



HAL
open science

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

G. Bourgoïn, Pascal Marchand, A. J. Mark Hewison, Kathreen E. Ruckstuhl,
Mathieu Garel

► **To cite this version:**

G. Bourgoïn, Pascal Marchand, A. J. Mark Hewison, Kathreen E. Ruckstuhl, Mathieu Garel. Social behaviour as a predominant driver of sexual, age-dependent and reproductive segregation in Mediterranean mouflon. *Animal Behaviour*, 2018, 136, pp.87-100. 10.1016/j.anbehav.2017.11.027. hal-02623393

HAL Id: hal-02623393

<https://hal.inrae.fr/hal-02623393>

Submitted on 16 Aug 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial - NoDerivatives 4.0
International License

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

3 Gilles BOURGOIN^{a,b,*}, Pascal MARCHAND^c, A. J. Mark HEWISON^d, Kathreen E.
4 RUCKSTUHL^e, Mathieu GAREL ^c

5

6

7 ^a Univ Lyon, VetAgro Sup, Marcy l'Etoile, France

8

9 ^b Univ Lyon, Université Lyon 1, CNRS, UMR 5558, Laboratoire de Biométrie et Biologie
10 Evolutive (LBBE), Villeurbanne, France

11

12 ^c Office National de la Chasse et de la Faune Sauvage, Unité Faune de montagne, Juvignac, France.

13

14 ^d CEFS, Université de Toulouse, INRA, Castanet Tolosan, France

15

16 ^e Department of Biological Sciences, University of Calgary, Calgary, AB, Canada

17

18

19 ***Correspondence:** G. Bourgoïn, VetAgro Sup, 1 avenue Bourgelat, BP 83, F-69280 Marcy
20 l'Etoile, France.

21 E-mail address: gilles.bourgoïn@vetagro-sup.fr

22

23

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 ± 3.7 °C and mean \pm SD cumulative precipitation =
176 151.5 ± 61.1 mm in June–August 2003–2014), wet autumns (mean \pm SD cumulative precipitation =
177 487.7 ± 197.3 mm in September–November 2003–2014), and fairly cold winters (mean \pm SD daily
178 temperature = 1.61 ± 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 ± 5.1 kg for females ≥ 1 year old (N
215 = 626) and 17.2 ± 3.8 kg, 25.0 ± 5.4 kg and 34.1 ± 5.5 for yearlings, 2–3- and ≥ 4 -year-old males,
216 respectively ($N = 114, 137$ and 175 , respectively; sexual size dimorphism of 66.4% between
217 females and ≥ 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 (≥ 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 ± 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 habitat²×e(log(1/100)/500²); 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 (ΔAICc) 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

588 **Acknowledgments**

589 We are grateful to all the professionals from the Institut National de la Recherche Agronomique (N.
590 Cransac), the Office National de la Chasse et de la Faune Sauvage (K. Martinetto, E. Marty, C. Itty,
591 J. Duhayer) and all the trainees for data collection. We also warmly thank Marina Tronchot for
592 providing the vegetation map and Météo France for providing the weather data. Thanks to two
593 anonymous referees for their useful and relevant comments allowing us to improve the manuscript.

594

595 **References**

- 596 Aivaz, A. N., & Ruckstuhl, K. E. (2011). Costs of behavioral synchrony as a potential driver behind
597 size-assorted grouping. *Behavioral Ecology*, 22(6), 1353–1363.
- 598 Alonso, J. C., Salgado, I., & Palacín, C. (2016). Thermal tolerance may cause sexual segregation in
599 sexually dimorphic species living in hot environments. *Behavioral Ecology*, 27(3), 717–724.

- 600 Alves, J., da Silva, A. A., Soares, A. M. V. M., & Fonseca, C. (2013). Sexual segregation in red
601 deer: is social behaviour more important than habitat preferences? *Animal Behaviour*, 85(2),
602 501–509.
- 603 Aublet, J.-F., Festa-Bianchet, M., Bergero, D., & Bassano, B. (2009). Temperature Constraints on
604 Foraging Behaviour of Male Alpine Ibex (*Capra ibex*) in Summer. *Oecologia*, 159(1), 237–
605 247.
- 606 Barboza, P. S., & Bowyer, R. T. (2001). Seasonality of sexual segregation in dimorphic deer:
607 extending the gastrocentric model. *Alces*, 37(2), 275–292.
- 608 Baudière, A. (1970). *Recherches phytogéographiques sur la bordure méridionale du Massif Central*
609 *français (Les Monts de l'Espinouse)* (PhD thesis). Montpellier, France: Université de
610 Montpellier.
- 611 Beier, P. (1987). Sex differences in quality of white-tailed deer diets. *Journal of Mammalogy*, 68(2),
612 323–329.
- 613 Benoist, S., Garel, M., Cugnasse, J.-M., & Blanchard, P. (2013). Human disturbances, habitat
614 characteristics and social environment generate sex-specific responses in vigilance of
615 Mediterranean mouflon. *PloS One*, 8(12), e82960.
- 616 Bleich, V. C., Bowyer, R. T., & Wehausen, J. D. (1997). Sexual segregation in mountain sheep:
617 resources or predation? *Wildlife Monographs*, 3–50.
- 618 Bon, R. 1991. Social and spatial segregation of males and females in polygamous ungulates:
619 proximate factors. In F. Spitz, G. Janeau, G. Gonzalez & S. Aulagnier (Eds) *Proceedings of*
620 *the International Symposium Ongules/Ungulates 1991*, pp. 195–198. Paris, France:
621 S.F.E.M.P.–I.R.G.M.
- 622 Bon, R., & Campan, R. (1996). Unexplained sexual segregation in polygamous ungulates: a defense
623 of an ontogenetic approach. *Behavioural Processes*, 38(2), 131–154.
- 624 Bon, R., Cugnasse, J.-M., Dubray, D., Gibert, P., Houard, P., & Rigaud, P. (1991). Le mouflon de
625 Corse. *Revue d'Écologie (La Terre et La Vie)*, (suppl. 6), 67–110.

- 626 Bon, R., Dardaillon, M., & Estevez, I. (1993). Mating and lambing periods as related to age of
627 female mouflon. *Journal of Mammalogy*, 74(3), 752–757.
- 628 Bon, R., Deneubourg, J.-L., & Michelena, P. (2005). Sexual segregation in ungulates: from
629 individual mechanisms to collective patterns. In K. E. Ruckstuhl & P. Neuhaus, *Sexual*
630 *segregation in vertebrates: ecology of the two sexes* (pp. 180–199). Cambridge, U.K.:
631 Cambridge University Press.
- 632 Bon, R., Dubois, M., & Maublanc, M.-L. (1993). Does age influence between-rams companionship
633 in mouflon (*Ovis gmelini*)? *Revue d'Écologie (La Terre et La Vie)*, 48(1), [57-64](#).
- 634 Bon, R., Gonzalez, G., Bosch, M. D., & Cugnasse, J.-M. (1992). Ram rut-involvement in a hunted
635 population of mouflons. *Acta Theriologica*, 37(1–2), 63–71.
- 636 Bon, R., Joachim, J., & Maublanc, M.-L. (1995). Do lambs affect feeding habitat use by lactating
637 female mouflons in spring in areas free of predators? *Journal of Zoology*, 235(1), 43–51.
- 638 Bon, R., Recarte, J. M., Gonzalez, G., & Cugnasse, J.-M. (1995). Courtship and behavioral
639 maturation of male mouflons. *Acta Theriologica*, 40(3), 283–294.
- 640 Bon, R., Rideau, C., Villaret, J.-C., & Joachim, J. (2001). Segregation is not only a matter of sex in
641 Alpine ibex, *Capra ibex ibex*. *Animal Behaviour*, 62(3), 495–504.
- 642 Bonenfant, C., Gaillard, J.-M., Dray, S., Loison, A., Royer, M., & Chessel, D. (2007). Testing
643 sexual segregation and aggregation: old ways are best. *Ecology*, 88(12), 3202–3208.
- 644 Bonenfant, C., Loe, L. E., Mysterud, A., Langvatn, R., Stenseth, N. C., Gaillard, J.-M., & Klein, F.
645 (2004). Multiple causes of sexual segregation in European red deer: enlightenments from
646 varying breeding phenology at high and low latitude. *Proceedings of the Royal Society of*
647 *London, Series B: Biological Sciences*, 271(1542), 883–892.
- 648 Bourgoin, G., Garel, M., Blanchard, P., Dubray, D., Maillard, D., & Gaillard, J.-M. (2011). Daily
649 responses of mouflon (*Ovis gmelini musimon* × *Ovis* sp.) activity to summer climatic
650 conditions. *Canadian Journal of Zoology*, 89(9), 765–773.

- 651 Bourgoïn, G., Garel, M., Dubray, D., Maillard, D., & Gaillard, J.-M. (2009). What determines
652 global positioning system fix success when monitoring free-ranging mouflon? *European*
653 *Journal of Wildlife Research*, 55(6), 603–613.
- 654 Bourgoïn, G., Garel, M., Van Moorter, B., Dubray, D., Maillard, D., Marty, E., & Gaillard, J.-M.
655 (2008). Determinants of seasonal variation in activity patterns of mouflon. *Canadian*
656 *Journal of Zoology*, 86(12), 1410–1418.
- 657 Boussès, P., & Réale, D. (1998). Biology of twinning and origin of an unusually high twinning rate
658 in an insular mouflon population. *Zeitschrift für Säugetierkunde*, 63, 147–153.
- 659 Bowyer, R. T. (1984). Sexual Segregation in Southern Mule Deer. *Journal of Mammalogy*, 65(3),
660 410–417.
- 661 Bowyer, R. T., & Kie, J. G. (2004). Effects of foraging activity on sexual segregation in mule deer.
662 *Journal of Mammalogy*, 85(3), 498–504.
- 663 Brask, J. B., Croft, D. P., Thompson, K., Dabelsteen, T., & Darden, S. K. (2011). Social preferences
664 based on sexual attractiveness: a female strategy to reduce male sexual attention.
665 *Proceedings of the Royal Society of London B: Biological Sciences*, rspb20112212.
- 666 Burnham, K. P., & Anderson, D. R. (2002). *Model Selection and Multimodel Inference: A Practical*
667 *Information-Theoretic Approach*. New York, NY: Springer Science & Business Media.
- 668 Calhim, S., Shi, J., & Dunbar, R. I. M. (2006). Sexual segregation among feral goats: testing
669 between alternative hypotheses. *Animal Behaviour*, 72(1), 31–41.
- 670 Cazau, M., Garel, M., & Maillard, D. (2011). Responses of heather moorland and mediterranean
671 mouflon foraging to prescribed-burning and cutting. *Journal of Wildlife Management*, 75,
672 967–972.
- 673 Ciuti, S., & Apollonio, M. (2008). Ecological sexual segregation in fallow deer (*Dama dama*): a
674 multispatial and multitemporal approach. *Behavioral Ecology and Sociobiology*, 62(11),
675 1747–1759.

- 676 Clutton-Brock, T. H., Guinness, F. E., & Albon, S. D. (1982). *Red deer: behavior and ecology of*
677 *two sexes*. Chicago, IL: University of Chicago Press.
- 678 Conradt, L. (1998a). Could asynchrony in activity between the sexes cause intersexual social
679 segregation in ruminants? *Proceedings of the Royal Society of London B: Biological*
680 *Sciences*, 265(1403), 1359–1368.
- 681 Conradt, L. (1998b). Measuring the degree of sexual segregation in group-living animals. *Journal*
682 *of Animal Ecology*, 67(2), 217–226.
- 683 Conradt, L. (1999). Social segregation is not a consequence of habitat segregation in red deer and
684 feral soay sheep. *Animal Behaviour*, 57(5), 1151–1157.
- 685 Conradt, L. (2005). Definitions, hypotheses, models and measures in the study of animal
686 segregation. In K. E. Ruckstuhl & P. Neuhaus, *Sexual segregation in vertebrates: ecology of*
687 *the two sexes* (pp. 11–34). Cambridge, U.K.: Cambridge University Press.
- 688 Conradt, L., Clutton-Brock, T. H., & Guinness, F. E. (2000). Sex differences in weather sensitivity
689 can cause habitat segregation: red deer as an example. *Animal Behaviour*, 59(5), 1049–1060.
- 690 Conradt, L., Clutton-Brock, T. H., & Thomson, D. (1999). Habitat segregation in ungulates: are
691 males forced into suboptimal foraging habitats through indirect competition by females?
692 *Oecologia*, 119(3), 367–377.
- 693 Cransac, N., Gérard, J.-F., Maublanc, M.-L., & Pépin, D. (1998). An example of segregation
694 between age and sex classes only weakly related to habitat use in mouflon sheep (*Ovis*
695 *gmelini*). *Journal of Zoology*, 244(03), 371–378.
- 696 Cransac, N., Valet, G., Cugnasse, J.-M., & Rech, J. (1997). Seasonal diet of mouflon (*Ovis*
697 *gmelini*): comparison of population sub-units and age/sex classes.
- 698 Cugnasse, J.-M. (1990). *Inventaire faunistique du massif du Caroux et des monts de l'Espinouse*
699 *(Hérault):(mammifères, oiseaux, reptiles et batraciens)*. Paris, France: Office national de la
700 chasse, Station d'étude sur la faune des milieux méditerranéens.

- 701 Cugnasse, J.-M. (1994). Révision taxinomique des mouflons des îles méditerranéennes. *Mammalia*,
702 58(3), 507–512.
- 703 Darmon, G., Bourgoïn, G., Marchand, P., Garel, M., Dubray, D., Jullien, J.-M., & Loison, A.
704 (2014). Do ecologically close species shift their daily activities when in sympatry? A test on
705 chamois in the presence of mouflon. *Biological Journal of the Linnean Society*, 111(3),
706 621–626.
- 707 Faliu, L., Cugnasse, J.-M., Auvray, F., Orliac, D., & Rech, J. (1990). Le régime alimentaire du
708 mouflon de Corse (*Ovis ammon musimon*) dans le massif du Caroux-Espinouse d’après
709 l’analyse du contenu de 125 panses. *Revue de Médecine Vétérinaire*, 141, 545–556.
- 710 Festa-Bianchet, M. (1988). Seasonal range selection in bighorn sheep: conflicts between forage
711 quality, forage quantity, and predator avoidance. *Oecologia*, 75(4), 580–586.
- 712 Garel, M., Cugnasse, J.-M., Gaillard, J.-M., Loison, A., Gibert, P., Douvre, P., & Dubray, D.
713 (2005). Reproductive output of female mouflon (*Ovis gmelini musimon* x *Ovis* sp.): a
714 comparative analysis. *Journal of Zoology*, 266(1), 65–71.
- 715 Garel, M., Cugnasse, J.-M., Hewison, A. J. M., & Maillard, D. (2006). Errors in age determination
716 of mouflon in the field. *Wildlife Society Bulletin*, 34(2), 300–306.
- 717 Garel, M., Cugnasse, J.-M., Loison, A., Gaillard, J.-M., Vuiton, C., & Maillard, D. (2005).
718 Monitoring the abundance of mouflon in South France. *European Journal of Wildlife*
719 *Research*, 51(2), 69–76.
- 720 Garel, M., Cugnasse, J.-M., & Maillard, D. (2005). Reliability of mouflon aging using
721 morphological characteristics from observations in the field. *Wildlife Biology*, 11(3), 229–
722 235.
- 723 Garel, M., Cugnasse, J.-M., Maillard, D., Gaillard, J.-M., Hewison, A. J., & Dubray, D. (2007).
724 Selective harvesting and habitat loss produce long-term life history changes in a mouflon
725 population. *Ecological Applications*, 17(6), 1607–1618.

- 726 Garel, M., Loison, A., Gaillard, J.-M., Cugnasse, J.-M., & Maillard, D. (2004). The effects of a
727 severe drought on mouflon lamb survival. *Proceedings of the Royal Society of London B:*
728 *Biological Sciences*, 271(Suppl 6), S471–S473.
- 729 Garnick, S., Di Stefano, J., Elgar, M. A., & Coulson, G. (2014). Inter-and intraspecific effects of
730 body size on habitat use among sexually-dimorphic macropodids. *Oikos*, 123(8), 984–992.
- 731 Gaudin, S., Chaillou, E., Cornilleau, F., Moussu, C., Boivin, X., & Nowak, R. (2015). Daughters
732 are more strongly attached to their mother than sons: a possible mechanism for early social
733 segregation. *Animal Behaviour*, 102, 33–43.
- 734 Geist, V. (1971). *Mountain sheep: a study in behaviour and evolution*. Chicago, IL: University of
735 Chicago.
- 736 Gittleman, J. L., & Thompson, S. D. (1988). Energy allocation in mammalian reproduction.
737 *American Zoologist*, 28(3), 863–875.
- 738 Guilhem, C., Bideau, E., Gerard, J.-F., Maublanc, M.-L., & Pépin, D. (2006). Early differentiation
739 of male and female interactive behaviour as a possible mechanism for sexual segregation in
740 mouflon sheep (*Ovis gmelini*). *Applied Animal Behaviour Science*, 98(1), 54–69.
- 741 Guisan, A., & Thuiller, W. (2005). Predicting species distribution: offering more than simple
742 habitat models. *Ecology Letters*, 8(9), 993–1009.
- 743 Hamel, S., & Côté, S. D. (2007). Habitat use patterns in relation to escape terrain: are alpine
744 ungulate females trading off better foraging sites for safety? *Canadian Journal of Zoology*,
745 85(9), 933–943.
- 746 Hamel, S., & Côté, S. D. (2008). Trade-offs in activity budget in an alpine ungulate: contrasting
747 lactating and nonlactating females. *Animal Behaviour*, 75(1), 217–227.
- 748 Hofmann, R. R. (1989). Evolutionary steps of ecophysiological adaptation and diversification of
749 ruminants: a comparative view of their digestive system. *Oecologia*, 78, 443–457.
- 750 Jackes, A. (1973). *The use of wintering grounds by red deer in Ross-shire, Scotland*. [Ph.D. thesis],
751 Edinburgh, U.K.: University of Edinburgh.

- 752 Jakimchuk, R. D., Ferguson, S. H., & Sopuck, L. G. (1987). Differential habitat use and sexual
753 segregation in the Central Arctic caribou herd. *Canadian Journal of Zoology*, 65(3), 534–
754 541.
- 755 Jarman, P. J. (1974). The social organisation of antelope in relation to their ecology. *Behaviour*,
756 48(3/4), 215–267.
- 757 Kamler, J. (2001). Morphological variability of forestomach mucosal membrane in red deer, fallow
758 deer, roe deer and mouflon. *Small Ruminant Research*, 41(2), 101–107.
- 759 Le Pendu, Y., Briedermann, L., Gerard, J.-F., & Maublanc, M.-L. (1995). Inter-individual
760 associations and social structure of a mouflon population (*Ovis orientalis musimon*).
761 *Behavioural Processes*, 34(1), 67–80.
- 762 Le Pendu, Y., Maublanc, M.-L., Briedermann, L., & Dubois, M. (1996). Spatial structure and
763 activity in groups of Mediterranean mouflon (*Ovis gmelini*): a comparative study. *Applied*
764 *Animal Behaviour Science*, 46(3), 201–216.
- 765 Lewis, S., Phillips, R. A., Burthe, S. J., Wanless, S., & Daunt, F. (2015). Contrasting responses of
766 male and female foraging effort to year-round wind conditions. *Journal of Animal Ecology*,
767 84(6), 1490–1496.
- 768 Liao, J., & McGee, D. (2003). Adjusted coefficients of determination for logistic regression. *The*
769 *American Statistician*, 57(3), 161–165.
- 770 Loe, L. E., Irvine, R. J., Bonenfant, C., Stien, A., Langvatn, R., Albon, S. D., ... Stenseth, N. C.
771 (2006). Testing five hypotheses of sexual segregation in an arctic ungulate. *Journal of*
772 *Animal Ecology*, 75(2), 485–496.
- 773 Loudon, A. S. I. (1985). Lactation and neonatal survival of mammals. *Symposia of the Zoological*
774 *Society of London*, 54, 183–207.
- 775 Maier, J. A., & White, R. G. (1998). Timing and synchrony of activity in caribou. *Canadian*
776 *Journal of Zoology*, 76(11), 1999–2009.

- 777 Main, M. B., & Coblentz, B. E. (1990). Sexual segregation among ungulates: a critique. *Wildlife*
778 *Society Bulletin (1973-2006)*, 18(2), 204–210.
- 779 Main, M. B., & Coblentz, B. E. (1996). Sexual segregation in Rocky Mountain mule deer. *The*
780 *Journal of Wildlife Management*, 60(3), 497–507.
- 781 Main, M. B., & Du Toit, J. (2005). Sex differences in reproductive strategies affect habitat choice in
782 ungulates. In K. E. Ruckstuhl & P. Neuhaus, *Sexual segregation in vertebrates: ecology of*
783 *the two sexes* (pp. 148–163). Cambridge, U.K.: Cambridge University Press.
- 784 Main, M. B., Weckerly, F. W., & Bleich, V. C. (1996). Sexual segregation in ungulates: new
785 directions for research. *Journal of Mammalogy*, 77(2), 449–461.
- 786 Marchand, P., Garel, M., Bourgoïn, G., Dubray, D., Maillard, D., & Loison, A. (2014). Impacts of
787 tourism and hunting on a large herbivore’s spatio-temporal behavior in and around a French
788 protected area. *Biological Conservation*, 177, 1–11.
- 789 Marchand, P., Garel, M., Bourgoïn, G., Dubray, D., Maillard, D., & Loison, A. (2015a). Coupling
790 scale-specific habitat selection and activity reveals sex-specific food/cover trade-offs in a
791 large herbivore. *Animal Behaviour*, 102, 169–187.
- 792 Marchand, P., Garel, M., Bourgoïn, G., Dubray, D., Maillard, D., & Loison, A. (2015b). Sex-
793 specific adjustments in habitat selection contribute to buffer mouflon against summer
794 conditions. *Behavioral Ecology*, 26(2), 472–482.
- 795 Marchand, P., Garel, M., Bourgoïn, G., Michel, P., Maillard, D., & Loison, A. (2014). Habitat-
796 related variation in carcass mass of a large herbivore revealed by combining hunting and
797 GPS data. *The Journal of Wildlife Management*, 78(4), 657–670.
- 798 Marchand, P., Redjadj, C., Garel, M., Cugnasse, J.-M., Maillard, D., & Loison, A. (2013). Are
799 mouflon *Ovis gmelini musimon* really grazers? a review of variation in diet composition.
800 *Mammal Review*, 43(4), 275–291.

- 801 Martinetto, K., Cugnasse, J.-M., & Gilbert, Y. (1998). La cohabitation du mouflon méditerranéen
802 (*Ovis gmelini musimon* x *Ovis* sp.) et des touristes dans le massif du Caroux-Espinouse
803 (Hérault). *Gibier Faune Sauvage*, 15, 905–919.
- 804 Michelena, P., Noël, S., Gautrais, J., Gerard, J.-F., Deneubourg, J.-L., & Bon, R. (2006). Sexual
805 dimorphism, activity budget and synchrony in groups of sheep. *Oecologia*, 148(1), 170–180.
- 806 Montgelard, C., Nguyen, T. C., & Dubray, D. (1994). Genetic variability in French populations of
807 the Corsican mouflon (*Ovis ammon musimon*): analysis of 2 blood proteins and red-cell
808 blood groups. *Genetics Selection Evolution*, 26(4), 303–315.
- 809 Nekola, J. C., & White, P. S. (1999). The distance decay of similarity in biogeography and ecology.
810 *Journal of Biogeography*, 26(4), 867–878.
- 811 Oftedal, O. T. (1985). Pregnancy and lactation. In R. J. Hudson & R. G. White, *Bioenergetics of*
812 *wild herbivores* (pp. 215–238). Boca Raton, FL: CRC Press.
- 813 Pérez-Barbería, F. J., Robertson, E., & Gordon, I. J. (2005). Are social factors sufficient to explain
814 sexual segregation in ungulates? *Animal Behaviour*, 69(4), 827–834.
- 815 Pérez-Barbería, F. J., Robertson, E., Soriguer, R., Aldezabal, A., Mendizabal, M., & Pérez-
816 Fernández, E. (2007). Why do polygynous ungulates segregate in space? Testing the
817 activity-budget hypothesis in Soay sheep. *Ecological Monographs*, 77(4), 631–647.
- 818 Porter, W. P., & Kearney, M. (2009). Size, shape, and the thermal niche of endotherms.
819 *Proceedings of the National Academy of Sciences*, 106(Supplement 2), 19666–19672.
- 820 R Core Team. (2016). *R: a language and environment for statistical computing*. Vienna, Austria: R
821 Foundation for Statistical Computing.
- 822 Ruckstuhl, K. E. (1998). Foraging behaviour and sexual segregation in bighorn sheep. *Animal*
823 *Behaviour*, 56(1), 99–106.
- 824 Ruckstuhl, K. E. (1999). To synchronise or not to synchronise: a dilemma for young bighorn males?
825 *Behaviour*, 136(6), 805–818.

- 826 Ruckstuhl, K. E. (2007). Sexual segregation in vertebrates: proximate and ultimate causes.
827 *Integrative and Comparative Biology*, 47(2), 245–257.
- 828 Ruckstuhl, K. E., & Neuhaus, P. (2002). Sexual segregation in ungulates: a comparative test of
829 three hypotheses. *Biological Reviews of the Cambridge Philosophical Society*, 77(01), 77–
830 96.
- 831 Ruckstuhl, K. E., & Neuhaus, P. (2005). *Sexual segregation in vertebrates: ecology of the two*
832 *sexes*. Cambridge, U.K.: Cambridge University Press.
- 833 Shrestha, A., Van Wieren, S., Van Langevelde, F., Fuller, A., Hetem, R., Meyer, L., ... Prins, H.
834 (2014). Larger antelopes are sensitive to heat stress throughout all seasons but smaller
835 antelopes only during summer in an African semi-arid environment. *International Journal*
836 *of Biometeorology*, 58(1), 41–49.
- 837 Singh, N. J., Bonenfant, C., Yoccoz, N. G., & Côté, S. D. (2010). Sexual segregation in Eurasian
838 wild sheep. *Behavioral Ecology*, 21(2), 410–418.
- 839 Sundaresan, S. R., Fischhoff, I. R., & Rubenstein, D. I. (2007). Male harassment influences female
840 movements and associations in Grevy's zebra (*Equus grevyi*). *Behavioral Ecology*, 18(5),
841 860–865.
- 842 Thiebaut, B. (1971). La transition climatique dans le massif de l'Agoût. *Vie Milieu*, 22, 167–206.
- 843 Tronchot, M. (2008). *Cartographie des habitats du massif du Caroux-Espinouse (Hérault) à partir*
844 *de photos aériennes de 2005* (Technical report). Paris, France: Groupement d'Intérêt
845 Environnemental et Cynégétique du Caroux-Espinouse–Office National de la Chasse et de
846 la Faune Sauvage.
- 847 Türcke, F., & Schmincke, S. (1965). *Das Muffelwild: Naturgeschichte, Hege, und Jagd*. Hamburg,
848 Germany: Parey.
- 849 Uloth, W. (1972). To the history of the distribution, introduction and cross-breeding of the
850 Tyrrhenis mouflon in Europe and oversea. *Acta Theriologica*, 17(31), 412–413.

- 851 Villaret, J. C., & Bon, R. (1995). Social and Spatial Segregation in Alpine Ibex (*Capra ibex*) in
852 Bary, French Alps. *Ethology*, *101*(4), 291–300.
- 853 Weckerly, F. W. (2001). Are large male Roosevelt elk less social because of aggression? *Journal of*
854 *Mammalogy*, *82*(2), 414–421.
- 855 Xu, F., Ma, M., Yang, W., Blank, D., & Wu, Y. (2012). Test of the activity budget hypothesis on
856 Asiatic ibex in Tian Shan Mountains of Xinjiang, China. *European Journal of Wildlife*
857 *Research*, *58*(1), 71–75.

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	Females with lambs closer to refuge habitats during early lactation	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)	Males in habitats with abundant but lower quality food	Different nutritional requirements during the end of gestation and early lactation for reproductive females → Higher segregation	Increased use of habitats with abundant low-quality food as males become older	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	Large males in habitats buffering harsh climatic conditions	<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	Segregation, except during rut	No specific patterns	As males become older, segregation with females increases but decreases with adult males	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)	Lower synchrony in mixed-sex groups	<i>Lower synchrony</i>	Lower synchrony in heterogeneous reproductive status groups	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.

863 **Table 2.**

864 Monthly differences in habitat use for each combination of age, sex and-reproductive status classes based on generalized linear models with binomial
 865 error structure

Class	Selected habitat	Month											
		1	2	3	4	5	6	7	8	9	10	11	12
Females– adult males	Moorlands		M**			M**	M***	M**					
	Grass					F*	F***	F***					
	Slope	F***	F*	F***	F***	F***	F***	F***	M**	M***		F*	F***
Females with lambs– adult males	Moorlands		M***		M**	M**	M***	M**					
	Grass		F _{wL} *			F _{wL} *	F _{wL} ***	F _{wL} ***			F _{wL} *		
	Slope	F _{wL} ***	F _{wL} *	F _{wL} ***	F _{wL} ***	F _{wL} ***	F _{wL} **	F _{wL} ***	M**	M**			F _{wL} ***
Females without lambs–adult males	Moorlands		M*			M**	M***	M**					
	Grass					F _{w/oL} *	F _{w/oL} ***	F _{w/oL} **	F _{w/oL} *				
	Slope	F _{w/oL} *		F _{w/oL} ***	F _{w/oL} ***	F _{w/oL} ***	F _{w/oL} ***	F _{w/oL} **	M*	M***		F _{w/oL}	F _{w/oL} ***
Females with lambs– females without lambs	Moorlands					F _{w/oL} **							
	Grass								F _{wL} **	F _{w/oL} **			
	Slope	F _{wL} **		F _{wL} *	F _{wL} ***					F _{wL} *			
Females– yearling males	Moorlands												
	Grass												
Females– young adult males	Slope	M ₁ *	M ₁ *		F***	F***						F*	
	Moorlands				M ₂₃ ***	M ₂₃ ***							
	Grass				F*	F*							
Adult– yearling males	Slope			F**	F***	F***	F***	F***	M ₂₃ **			F*	
	Moorlands												
	Grass			M*			M***	M**					
Adult– yearling males	Slope	M ₁ ***	M ₁ *	M ₁ *	M ₁ ***	M ₁ ***	M ₁ **	M ₁ **			M*	M**	M ₁ *

Adult–young adult males	Moorlands Grass Slope	M ₂₃ [*]	M ₂₃ [*] M [*] M ₂₃ ^{***}	M ₂₃ ^{***}	M [*] M ₂₃ [*]	M ₂₃ [*] M [*]	M ^{**}	M ₂₃ ^{***}
----------------------------	-----------------------------	------------------------------	--	--------------------------------	--	--	-----------------	--------------------------------

866 Moorlands: proximity to moorlands, Grass: proximity to grass, Slope: proximity to slope; F: females; F_{wL}: females with lambs; F_{w/oL}: females without
867 lambs; M: adult males; M₁: yearling males; M₂₃: 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; M₁: yearling males; M₂₃: 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; M₂₃: young
906 adult males; M₁: 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).

913