351 lambing and early lactation (April–June). Randomization tests were performed ( $N = 10\,000$ ) for  
352 each group type to compute confidence intervals and to test for differences between groups. All  
353 analyses were implemented in R 3.3.1 (R Core Team, 2016).

## 354 <H1>RESULTS

### 355 <H2>Variation in patterns of segregation

#### 356 <H3>Segregation between sex and age classes

357 Adult males and females were strongly segregated from each other all year round (all SSAS tests  
358 for segregation:  $P_{\text{segregation}} < 0.001$ ; Fig. 1a). The level of segregation increased during spring and  
359 remained high until September (highest differences between observed SSAS and random  
360 association (grey area in Fig. 1a) before decreasing during autumn. Although the differences in  
361 observed SSAS versus random association between males and females were lowest during the  
362 rutting period, segregation remained significant ( $P_{\text{segregation}} < 0.001$  from October to December). As  
363 males aged, segregation from females increased (SSAS tests for segregation: females versus  
364 yearling males:  $P_{\text{segregation}} \leq 0.01$  during only 3 months; females versus young adult males:  $P_{\text{segregation}}$   
365  $< 0.05$  for 11 months, including 9 months with  $P_{\text{segregation}} < 0.001$ ; Fig. 1a, b, c). Yearling males and  
366 females were significantly segregated from each other only during the lambing and rearing periods  
367 ( $P_{\text{segregation}} \leq 0.002$  in April–May;  $P_{\text{segregation}} = 0.012$  in July; Fig. 1c). Young adult males segregated  
368 from females most of the year (all  $P_{\text{segregation}} < 0.05$ , except in January), particularly during spring  
369 and summer (all  $P_{\text{segregation}} < 0.001$ ), but less so during the rutting period and the first part of the

370 winter ( $P_{\text{segregation}} = 0.029$  and  $0.169$  in December and January, respectively; Fig. 1b). Outside the  
371 November–January period, young males (yearling and young adult males) segregated less from  
372 adult males as they aged (all  $P_{\text{segregation}} < 0.001$  for both adult–yearling males and adult–young adult  
373 males from February to October, but with a larger difference between observed SSAS and random  
374 association for adult–yearling males than for adult–young adult males outside the rutting period;  
375 Fig. 2a, b).

### 376 <H3>Reproductive status of females

377 Females with lambs and adult males segregated from each other all year round (all  $P_{\text{segregation}} \leq$   
378  $0.001$ ; Fig. 3a), with the lowest differences in observed SSAS compared to random association  
379 during the rutting period and the highest during the lambing peak. A similar decrease in observed  
380 SSAS values during the rutting period was observed between females without lambs and adult  
381 males, and the highest values of SSAS were obtained in spring and summer (all  $P_{\text{segregation}} < 0.001$   
382 over the whole year), but without a peak in April (lambing peak; data not shown). We also observed  
383 significant segregation between females according to their reproductive status (all  $P_{\text{segregation}} \leq$   
384  $0.001$ ), except in June and July ( $P_{\text{segregation}} = 0.159$  and  $0.179$ , respectively), and with the highest  
385 values around the birth peak (Fig. 3b).

### 386 <H2>Differences in habitat use as a driver of segregation

387 Regarding the relative contribution of habitat variables for explaining segregation (i.e. adjusted  
388 coefficient of determination for logistic regression: adjusted  $R^2$ ; Liao & McGee, 2003), we observed  
389 low differences in habitat use between age, sex and reproductive status classes (Fig. 4), suggesting  
390 that, most of the year, differences in habitat use are not a main driver of segregation in our mouflon  
391 population. The lowest annual differences in habitat use were observed between females and  
392 yearling males (mean adjusted  $R^2 \pm \text{SD} = 0.6 \pm 0.7\%$ ), and between females with versus without  
393 lambs ( $0.8 \pm 1.0\%$ ; Fig. 4a, c). Females with lambs were generally observed closer to safer habitat  
394 around the peak of births than females without lambs (April:  $P < 0.001$ ; Table 2). The highest



395 differences in habitat use were observed between adult males and females (mean adjusted  $R^2 \pm SD =$   
396  $3.4 \pm 4.3\%$ ,  $3.1 \pm 4.2\%$  and  $5.1 \pm 5.3\%$  for all females, females without lambs and females with  
397 lambs, respectively), with the highest values occurring during the peak of births (i.e. in April;  
398  $15.4\%$ ,  $14.8\%$  and  $20.0\%$ , respectively; Fig. 4a, c). Consistently, females were observed closer to  
399 slopes most of the year (all  $P < 0.05$  for 8–9 months) and to grass-rich areas mostly during spring  
400 and summer (all  $P < 0.05$  for 3 - 5 months) compared to adult males (Table 2). Conversely, adult  
401 males were observed closer to moorlands (all  $P < 0.01$  during 4–5 months) more often than females,  
402 and particularly during the end of spring and summer. As yearling males tended to remain with their  
403 mothers (see above and Fig. 1c), they selected similar habitats to females (all  $P > 0.05$  for the  
404 proximity to moorlands and grass), but females remained closer to slopes during the lambing and  
405 early lactation period ( $P < 0.001$  in April–May). As males aged, differences in habitat use with  
406 females increased ( $1.2 \pm 1.8\%$  for females versus young males; paired Mann–Whitney test:  $P \leq$   
407  $0.002$  for females–adult males versus females–yearling males and for females–adult males versus  
408 females–young adult males;  $P = 0.179$  for females–young adult males versus females–yearling  
409 males; Bonferroni-corrected alpha level =  $0.0125$ ; Fig. 4a), but decreased with adult males ( $3.1 \pm$   
410  $2.7\%$  and  $1.2 \pm 1.3\%$  for adult males versus yearling and young males, respectively; paired Mann–  
411 Whitney test:  $P = 0.010$  for adult males–young adult males versus adult males–yearling males; Fig.  
412 4b).

413 Testing the influence of ambient temperature on the differential use of elevation between age/sex  
414 classes in July–August, we found stronger support for the full model including the interaction  
415 between temperature and elevation for females versus adult males and young adult males ( $\Delta AICc =$   
416  $4.495$  and  $14.495$ , respectively, compared to a model with elevation only). At low elevation,  
417 ambient temperature did not affect the proportion of females versus adult males and young adult  
418 males, but the proportion decreased at high elevation in hot weather, especially for young adult  
419 males (Fig. 5). We did not find support for the full model including the interaction between

420 temperature and elevation for adult versus yearling males ( $\Delta\text{AICc} = 1.129$ ), adult versus young  
421 adult males ( $\Delta\text{AICc} = 1.532$ ) and females versus yearling males ( $\Delta\text{AICc} = 3.612$ ).

## 422 <H2>Differences in activity budget as a driver of segregation

423 During the March–November period, behavioural synchrony within groups of adult males was  
424 significantly higher than within groups of females ( $P = 0.015$ ), and tended to be higher than in  
425 mixed groups ( $P = 0.086$ ; Fig. 6a). Considering all age classes of males, synchrony was higher in  
426 homogeneous age groups (i.e. with individuals of similar age) than in heterogeneous age groups ( $P$   
427  $= 0.034$ ). We observed higher behavioural synchrony in homogeneous groups of yearling and  
428 young adult males than in mixed groups of adult–young adult males ( $P = 0.006$  and  $0.001$ ,  
429 respectively) and adult–young adult–yearling males ( $P = 0.002$  and  $< 0.001$ , respectively; Fig. 6b).  
430 In addition, synchrony tended to be higher for young adult groups than for mixed groups of  
431 yearling–young adult males ( $P = 0.063$ ). Among groups of males, higher behavioural synchrony  
432 was observed in heterogeneous than homogeneous groups for groups of adult males only compared  
433 to mixed groups of adult–yearling males ( $P = 0.039$ ).

434 For females, synchrony in mixed groups of females with and without lambs increased from April to  
435 June (all  $P < 0.037$ ; Fig. 6c). During the lambing period and the first months of lactation, females in  
436 mixed groups were significantly less synchronized than homogeneous groups (April:  $P = 0.002$  and  
437  $0.029$  with heterogeneous groups of females with and without lambs, respectively; May:  $P = 0.005$   
438 with homogeneous groups of females without lambs; June:  $P = 0.055$  with homogeneous groups of  
439 females with lambs). A higher synchrony in groups of females with than without lambs was  
440 observed in April ( $P = 0.038$ ), while the opposite occurred in May ( $P = 0.03$ ), and no differences  
441 were observed in June ( $P = 0.354$ ).

## 442 <H1>DISCUSSION

443 We found marked segregation between adult males and females in this mouflon population which  
444 peaked in spring and reached its minimum at the end of autumn to early winter. We were able to

445 demonstrate not only an effect of age on the level of segregation between sexes, but also a variable  
446 level of segregation within the sexes related to age for males and to reproductive status for females.  
447 In relation to habitat segregation, we observed the expected pattern under the RSH and FSH  
448 hypotheses, with smaller individuals observed closer to habitat with high-quality food and,  
449 especially for females with lambs, closer to secure areas when lambs were highly vulnerable,  
450 compared to other age/sex classes. In addition, the higher proportion of young adult and adult males  
451 versus females at high elevations during hot summer days compared with cooler days indicates that  
452 males seek out lower temperatures under thermally stressful conditions (Marchand et al., 2015b).  
453 This result provides some support for the WSH. However, differences in habitat use only provided a  
454 partial explanation for segregation. In relation to social segregation, the marked annual grouping  
455 pattern and higher activity synchrony of groups composed of individuals of similar age, sex and  
456 reproductive classes compared to heterogeneous groups is in agreement with the SPH and the ABH.  
457 Although our study provides more support for social than habitat factors as the main driver of  
458 segregation, we highlighted the fact that multiple potential mechanisms may simultaneously  
459 contribute to patterns of segregation in populations of large wild herbivores.

460 The annual pattern of sexual segregation that we report, with a peak in spring and summer and a  
461 minimum at the end of autumn and early winter (peak rut; Bon, Recarte, Gonzalez, & Cugnasse,  
462 1995), is in agreement with previous studies on this population (Cransac et al., 1998) and on other  
463 sexually dimorphic wild ungulates (e.g. Alves et al., 2013; Bleich et al., 1997; Geist, 1971;  
464 Ruckstuhl & Neuhaus, 2005). During the rut, mouflon males roam from one female group to another  
465 (Bon et al., 1992), searching for ewes in oestrus, which leads to this low level of segregation.  
466 However, large mixed groups of mouflon were observed mostly from December to February (Bon  
467 et al., 1991), suggesting that mechanisms other than rutting behaviour could be involved, including  
468 environmental and physiological constraints. In winter, mouflon are mostly active during the few  
469 hours of daylight to limit heat loss and energy expenditure during the coldest period of the day (i.e.  
470 night; Bourgoïn et al., 2008; Darmon et al., 2014), which may lead to a higher synchrony of activity

471 and cohesion in mixed-sex groups. In addition, both sexes of mouflon have similar habitat use and  
472 diets during this period (Cransac et al., 1997; Marchand et al., 2015a), which can be explained by  
473 limited resource availability, leading animals to group on the remaining feeding patches. Hence,  
474 mouflon of different sex, age and reproductive status are more likely to be active at approximately  
475 the same time and in the same areas during winter, leading to a low level of segregation.

476 Adult and young adult males were observed less in proximity to slopes and grass-rich areas (i.e.  
477 secure and high-quality and quantity food areas, respectively), favouring areas close to moorlands  
478 as they aged and their body mass increased, compared with yearling males and females. This result  
479 is in line with the greater ability of larger animals to process more fibrous foods than smaller  
480 individuals (support for the FSH) and supports previous studies on cervids (Bonenfant et al., 2004;  
481 Conradt, Clutton-Brock, & Thomson, 1999). Most of the differences between males and females in  
482 their proximity to moorlands and grass-rich areas occurred during spring and early summer, when  
483 abundant and high-quality vegetation is widespread. While grass-rich areas seem to provide a high  
484 proportion of the diet of mouflon (Cransac et al., 1997; Faliu et al., 1990; Marchand et al., 2013)  
485 and to be valuable resources for their body condition (Marchand, Garel, Bourgoïn, Michel, et al.,  
486 2014), selection of shrub leaves, buds and twigs, and avoidance of woody parts of the plants, may  
487 provide highly digestible food (with low fibre content) for mouflon. It would be interesting to  
488 collect information on diet composition and quality in both sexes during the spring and summer  
489 period (i.e. the period with the highest segregation values and differences in habitat use). A recent  
490 study on habitat use based on GPS locations of mouflon in this population demonstrated strong  
491 selection for grass-rich areas on plateaus (slope < 10° and altitude > 900 m above sea level) by  
492 males in spring and summer, while females selected, to a lesser extent, grass-rich areas from mid-  
493 winter to early summer (Marchand et al., 2015a). These differences from our results can be  
494 explained by the habitat variables used in the analyses, as the grass-rich habitats of Marchand et al.  
495 (2015a) were divided into two groups (on plateaus versus slopes) and included heather and  
496 blueberry moorlands. In addition, our study used coarse location data and focused on proximity to

497 the three habitats of interest to test our hypotheses, while Marchand et al. (2015a) performed habitat  
498 selection analyses with fine scale GPS data. Differences may originate from the limits of data  
499 derived from direct observation of animals in a relatively forested and mountainous environment  
500 compared to GPS data which provide locations of animals during the day and night, in open and  
501 forested habitats (Bourgoin et al., 2009) and irrespective of environmental conditions.

502 Long-term fitness of females depends on both the survival of their lamb and on their own survival,  
503 while that of males is highly dependent on being in good enough physical condition to access  
504 females in this highly polygynous species (Clutton-Brock, Guinness, & Albon, 1982; Main & Du  
505 Toit, 2005). Even though it is not a general rule, some previous studies on other dimorphic species  
506 have demonstrated higher use of refuge areas by females with offspring than by males, sometimes  
507 at the expense of forage resources (e.g. Bleich et al., 1997; Festa-Bianchet, 1988; Hamel & Côté,  
508 2007; Main & Du Toit, 2005; Marchand et al., 2015a for this population of mouflon). Accordingly,  
509 we found that females with lambs segregated from all other age/sex classes, remaining closer to  
510 safer habitats during the lambing peak (i.e. April), when lambs are most vulnerable and less able to  
511 escape (Bon, Joachim, & Maublanc, 1995; Marchand et al., 2015a in the same population), in  
512 agreement with the RSH hypothesis. They also selected areas offering proximity to both secure and  
513 food-rich environments during the rearing period, when lambs are more agile and able to escape  
514 predation. This pattern of habitat use allowed females to fulfil their high energetic requirements  
515 associated with lactation (Gittleman & Thompson, 1988; Loudon, 1985; Oftedal, 1985), while  
516 ensuring a high level of security for their lamb, despite the absence of large natural predators in our  
517 study area since the introduction of mouflon in 1956 (but see Methods). Females without lambs  
518 showed a similar pattern of habitat use as females with lambs which may be explained by social  
519 preferences. Conversely, males occurred mostly near areas that were less secure, but that contained  
520 abundant foraging resources.

521 As males aged, they progressively separated from their mothers to form groups of young adult  
522 males, with increasing levels of segregation through spring and summer (Fig. 1b), before

523 associating with older males (Bon, Deneubourg, & Michelena, 2005; Bon, Dubois, & Maublanc,  
524 1993). These observations and the low proportion of segregation explained by differences in habitat  
525 use highlight the marked social preference of animals to group with individuals of the same sex and  
526 age classes, supporting the SPH (Bon, Rideau, Villaret, & Joachim, 2001; Le Pendu et al., 1995; Le  
527 Pendu, Maublanc, Briedermann, & Dubois, 1996; Pérez-Barbería et al., 2005; Villaret & Bon,  
528 1995). Previous studies in this population highlighted the negative consequences of dry and warm  
529 summers (Bourgoin et al., 2011; Garel, Loison, Gaillard, Cugnasse, & Maillard, 2004; Marchand et  
530 al., 2015b). According to the WSH, larger mouflon are expected to suffer more from extreme  
531 climatic conditions (here, high temperatures) than smaller ones and, therefore, to select habitats that  
532 buffer adverse climatic conditions (here, higher elevation; Alonso et al., 2016; Aublet et al., 2009;  
533 Conradt et al., 2000). In a previous study based on GPS location data and thermal sensors in this  
534 population (Marchand et al., 2015b), female mouflon traded thermal cover against safer habitats to  
535 promote lamb survival by avoiding unsafe plateaus and selecting steep rocky areas. In contrast, the  
536 larger adult males selected those habitats providing the best thermal cover (i.e. the plateaus). The  
537 combination of these findings collected at a fine scale and our observations suggests that larger  
538 individuals (i.e. young adult and adult males versus females) selected habitats offering better  
539 buffering against constraining summer climatic conditions. This mechanism may contribute to  
540 habitat segregation, at least during hot summers, in agreement with the WSH.

541 The higher activity synchrony in homogeneous versus mixed age/sex groups highlighted in several  
542 studies on wild and feral ungulates, including this study, provides support for the ABH (e.g.  
543 Calhim, Shi, & Dunbar, 2006; Conradt, 1998a; Ruckstuhl, 1998, 1999). Additionally, large group  
544 size and low synchrony in behaviour were linked to a higher probability of group fission, followed  
545 by higher synchrony among the remaining individuals in the group (Calhim et al., 2006). However,  
546 the authors of some studies, including experiments, found less support for the ABH, and considered  
547 that alone it cannot adequately explain segregation (Bowyer & Kie, 2004; Michelena et al., 2006;  
548 Pérez-Barbería et al., 2007). In an experiment on Soay sheep, differences in synchrony were mostly

549 explained by sex rather than by differences in body size (Pérez-Barbería et al., 2007). This  
550 contrasting result could be because the sheep in this experiment segregated by sex and not by body  
551 mass, and because ungulates tend to be more synchronized within a group than between groups  
552 (Maier & White, 1998). To disentangle the mechanism explaining these contrasting results between  
553 experiments with domestic animals (Pérez-Barbería et al., 2007) and studies on free-ranging  
554 ungulates (our results; Alves et al., 2013; Bon et al., 2001), observations on captive wild ungulates  
555 in similar experimental conditions (relatively homogeneous and space-limited habitat), or on larger  
556 groups of free-ranging domestic ungulates, should be performed.

557 We also observed differences in the degree of synchrony in activity between females with and  
558 without lambs during the lambing and lactating period. Differences were most pronounced during  
559 the lambing peak, when the differences in energetic requirements and sensitivity to risk between  
560 females with and without lambs were maximal. Females with lambs were observed to spend more  
561 time feeding (Hamel & Côté, 2008; Ruckstuhl, 1998) and/or more time in vigilance than females  
562 without lambs (Benoist et al., 2013; Singh et al., 2010), at the expense of resting. In addition,  
563 females classified as females without lambs may include not only true nonreproductive females but  
564 also late-pregnant females that have high energetic requirements compared to nonreproductive  
565 females, and low predation risk compared to females with a new-born lamb at heel. In this context,  
566 the ABH postulates that remaining in a group with individuals that have different activity patterns  
567 should be potentially costly (e.g. Conradt, 1998a; Ruckstuhl, 1998, 1999; Ruckstuhl & Neuhaus,  
568 2002; Xu, Ma, Yang, Blank, & Wu, 2012), so that differences in activity synchrony should  
569 therefore also contribute to social segregation between females around the lambing period.

570 Our study confirms the strong multifactorial origins of segregation in mouflon, mostly between  
571 adult males and females, but also between age (e.g. Alves et al., 2013) and reproductive classes  
572 (Alves et al., 2013; Bonenfant et al., 2004; Loe et al., 2006; Singh et al., 2010). The relative  
573 contribution of the different factors to segregation may vary according to the species, the  
574 environment (e.g. predation risk, habitat heterogeneity) and the season (e.g. reproductive period,

575 climatic conditions, resource availability). In our study area, the summer climatic conditions are the  
576 most constraining for mouflon (Bourgoin et al., 2008, 2011; Garel et al., 2004) and may lead to the  
577 two sexes selecting different habitats (our results; Marchand et al., 2015b). In a context of global  
578 warming, such differences between the sexes in response to hot climatic conditions may increase  
579 and occur during longer periods in the future. In addition to changes in habitat use, as a response to  
580 limiting climatic conditions, animals may also modify their activity (Alonso et al., 2016; Lewis,  
581 Phillips, Burthe, Wanless, & Daunt, 2015), at least with mouflon females (Bourgoin et al., 2008,  
582 2011). Investigating how males and females change their activity in response to stressful summer  
583 climatic conditions would help disentangle the relative contribution of weather in driving  
584 segregation patterns. This better understanding of behavioural processes will ultimately help to  
585 identify the pathways through which climate change impacts the species' population dynamics and  
586 distribution (Guisan & Thuiller, 2005).

587

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594

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858

859 **Appendix**

860 **Table 1.** Hypotheses tested in this study and the corresponding predictions according to sex, reproductive status and age for the Mediterranean  
 861 mouflon

Hypotheses	General predictions		Detailed predictions			Source	
	Main assumptions	Seasonal pattern (outside rut)	Females–adult males	Reproductive status of females	Age of males		
				Reproductive females–adult males	Reproductive–nonreproductive females	Females–males of different age classes	Adult males–younger males
Reproductive strategy hypothesis (RSH)	Each sex chooses habitat favouring reproductive success	Mostly around lambing and early lactation periods	Males closer to food-rich habitats, even if less secure	<b>Females with lambs closer to refuge habitats during early lactation</b>		Use of food-rich habitats, even if less secure, increases as males become older	Bowyer, 1984; Jakimchuk et al., 1987; Main & Coblentz, 1990, 1996; Main et al., 1996
Forage selection hypothesis (FSH)	Different nutritional requirements and processing abilities. Smaller individuals in habitats with higher quality food compared to larger individuals selecting abundant and lower quality food	No pattern (except around lambing and lactation for reproductive females)	<b>Males in habitats with abundant but lower quality food</b>	<b>Different nutritional requirements during the end of gestation and early lactation for reproductive females</b> → Higher segregation		<b>Increased use of habitats with abundant low-quality food as males become older</b>	Barboza & Bowyer, 2001; Beier, 1987; Bowyer, 1984

Weather sensitivity hypothesis (WSH)	Large individuals are more sensitive to harsh weather. They select habitats buffering harsh climatic conditions	During season with harsh weather conditions	<b>Large males in habitats buffering harsh climatic conditions</b>	<i>Not related to reproductive status</i>	Increased use of habitats buffering harsh climatic conditions as males become older	Conradt et al., 2000
Social-preference hypothesis (SPH)	Individuals prefer to interact and group with peers	No pattern	<b>Segregation, except during rut</b>	No specific patterns	<b>As males become older, segregation with females increases but decreases with adult males</b>	Bon, 1991; Bon & Campan, 1996
Activity budget hypothesis (ABH)	Differences in activity associated with body mass and/or different nutritional requirements lead to segregation	No pattern (except around lambing and lactation for reproductive females)	<b>Lower synchrony in mixed-sex groups</b>	<i>Lower synchrony</i>	<b>Lower synchrony in heterogeneous reproductive status groups</b>	Conradt, 1998a; Ruckstuhl, 1998, 1999

862 Supported, or partially supported, detailed predictions in this study are in bold. Predictions in italics were not tested here.



Adult–young adult males	Moorlands Grass Slope	M <sub>23</sub> <sup>*</sup>	M <sub>23</sub> <sup>*</sup> M <sup>*</sup> M <sub>23</sub> <sup>***</sup>	M <sub>23</sub> <sup>***</sup>	M <sup>*</sup> M <sub>23</sub> <sup>*</sup>	M <sub>23</sub> <sup>*</sup> M <sup>*</sup>	M <sup>**</sup>	M <sub>23</sub> <sup>***</sup>
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866 Moorlands: proximity to moorlands, Grass: proximity to grass, Slope: proximity to slope; F: females; F<sub>wL</sub>: females with lambs; F<sub>w/oL</sub>: females without  
867 lambs; M: adult males; M<sub>1</sub>: yearling males; M<sub>23</sub>: young adult males. Only the class observed closer to the corresponding habitat and significant results  
868 ( $P < 0.05$ ) are reported.

869 \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

870

871 **Figure captions**

872 **Figure 1.** Annual patterns of segregation for females and (a) adult, (b) young adult and (c) yearling  
873 males using the sexual segregation and aggregation statistic (SSAS). SSAS values are represented  
874 by the points (one value per month, with value computed from the first to the last day of the  
875 corresponding month) and the line in black. Significant segregation occurs if the observed SSAS  
876 value is above the grey shaded area (95% confidence interval). Light grey vertical shading: main  
877 rutting period; dark grey vertical shading: main lambing period; diagonal stripes: less intense rutting  
878 and lambing periods (note that tick marks on the x-axis indicate the 15th day of each month).  
879 Numbers above the x-axis (from top to bottom): (1) number of groups/solitary individuals, (2) and  
880 (3) total number of individuals of each age, sex and reproductive status class (i.e. females and adult  
881 males in (a), females and young adult males in (b) and females and yearling males in (c)) used to  
882 compute the SSAS for the corresponding month.

883

884 **Figure 2.** Annual patterns of segregation for adult and (a) young adult and (b) yearling males using  
885 the sexual segregation and aggregation statistic (SSAS). See Fig. 1 for details.

886

887 **Figure 3.** Annual patterns of segregation for females with lambs and (a) adult males and (b)  
888 females without lambs using the sexual segregation and aggregation statistic (SSAS). See Fig. 1 for  
889 details.

890

891 **Figure 4.** Annual patterns of the adjusted coefficient of determination for logistic regressions  
892 (adjusted  $R^2$ ; Liao & McGee, 2003) quantifying the global role of the habitat variables in explaining  
893 segregation for each combination of age, sex and reproductive status classes, based on generalized  
894 linear models with binomial error structure. F: females; FwL: females with lambs; Fw/oL: females  
895 without lambs; M: adult males; M<sub>1</sub>: yearling males; M<sub>23</sub>: young adult males.



896 **Figure 5.** Predicted values ( $\pm$  95% confidence interval) of the proportion of females compared to  
897 (a) adult males and (b) young adult males at low and high elevations (10 and 90% quantiles of  
898 observations = 530 and 1047 m above sea level, respectively) under cool and hot weather  
899 conditions (10 and 90% quantiles of corrected temperature = -4.5 and 2.3 °C, respectively).

900

901 **Figure 6.** Observed synchrony ( $\pm$  95% confidence interval based on 10 000 resamplings) in groups  
902 of (a) females and adult males and (b) males according to their age, during the March–November  
903 period, and (c) females according to their reproductive status during the lambing and early lactation  
904 periods (April–June). Numbers above the x-axis are numbers of groups used for computation. F:  
905 females; FwL: females with lambs; Fw/oL: females without lambs; M: adult males; M<sub>23</sub>: young  
906 adult males; M<sub>1</sub>: yearling males; ‘-’: mixed group.

907

908 **Figure A1.** Yearly variation in sexual segregation between females and adult male mouflon during  
909 the April–June period using the sexual segregation and aggregation statistic (SSAS). Age/sex  
910 classes and period were fixed to those when segregation was maximal. No temporal trend was  
911 detected between the arcsine square root transformation of the SSAS value and covariate ‘year’  
912 (slope = -0.0005, SE = 0.003,  $P$  = 0.885). See Fig. 1 for details (numbers are sample sizes).

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