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

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Segregation between the sexes or related to age and/or reproductive status is common in many animal taxa, particularly in dimorphic species. The causes of this segregation remain difficult to disentangle, despite numerous attempts. This is probably due to the difficulty of obtaining sufficient data on animal behaviour (e.g. habitat use, activity budgets) and group composition (age/sex and reproductive status) during the various phases of the species' reproductive cycle. Based on an intensive long-term monitoring of a Mediterranean mouflon, *Ovis gmelini musimon* x *Ovis* sp., population, we concurrently assessed five hypotheses for segregation linked to forage selection (FSH), reproductive strategy (RSH), social preference (SPH), activity budget (ABH) and weather sensitivity (WSH). We found marked segregation between most age/sex classes. Age-dependent segregation among males was increasingly marked as their age difference increased and segregation between the sexes also increased as males became older and larger. Over the year, segregation between sex, age and reproductive status classes was lowest during the rut. We also observed the highest synchrony of activity in groups composed of individuals of similar age/sex class or reproductive status. Females occurred closer to both secure and high-quality food habitats, especially during the lambing and rearing periods, whereas males used less secure and lower quality habitats as they aged. Differences in habitat use between age/sex classes provided partial or full support for the RSH and FSH. Large males were preferentially observed at higher altitude than females during hot summer days to buffer against heat stress, in agreement with the WSH. A preference for interacting and grouping with peers that express similar activity patterns (ABH and SPH) appears to be the main driver of segregation in this population. Our study confirms the strong multifactorial nature of segregation in ungulates.

Keywords:

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

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

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

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

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

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

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

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

These different drivers of segregation may have independent effects or may work in tandem and fluctuate across the year to generate the observed patterns of segregation (e.g. Alves et al., 2013; Conradt, 1999; Singh et al., 2010). Thus, the relative importance of these drivers should depend on the physiological status of individuals and on environmental conditions encountered (Alves et al., 2013; Bonenfant et al., 2004; Ciuti & Apollonio, 2008; Loe et al., 2006). Despite an abundant literature on segregation in large herbivores, most studies have focused on certain components of segregation only (i.e. either segregation between individuals of different age/sex classes, or segregation between females with or without offspring) and restricted their analyses to the corresponding hypotheses (but see e.g. Alves et al., 2013; Bonenfant et al., 2004; Loe et al., 2006). This may be due to the difficulty of simultaneously collecting (at the same time or in the same study area) sufficient data on the behaviour (e.g. habitat use, activity budget) of individuals with variable characteristics (sex, age, reproductive status). In addition, to explain segregation between sex and age classes, especially in hot environments, the WSH has been largely ignored, despite an increasing number of studies revealing specific behaviours in animals with contrasting body size, when facing adverse weather conditions (Alonso et al., 2016; Aublet, Festa-Bianchet, Bergero, & Bassano, 2009; Conradt et al., 2000; Garnick, Di Stefano, Elgar, & Coulson, 2014; Shrestha et al., 2014).

To tease apart the relative contribution of habitat, social and climatic factors for explaining segregation, we analysed a large data set composed of more than 7800 spatially explicit observations of groups of the polygynous, dimorphic Mediterranean mouflon, *Ovis gmelini musimon* x *Ovis* sp., in the south of France, between 1994 and 2014. We combined this data set with detailed information on the activity states of each individual recorded from almost 3000 scan observations of these groups, between 1996 and 1997. We first assessed the temporal patterns of segregation in relation to sex, age and reproductive status of females. We then investigated the degree to which differential habitat use and weather conditions drive this pattern. We tested the influence of stressful climatic conditions on segregation during summer, the critical season for mouflon in our study area (see Bourgoin et al., 2008, 2011 and Marchand et al. 2015b for details on adult behavioural responses to hot conditions, and Garel, Loison, Gaillard, Cugnasse, & Maillard, 2004 for consequences for the survival of young and body mass of adults). We thus expected habitat segregation between the smallest individuals (i.e. females), individuals of intermediate size (i.e. young adult males) and large males to be more pronounced during summer because of an increasing use of high altitudes (providing thermal shelter, Marchand et al 2015b) with increasing body size and hence sensitivity to the hottest conditions. Finally, we assessed whether differences in activity synchrony between individuals could explain segregation. Based on these analyses, we assessed the support for the above-mentioned hypotheses underlying segregation in large herbivores (FSH, RSH, WSH, SPH, ABH; Table 1).

<H1>METHODS

<H2>Study Area

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

No large predators were present in the study area during most of the study period, although evidence of wolf, *Canis lupus*, presence (mouflon killed by wolf, visual/camera trap observations) were recently recorded (since spring–summer 2014), with a maximum of one wolf observed at a time. Other potential predators for new-born and sick mouflon are free-roaming dogs, golden eagles, *Aquila chrysaetos*, and red foxes, *Vulpes vulpes*. Stalking and drive hunting were permitted each year, from 1 September to the end of February, except in a central Wildlife Reserve of 1658 ha (Garel et al., 2007; Marchand, Garel, Bourgoin, Dubray, et al., 2014; Marchand et al., 2015a). Between 200 and 600 mouflon were harvested per year during the study period 2002–2014. Population monitoring from foot ground counts (Garel, Cugnasse, Loison, et al., 2005) did not reveal any marked population trends in abundance.

<H2>Study population and species

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

The Mediterranean mouflon is a gregarious, sexually dimorphic species. In this population during the 2002–2014 period, mean spring body mass ± SD was 22.7 ± 5.1 kg for females ≥ 1 year old (*N* = 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, respectively (*N* = 114, 137 and 175, respectively; sexual size dimorphism of 66.4% between females and ≥ 4-year-old males; see also Garel et al., 2007 for similar differences in autumn).

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

<H2>Observational data

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

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

<H2>Habitat types

Mouflon are grazers (sensu Hofmann, 1989) with digestive ability to process a diet dominated by grass species (Hofmann, 1989; Kamler, 2001). They mainly feed in open habitats such as pastures, meadows and sown crops devoted to wildlife (i.e. grass-rich areas), consuming a large proportion of herbaceous species (40–50% grasses in our study population), and, to a lesser extent, in moorland habitat with abundant ligneous species (broom, heather, fern and blueberry; Cransac, Valet, Cugnasse, & Rech, 1997; Faliu, Cugnasse, Auvray, Orliac, & Rech, 1990; Marchand et al., 2013). In our population, previous analyses of vegetation in grass-rich areas have shown higher digestive and energetic values for plant species present in this habitat than in areas rich in ligneous species (Cazau, Garel, & Maillard, 2011). Accordingly, mouflon were in better condition when their home range included a large proportion of grass-rich areas (Marchand, Garel, Bourgoin, Michel, et al., 2014). For these reasons, we considered this habitat to be higher quality for mouflon than moorlands. We used this contrast to investigate the role of resource quality (see also Benoist et al., 2013) on segregation (FSH hypothesis). Based on a land cover map (derived from the processing of a SPOT satellite image from July 2005 and field validation; 25 m grid resolution; Tronchot, 2008), we computed two distance maps (distance to grass-rich areas and distance to moorland areas). The resolution of these maps was four times higher than the resolution of animal observations (125 m). We thus downgraded them to 125 m to match the grid map historically used for recording locations of observed animals. We used these maps to compute the proximity to grass-rich and to moorland areas (distance to habitat^2×e(log(1/100)/500^2); adapted from Nekola & White, 1999) for each animal location. Proximity ranged in a nonlinear manner from 1 (mean estimated location of the animal (i.e. centre of a 125x125 m pixel; see above 'Observational data') in the focal habitat) to near 0 (beyond a cut-off distance of 500 m). The cut-off distance of 500 m corresponded to the upper limit within which 95% of the distances travelled by 26 adult GPS-collared mouflon over 2 h were included (Marchand et al., 2015b). We considered habitat beyond this cut-off distance to have low or no influence on movements or habitat selection. We also used a digital elevation model (25 m grid resolution downgraded to 125 m resolution; source: BD ALTI data set from the Institut Géographique National, France) to get elevations and derive a map of proximity to refuge areas (i.e. proximity to steep slopes (> 30°); see Marchand, Garel, Bourgoin, Dubray, et al., 2014; Marchand et al., 2015a). As precise information on habitat-specific climate was not available, we focused on elevation as a proxy for ambient temperature: as temperature decreases with elevation, selection for elevation is one of the ways by which mountain ungulates buffer against summer conditions (ibex, *Capra ibex*: Aublet et al., 2009; mouflon: Marchand et al., 2015b). Maps of elevation and proximity to refuge areas allowed us to specifically test the WSH and RSH hypotheses, respectively.

<H2>Weather data

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

<H2>Statistical analyses

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

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

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

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

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

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

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

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

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

Finally, we computed the synchronization coefficient developed by Conradt (1998a) on our activity data recorded in 1996–1997. We considered individuals that were eating, moving and vigilant as active. The synchronization coefficient ranges from 0 (no synchronization of activity within groups) to 1 (complete synchronization). This coefficient was computed with data recorded from March to November for (1) females only, adult males only and mixed groups; (2) groups of males, considering all groups composed of males of similar age class (i.e. groups of adults, of young adults and of yearling males) and groups composed of males of different age classes. We computed synchrony also for (3) groups of females with lambs (i.e. groups with $N_{\mathrm{lambs}} \geq N_{\mathrm{females}}$), females without lambs and mixed (i.e. groups with $N_{\mathrm{females}} > N_{\mathrm{lambs}} > 0$) females for each month around lambing and early lactation (April–June). Randomization tests were performed ($N = 10\,000$) for each group type to compute confidence intervals and to test for differences between groups. All analyses were implemented in R 3.3.1 (R Core Team, 2016).

<H1>RESULTS

<H2>Variation in patterns of segregation

<H3>Segregation between sex and age classes

Adult males and females were strongly segregated from each other all year round (all SSAS tests for segregation: $P_{\mathrm{segregation}} < 0.001$; Fig. 1a). The level of segregation increased during spring and remained high until September (highest differences between observed SSAS and random association (grey area in Fig. 1a) before decreasing during autumn. Although the differences in observed SSAS versus random association between males and females were lowest during the rutting period, segregation remained significant ($P_{\mathrm{segregation}} < 0.001$ from October to December). As males aged, segregation from females increased (SSAS tests for segregation: females versus yearling males: $P_{\mathrm{segregation}} \leq 0.01$ during only 3 months; females versus young adult males: $P_{\mathrm{segregation}} < 0.05$ for 11 months, including 9 months with $P_{\mathrm{segregation}} < 0.001$; Fig. 1a, b, c). Yearling males and females were significantly segregated from each other only during the lambing and rearing periods ($P_{\mathrm{segregation}} \leq 0.002$ in April–May; $P_{\mathrm{segregation}} = 0.012$ in July; Fig. 1c). Young adult males segregated from females most of the year (all $P_{\mathrm{segregation}} < 0.05$, except in January), particularly during spring and summer (all $P_{\mathrm{segregation}} < 0.001$), but less so during the rutting period and the first part of the winter ($P_{\text{segregation}}$ = 0.029 and 0.169 in December and January, respectively; Fig. 1b). Outside the November–January period, young males (yearling and young adult males) segregated less from adult males as they aged (all $P_{\text{segregation}} < 0.001$ for both adult–yearling males and adult–young adult males from February to October, but with a larger difference between observed SSAS and random association for adult–yearling males than for adult–young adult males outside the rutting period; Fig. 2a, b).

<H3>Reproductive status of females

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

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

Regarding the relative contribution of habitat variables for explaining segregation (i.e. adjusted coefficient of determination for logistic regression: adjusted R^2; Liao & McGee, 2003), we observed low differences in habitat use between age, sex and reproductive status classes (Fig. 4), suggesting that, most of the year, differences in habitat use are not a main driver of segregation in our mouflon population. The lowest annual differences in habitat use were observed between females and yearling males (mean adjusted R^2 ± SD = 0.6 ± 0.7%), and between females with versus without lambs (0.8 ± 1.0%; Fig. 4a, c). Females with lambs were generally observed closer to safer habitat around the peak of births than females without lambs (April: $P < 0.001$; Table 2). The highest differences in habitat use were observed between adult males and females (mean adjusted R^2 ± SD = 3.4 ± 4.3%, 3.1 ± 4.2% and 5.1 ± 5.3% for all females, females without lambs and females with lambs, respectively), with the highest values occurring during the peak of births (i.e. in April; 15.4%, 14.8% and 20.0%, respectively; Fig. 4a, c). Consistently, females were observed closer to slopes most of the year (all $P< 0.05$ for 8–9 months) and to grass-rich areas mostly during spring and summer (all $P< 0.05$ for 3 - 5 months) compared to adult males (Table 2). Conversely, adult males were observed closer to moorlands (all $P < 0.01$ during 4–5 months) more often than females, and particularly during the end of spring and summer. As yearling males tended to remain with their mothers (see above and Fig. 1c), they selected similar habitats to females (all $P > 0.05$ for the proximity to moorlands and grass), but females remained closer to slopes during the lambing and early lactation period ($P < 0.001$ in April–May). As males aged, differences in habitat use with females increased (1.2 ± 1.8% for females versus young males; paired Mann–Whitney test: $P\leq 0.002$ for females–adult males versus females–yearling males and for females–adult males versus females–young adult males; $P = 0.179$ for females–young adult males versus females–yearling males; Bonferroni-corrected alpha level = 0.0125; Fig. 4a), but decreased with adult males (3.1 ± 2.7% and 1.2 ± 1.3% for adult males versus yearling and young males, respectively; paired Mann–Whitney test: $P = 0.010$ for adult males–young adult males versus adult males–yearling males; Fig. 4b).

Testing the influence of ambient temperature on the differential use of elevation between age/sex classes in July–August, we found stronger support for the full model including the interaction between temperature and elevation for females versus adult males and young adult males (ΔAICc = 4.495 and 14.495, respectively, compared to a model with elevation only). At low elevation, ambient temperature did not affect the proportion of females versus adult males and young adult males, but the proportion decreased at high elevation in hot weather, especially for young adult males (Fig. 5). We did not find support for the full model including the interaction between temperature and elevation for adult versus yearling males (ΔAICc = 1.129), adult versus young adult males (ΔAICc = 1.532) and females versus yearling males (ΔAICc = 3.612).

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

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

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

<H1>DISCUSSION

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

The annual pattern of sexual segregation that we report, with a peak in spring and summer and a minimum at the end of autumn and early winter (peak rut; Bon, Recarte, Gonzalez, & Cugnasse, 1995), is in agreement with previous studies on this population (Cransac et al., 1998) and on other sexually dimorphic wild ungulates (e.g. Alves et al., 2013; Bleich et al., 1997; Geist, 1971; Ruckstuhl & Neuhaus, 2005).During the rut, mouflon males roam from one female group to another (Bon et al., 1992), searching for ewes in oestrus, which leads to this low level of segregation. However, large mixed groups of mouflon were observed mostly from December to February (Bon et al., 1991), suggesting that mechanisms other than rutting behaviour could be involved, including environmental and physiological constraints. In winter, mouflon are mostly active during the few hours of daylight to limit heat loss and energy expenditure during the coldest period of the day (i.e. night; Bourgoin et al., 2008; Darmon et al., 2014), which may lead to a higher synchrony of activity and cohesion in mixed-sex groups. In addition, both sexes of mouflon have similar habitat use and diets during this period (Cransac et al., 1997; Marchand et al., 2015a), which can be explained by limited resource availability, leading animals to group on the remaining feeding patches. Hence, mouflon of different sex, age and reproductive status are more likely to be active at approximately the same time and in the same areas during winter, leading to a low level of segregation.

Adult and young adult males were observed less in proximity to slopes and grass-rich areas (i.e. secure and high-quality and quantity food areas, respectively), favouring areas close to moorlands as they aged and their body mass increased, compared with yearling males and females. This result is in line with the greater ability of larger animals to process more fibrous foods than smaller individuals (support for the FSH) and supports previous studies on cervids (Bonenfant et al., 2004; Conradt, Clutton-Brock, & Thomson, 1999). Most of the differences between males and females in their proximity to moorlands and grass-rich areas occurred during spring and early summer, when abundant and high-quality vegetation is widespread. While grass-rich areas seem to provide a high proportion of the diet of mouflon (Cransac et al., 1997; Faliu et al., 1990; Marchand et al., 2013) and to be valuable resources for their body condition (Marchand, Garel, Bourgoin, Michel, et al., 2014), selection of shrub leaves, buds and twigs, and avoidance of woody parts of the plants, may provide highly digestible food (with low fibre content) for mouflon. It would be interesting to collect information on diet composition and quality in both sexes during the spring and summer period (i.e. the period with the highest segregation values and differences in habitat use). A recent study on habitat use based on GPS locations of mouflon in this population demonstrated strong selection for grass-rich areas on plateaus (slope $< 10°$ and altitude > 900 m above sea level) by males in spring and summer, while females selected, to a lesser extent, grass-rich areas from mid-winter to early summer (Marchand et al., 2015a). These differences from our results can be explained by the habitat variables used in the analyses, as the grass-rich habitats of Marchand et al. (2015a) were divided into two groups (on plateaus versus slopes) and included heather and blueberry moorlands. In addition, our study used coarse location data and focused on proximity to the three habitats of interest to test our hypotheses, while Marchand et al. (2015a) performed habitat selection analyses with fine scale GPS data. Differences may originate from the limits of data derived from direct observation of animals in a relatively forested and mountainous environment compared to GPS data which provide locations of animals during the day and night, in open and forested habitats (Bourgoin et al., 2009) and irrespective of environmental conditions.

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

As males aged, they progressively separated from their mothers to form groups of young adult males, with increasing levels of segregation through spring and summer (Fig. 1b), before associating with older males (Bon, Deneubourg, & Michelena, 2005; Bon, Dubois, & Maublanc, 1993). These observations and the low proportion of segregation explained by differences in habitat use highlight the marked social preference of animals to group with individuals of the same sex and age classes, supporting the SPH (Bon, Rideau, Villaret, & Joachim, 2001; Le Pendu et al., 1995; Le Pendu, Maublanc, Briedermann, & Dubois, 1996; Pérez-Barbería et al., 2005; Villaret & Bon, 1995). Previous studies in this population highlighted the negative consequences of dry and warm summers (Bourgoin et al., 2011; Garel, Loison, Gaillard, Cugnasse, & Maillard, 2004; Marchand et al., 2015b). According to the WSH, larger mouflon are expected to suffer more from extreme climatic conditions (here, high temperatures) than smaller ones and, therefore, to select habitats that buffer adverse climatic conditions (here, higher elevation; Alonso et al., 2016; Aublet et al., 2009; Conradt et al., 2000). In a previous study based on GPS location data and thermal sensors in this population (Marchand et al., 2015b), female mouflon traded thermal cover against safer habitats to promote lamb survival by avoiding unsafe plateaus and selecting steep rocky areas. In contrast, the larger adult males selected those habitats providing the best thermal cover (i.e. the plateaus). The combination of these findings collected at a fine scale and our observations suggests that larger individuals (i.e. young adult and adult males versus females) selected habitats offering better buffering against constraining summer climatic conditions. This mechanism may contribute to habitat segregation, at least during hot summers, in agreement with the WSH.

The higher activity synchrony in homogeneous versus mixed age/sex groups highlighted in several studies on wild and feral ungulates, including this study, provides support for the ABH (e.g. Calhim, Shi, & Dunbar, 2006; Conradt, 1998a; Ruckstuhl, 1998, 1999). Additionally, large group size and low synchrony in behaviour were linked to a higher probability of group fission, followed by higher synchrony among the remaining individuals in the group (Calhim et al., 2006). However, the authors of some studies, including experiments, found less support for the ABH, and considered that alone it cannot adequately explain segregation (Bowyer & Kie, 2004; Michelena et al., 2006; Pérez-Barbería et al., 2007). In an experiment on Soay sheep, differences in synchrony were mostly explained by sex rather than by differences in body size (Pérez-Barbería et al., 2007). This contrasting result could be because the sheep in this experiment segregated by sex and not by body mass, and because ungulates tend to be more synchronized within a group than between groups (Maier & White, 1998). To disentangle the mechanism explaining these contrasting results between experiments with domestic animals (Pérez-Barbería et al., 2007) and studies on free-ranging ungulates (our results; Alves et al., 2013; Bon et al., 2001), observations on captive wild ungulates in similar experimental conditions (relatively homogeneous and space-limited habitat), or on larger groups of free-ranging domestic ungulates, should be performed.

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

Our study confirms the strong multifactorial origins of segregation in mouflon, mostly between adult males and females, but also between age (e.g. Alves et al., 2013) and reproductive classes (Alves et al., 2013; Bonenfant et al., 2004; Loe et al., 2006; Singh et al., 2010). The relative contribution of the different factors to segregation may vary according to the species, the environment (e.g. predation risk, habitat heterogeneity) and the season (e.g. reproductive period, climatic conditions, resource availability). In our study area, the summer climatic conditions are the most constraining for mouflon (Bourgoin et al., 2008, 2011; Garel et al., 2004) and may lead to the two sexes selecting different habitats (our results; Marchand et al., 2015b). In a context of global warming, such differences between the sexes in response to hot climatic conditions may increase and occur during longer periods in the future. In addition to changes in habitat use, as a response to limiting climatic conditions, animals may also modify their activity (Alonso et al., 2016; Lewis, Phillips, Burthe, Wanless, & Daunt, 2015), at least with mouflon females (Bourgoin et al., 2008, 2011). Investigating how males and females change their activity in response to stressful summer climatic conditions would help disentangle the relative contribution of weather in driving segregation patterns. This better understanding of behavioural processes will ultimately help to identify the pathways through which climate change impacts the species' population dynamics and distribution (Guisan & Thuiller, 2005).

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Appendix

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

General predictions				Detailed predictions				Source
Hypotheses	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**	**➔ 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**	*Not related to reproductive status*		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 dimorphism and/or different nutritional requirements lead to segregation	No pattern (except around lambing and lactation for reproductive females)	**Lower synchrony in mixed-sex groups**	*Lower synchrony*	**Lower synchrony in heterogeneous reproductive status groups**	**Synchrony decreases with higher body size dimorphism**	Conradt, 1998a; Ruckstuhl, 1998, 1999

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

Table 2.

Monthly differences in habitat use for each combination of age, sex and-reproductive status classes based on generalized linear models with binomial 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^{**}	$F_{w/oL}^{*}$				
	Grass					$F_{w/oL}^{*}$	$F_{w/oL}^{***}$	$F_{w/oL}^{**}$	M^{**}				
	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				$F_{w/oL}^{**}$					$F_{w/oL}^{**}$			
	Grass								F_{wL}^{**}	F_{wL}^{*}			
	Slope	F_{wL}^{**}		F_{wL}^{*}	F_{wL}^{***}								
Females–yearling males	Moorlands												
	Grass												
	Slope	M_1^{*}	M_1^{*}		F^{***}	F^{***}					F^{*}		
Females–young adult males	Moorlands				M_{23}^{***}	M_{23}^{***}							
	Grass				F^{*}	F^{*}							
	Slope			F^{**}	F^{***}	F^{***}	F^{***}	F^{***}	M_{23}^{**}		F^{*}		
Adult–yearling males	Moorlands						M^{***}	M^{**}					
	Grass			M^{*}			M_1^{**}	M_1^{**}					
	Slope	M_1^{***}	M_1^{*}	M_1^{*}	M_1^{***}	M_1^{***}				M^{*}	M^{**}		M_1^{*}

Adult–young adult males	Moorlands		M_{23}^{*}		M^{*}	M_{23}^{*}		
	Grass		M^{*}		M_{23}^{*}	M^{*}		
	Slope	M_{23}^{*}	M_{23}^{***}	M_{23}^{***}			M^{**}	M_{23}^{***}

Moorlands: proximity to moorlands, Grass: proximity to grass, Slope: proximity to slope; F: females; F_{wL}: females with lambs; $F_{w/oL}$: females without lambs; M: adult males; M_1: yearling males; M_{23}: young adult males. Only the class observed closer to the corresponding habitat and significant results ($P<0.05$) are reported.

$^{*}P<0.05$; $^{**}P<0.01$; $^{***}P<0.001$.

Figure captions

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

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

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

Figure 4. Annual patterns of the adjusted coefficient of determination for logistic regressions (adjusted R^2; Liao & McGee, 2003) quantifying the global role of the habitat variables in explaining segregation for each combination of age, sex and reproductive status classes, based on generalized linear models with binomial error structure. F: females; FwL: females with lambs; Fw/oL: females without lambs; M: adult males; M_1: yearling males; M_{23}: young adult males.

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

Figure 6. Observed synchrony (± 95% confidence interval based on 10 000 resamplings) in groups of (a) females and adult males and (b) males according to their age, during the March–November period, and (c) females according to their reproductive status during the lambing and early lactation periods (April–June). Numbers above the x-axis are numbers of groups used for computation. F: females; FwL: females with lambs; Fw/oL: females without lambs; M: adult males; M_{23}: young adult males; M_1: yearling males; '-': mixed group.

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