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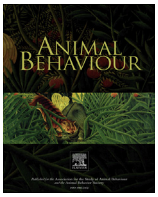

Coupling scale-specific habitat selection and activity reveals sex-specific food/cover trade-offs in a large herbivore

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The balance between food and perceived predation risk has been revealed as one of the primary drivers of animal habitat selection. However, few studies have investigated how spatiotemporal scales and movement/activity patterns shape responses to this food/cover trade-off while accounting for individual characteristics (e.g. sex) and for variation in predation risk (e.g. hunting) and in resource abundance/quality. We hence studied temporal changes in habitat selection of 30 GPS-collared females and 15 males of Mediterranean mouflon, *Ovis gmelini musimon*×*Ovis* sp., at two scales, i.e. 48 h home range selection within a subpopulation area (broad scale) and choice of movement steps (defined as the linear segment between two consecutive locations) according to activity state (fine scale), in southern France. During the hunting-free/food-abundant period, males selected at both scales the foraging habitats providing the best conditions for optimizing their future reproductive success and only selected areas perceived as safe during inactive steps. During the corresponding lambing period, and at both scales, females selected areas perceived as safe that should optimize lamb survival. They switched to the best foraging habitats only when lambs were weaned and only for active steps. By contrast, during hunting, when food was also scarce, both sexes selected home ranges with high proportions of the habitats perceived as safe, in which they performed all their activities. This result suggested that risk avoidance exceeded all the other individual and environmental factors in the hierarchy of the determinants of habitat selection during the hunting period. Coupling scale-specific habitat selection and activity patterns was hence decisive in disclosing how individuals fulfil their specific needs under seasonally changing levels of habitat attributes important for fitness.

The analysis of how, when and why animals select particular habitats is a central issue in ecology. It has become crucial for conservation given that habitat loss and fragmentation have been identified as major threats to biodiversity (Fahrig, 2003; Vitousek, Mooney, Lubchenco, & Melillo, 1997). Habitat selection is indeed not only the primary driver of population distribution but also contributes to individuals' survival and reproductive performance, and hence to population dynamics (Gaillard et al., 2010; Pulliam & Danielson, 1991).

Animals confronted with heterogeneous landscapes continuously assess the resources and conditions available in their surroundings. They should select the habitats allowing them to fulfil their internal needs and ultimately to ensure survival and reproduction (Hall, Krausman, & Morrison, 1997). Decisions taken at a given spatiotemporal scale may, however, depend on resources, environmental conditions, perceived predation risk and presence of conspecifics in the area chosen at broader scales. Habitat selection is hence a complex hierarchical decision-making process (Gaillard et al., 2010; Johnson, 1980; Morris, 1987; Senft et al., 1987) in which trade-offs are common. Indeed, foraging and protection attributes are rarely maximized in the same habitat type (Brown, 1999; Houston, McNamara, & Hutchinson, 1993; Lima & Dill,

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1990). As an example, this pervasive food/cover trade-off has repeatedly been reported in empirical studies on large herbivores (e.g. red deer, *Cervus elaphus*: Mysterud & Ostbye, 1999; moose, *Alces alces:* Dussault et al., 2005).

The relative importance of each of the components of this trade-off may, however, vary with spatiotemporal scale, the most important factors in terms of fitness being expected to be selected at the highest scales (Rettie & Messier, 2000; Senft et al., 1987). Furthermore, habitat selection can also vary through time as resource quantity, quality and availability are dynamic, as well as other ecosystem characteristics (e.g. presence of predators or human activities). Again, scale is important, as selection criteria can vary at the interannual, seasonal and even within-day scales (night versus day; Godvik et al., 2009; McLoughlin, Wal, Lowe, Patterson, & Murray, 2011).

In addition to space and time, spatial behaviours should also depend on individuals' own traits (e.g. sex and age, Miquelle, Peek, & Van Ballenberghe, 1992) and states (e.g. reproductive status, Bjørneraas et al., 2011), which modify their energy requirements and their perception of or susceptibility to risk factors (Ruckstuhl and Neuhaus, 2006). The presence of an offspring at heel, and ultimately the need to ensure offspring survival, are, for example, common explanations for ungulate females selecting areas perceived as safe during the rearing period (bighorn sheep, *Ovis canadensis*: Festa-Bianchet, 1988; Stone's sheep, *Ovis dalli stonei*: Rachlow & Bowyer, 1998; fallow deer, *Dama dama*: Ciuti, Bongi, Vassale, & Apollonio, 2006; mountain goat, *Oreamnos americanus*: Hamel & Côté, 2007). This pattern, which is observed even in areas where natural predators have disappeared for a long time or in protected ones (e.g. Alpine ibex, *Capra ibex*: Grignolio, Rossi, Bertolotto, Bassano, & Apollonio, 2007), may be related to the long past evolution of species with natural predators (Byers, 1997).

In ruminant herbivores, an overlooked constraint on individuals at the daily level is imposed by their foraging and digestive features (Belovsky & Slade, 1986; Mysterud, 1998). Indeed, acquisition of energy can be decomposed into food searching, food acquisition and food processing (Cederlund, 1989; Hanley, 1982). The activity pattern of ruminants is consequently characterized by successive foraging and ruminating–resting bouts (Bourgoin et al., 2011; Gillingham, Parker, & Hanley, 1997; Pagon et al., 2013) that should influence which habitats are selected at the within-home range scale (Ager, Johnson, Kern, & Kie, 2003; Godvik et al., 2009; Mysterud, Larsen, Ims, & Ostbye, 1999). Fully exploring at which scale and how individuals with specific attributes adjust the balance between their ever-changing needs should allow researchers to decipher how populations are distributed in space in a dynamic context.

The increasing deployment of GPS technology and associated recording devices on animals ('biologgers', Ropert-Coudert and Wilson 2005), together with the development of GIS software and analytical methods, has greatly improved our ability to understand habitat selection patterns at multiple scales (Cagnacci, Boitani, Powell, & Boyce, 2010). Up to now, however, few studies on large terrestrial herbivores have combined information obtained from activity loggers and GPS locations (but see Bjørneraas et al., 2011; Ewald, Dupke, Heurich, Müller, & Reineking, 2014; Godvik et al., 2009; Van Moorter, Visscher, Jerde, Frair, & Merrill, 2010).

In this study, we aimed at determining how activity patterns influence habitat selection in males and females of a large herbivore, the Mediterranean mouflon, *Ovis gmelini musimon*×*Ovis* sp., in the Caroux-Espinouse massif, southern France. In this area, two of the main drivers of habitat selection, namely the 'predation' pressure (here, hunting) and food abundance/quality, vary strongly through time (contrast between a hunting and food-restricted period versus a nonhunting and food-abundant period; Fig. 1). We took advantage of the recent advances in GPS collars including head motion sensors allowing us to combine the analyses of activity data at the daily scale with location data at both daily and seasonal scales.

We hypothesized that factors determining habitat selection act as a hierarchical cascade from the home range to the within-home range scales (Fig. 1). At the top of the hierarchy, we expected the predominant factor to be risk avoidance when the risk of being killed is high and foraging in good-quality areas when the risk of being killed is low. The highest risk is during the hunting period, when food abundance and quality are low and the weather is generally inclement. We hence expected that the main habitats selected during this period should correspond to areas perceived as safe at all scales, for both males and females and irrespective of the activity level (Dussault et al., 2005; Herfindal et al., 2009; Mysterud & Ostbye, 1999). Even though food resources are senescent, autumn forage contributes to improving body condition before winter in large herbivores (Hurley et al., 2014), so that the baseline expectation in the absence of hunting would have been a selection for foraging areas. When disturbance and predation risks are low and forage is abundant and of high quality (spring and summer; no hunting), mouflon should select the habitat types providing the best foraging conditions at the home range scale. However, ungulate females with young offspring at heel have been consistently shown to trade off favourable foraging conditions with areas perceived as safe even in the absence of predators (e.g. Grignolio et al., 2007). Sex differences in habitat selection at the home range scale should therefore be greatest in spring with females favouring perceived risk avoidance over food before weaning and males expected to make the opposite choice. At a fine scale and for both sexes, habitat selection criteria were expected to be influenced by the foraging/ruminating–resting cycle. They should therefore differ between active and inactive phases (Bjørneraas et al., 2011; Godvik et al., 2009), with a selection of areas perceived as safe during resting/rumination bouts that may allow individuals to offset choices expected at a broader scale, in particular for males. Coupling analyses of activity level with fine and home range scale habitat selection allowed us to test the aforementioned hypotheses and to disclose the multiscale adjustments made by individuals when selecting habitats under different levels of perceived risk and foraging conditions.

METHODS

Study Site and Population

We collected data in the Mediterranean mouflon population inhabiting the Caroux-Espinouse massif (43°38′N, 2°58′E, 17 000 ha, 150–1124 m above sea level), in southern France (Fig. 2). The study site was characterized by a Mediterranean climate with both oceanic and mountainous influences (Baudière, 1962). Droughts often happened during the summer (Garel, Loison, Gaillard, Cugnasse, & Maillard, 2004) whereas snowfalls during winter were often limited to plateaux and variable from year to year.

Since 1973, hunting has been the main source of regulation for this population. It has also involved behavioural and life history consequences for mouflon (Benoist, Garel, Cugnasse, & Blanchard, 2013; Garel et al., 2007; Marchand et al., 2014). During the study period (2003–2010), hunting occurred from 1 September to the end of February. On average 378 (SD = 109) animals were harvested per year (out of probably more than 2500 individuals; Marchand et al., 2014), evenly distributed between both sexes. Driven hunts with hounds were carried out on Wednesdays, Saturdays, Sundays and public holidays, target species being wild boar, *Sus scrofa scrofa*,

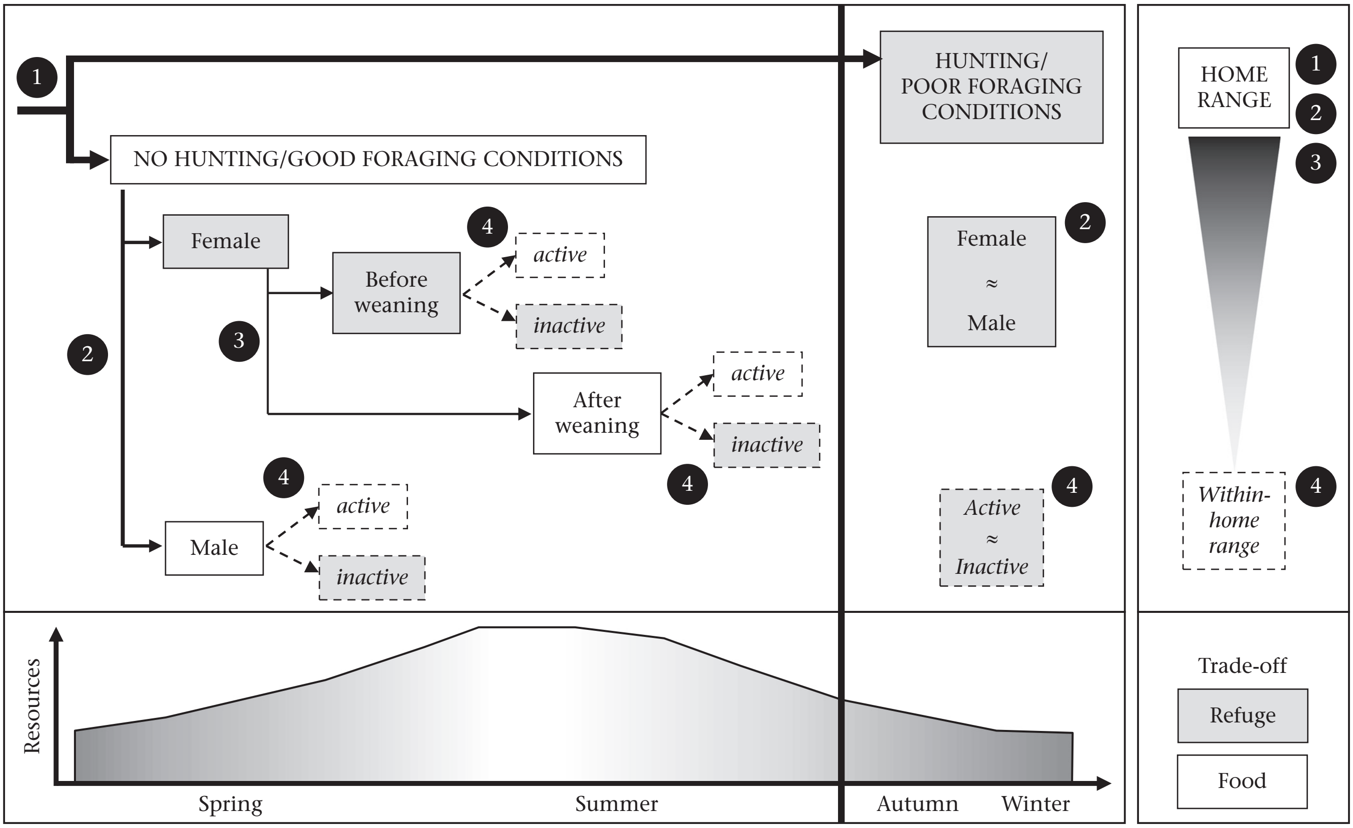

Figure 1. Schematic representation of our main hypotheses concerning variations in sex-, scale- and activity-specific habitat selection of Mediterranean mouflon. Habitat selection was expected to vary according to temporal variations in the food/cover trade-off resulting from the main constraints affecting large herbivores' habitat selection (food abundance/quality, 'predation' pressure [here, hunting] and rearing of young for females). Numbers indicate the scale at which a specific decision was expected to be taken (1 = home range to 4 = within home range). Background colour indicates priority is expected to be given to cover (grey) or food (white).

female mouflon (68% of harvested females) and occasionally roe deer, *Capreolus capreolus*. On all the other weekdays, male mouflon were the main target of hunters (66% of harvested males) and these were stalked. Hunting was forbidden in a 1658 ha central wildlife reserve, in which 16% of GPS-collared animals locations were recorded during the hunting period. As behavioural responses of mouflon to hunting disturbance also occurred in this protected area (Benoist et al., 2013; Marchand et al., 2014), these data were not distinguished in our analyses.

Roe deer and wild boar (at low density compared to mouflon) were the other two free-ranging ungulates inhabiting this massif. Mouflon had no natural predators in the study area, except for free-roaming dogs, golden eagles, *Aquila chrysaetos*, and red foxes, *Vulpes vulpes*, which are anecdotally reported to kill newborns and sick mouflon.

The lambing season was late March to June, with most births occurring from early April to mid-May, and lambs were strongly dependent on their mothers until weaning, by the end of June (Bon, Dardaillon, & Estevez, 1993). The lambing period was hence considered as the whole period from birth to weaning, i.e. from early April to the end of June. A high percentage of females reproduce every year (81% of yearlings and 91% of adults, Garel et al., 2005; see also section GPS Locations and Head Motion Sensors). The gestation period is 5 months, implying that most of the females were impregnated between early November and mid-December (Garel et al., 2005). Reproductive males roam from one female group to another and exhibit courtship behaviour from the beginning of October to early January (Bon, Gonzales, Bosch, & Cugnasse, 1992). As the habitat selection of males may be strongly related to females' choices during the rutting period, we did not expect sex-specific habitat selection during this period.

Vegetation Structure and Habitat Maps

The vegetation structure was markedly influenced by topography, with deep valleys indenting plateaux (altitude >900 m above sea level and slope <10°) and originating in steep slopes (Fig. 2), and by land use changes that occurred during the last few decades (Fig. 2, Table 1; Garel et al., 2007). Plateaux were either exploited for coniferous forestry (*Pinus sylvestris*, *Pinus nigra*, *Picea abies*), or mainly composed of heather moorlands (*Erica cinerea* and *Calluna vulgaris*) and other grass-rich areas (pastures, meadows, artificial cultures devoted to wildlife and blueberry moorlands, *Vaccinium myrtillus*). These grass-rich areas provided abundant food for mouflon (*Brachypodium sylvaticum*, *Festuca rubra*, *Festuca paniculata*, *Festuca ovina*, *Carex* sp.; Baudière, 1970; Cransac, Valet, Cugnasse, & Rech, 1997; Marchand et al., 2013). As elevation decreased and slope increased, heather moorlands tended to be replaced by encroaching broom (*Cytisus oromediterraneus*, *Cytisus scoparius*) and fern, *Pteridium aquilinum*, moorlands, providing less favourable foraging conditions for mouflon (Baudière, 1970; Cazau, Garel, & Maillard, 2011). The bottom of the valleys were largely covered with deciduous trees (mainly beech, *Fagus sylvatica*, chestnut trees, *Castanea sativa*, and evergreen oak, *Quercus ilex*), whereas the last uncovered slopes were composed of rocky areas.

We categorized habitats into seven significant types encompassing this marked structure and the conditions they provided in terms of forage, perceived predation risk or cover against inclement

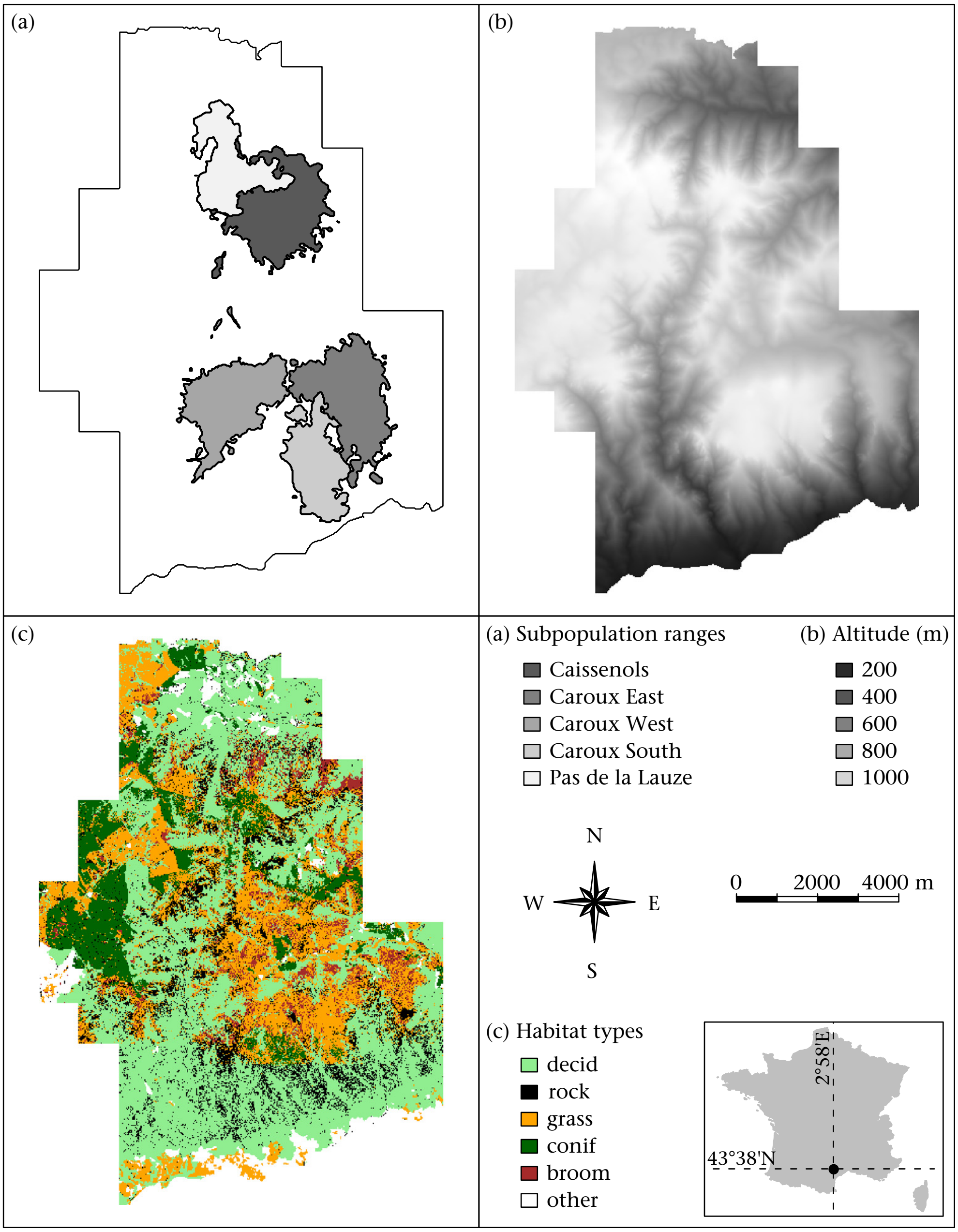

Figure 2. Description of the Caroux-Espinouse massif, southern France (inset map), where habitat selection by Mediterranean mouflon was investigated during 2003–2010. (a) Ranges of the five subpopulations considered (see Table 1 and section Home Range Selection for details). (b) Digital elevation model. (c) Habitat types (for details of classification, see Table 1). Villages and hamlets were grouped in the 'other' category, which was excluded from analyses since it represented a tiny percentage of the available areas (on average 0.8%, range 0.01–1.8%).

weather conditions (Table 1). We did not consider actual risk of being killed given that harvests may preferentially occur in habitats selected by animals because they feel safer there. We rather positioned each habitat on a gradient of perceived risk based on the literature showing the importance of steep slopes in antipredator behaviours (and distance to these areas perceived as safer; Hopewell, Rossiter, Blower, Leaver, & Goto, 2005; Singh, Bonenfant, Yoccoz, & Côté, 2010). We also accounted for criteria that are involved in determining the perceived risk of being killed by hunters, such as visibility (related to hunters being detected by animals; Benoist et al., 2013) or accessibility for humans. Mouflon should hence perceive plateaux as risky because of the low slope and large distance to steep areas (Table 1). By contrast, we expected slopes, in particular the steepest ones offering high visibility while being difficult to access for potential predators and hunters, to be perceived as safer by mouflon (Table 1). Two types of grass-rich areas were hence distinguished depending on the position either on slopes or on plateaux (grass and grass.p; Table 1). Similarly, rocky areas were divided into two classes (rock: slopes $<30°$; rock.sl: slope $\geq 30°$) to account for varying degrees of perceived risk. Finally, we distinguished between coniferous and deciduous forests, both providing cover from inclement weather but the latter being steeper (Table 1) and providing fruits in autumn that may represent a significant part of the mouflon's diet in this population (Cransac, Valet, et al., 1997; Faliu, Cugnasse, Auvray, Orliac, & Rech, 1990). We derived habitat types from the processing (*k*-means

Table 1

Characteristics (mean [SD]) of the seven habitat types defined in this study of habitat selection of Mediterranean mouflon during 2003–2010 in the Caroux-Espinouse massif, southern France, and their relative percentages within the five subpopulations studied

Code	Description	Altitude (m)	Slope (°)	Visibility	Distance to slope ≥ 30°	Caissenols	Pas de la Lauze	Caroux West	Caroux South	Caroux East	Perceived predation risk	Cover against bad weather	Foraging conditions
conif	Coniferous trees	998 [100]	10 [7]	0*	641 [554]	11.6	9.2	1.5	4.7	1.0	0	++	–
grass.p	Grass-rich areas on plateaux: heather and blueberry moorlands, pastures, meadows and artificial cultures devoted to wildlife with slope <10° and altitude >900 m above sea level	1035 [42]	5 [2]	146 [162]	663 [548]	3.1	2.4	8.9	15.8	14.6	++	– –	+++
grass	Grass-rich areas in slopes: heather and blueberry moorlands, pastures, meadows and artificial cultures devoted to wildlife with slope >10° and altitude <900 m above sea level	823 [224]	19[10]	143 [185]	262 [274]	15.9	13.1	18.3	6.5	20.5	+	–	++
broom	Broom and fern moorlands	890 [130]	20 [10]	63 [113]	272 [321]	5.5	6.1	8.1	2.3	8.0	+	+	+
rock	Rocky areas with slope <30°	846 [204]	19 [8]	94 [128]	208 [364]	7.8	3.8	6.0	8.8	5.6	–	–	– –
rock.sl	Rocky areas with slope ≥30°	738 [190]	39[7]	110 [124]	0	8.4	10.3	7.9	12.0	8.0	– –	–	– –
decid	Deciduous trees: beech, *Fagus sylvatica*, chestnut tree, *Castanea sativa*, holm oak, *Quercus ilex*, and mixed deciduous patches	674 [228]	26 [10]	0*	129 [241]	46.8	53.2	49.1	49.3	42.3	–	++	0

The expected benefits of each habitat type in terms of food and perceived predation risk are based on previous knowledge of wild sheep requirements (Cransac, Valet, et al., 1997; Geist, 1971; Marchand et al., 2013; Risenhoover & Bailey, 1985; Risenhoover, Bailey, & Wakelyn, 1988; Wakelyn, 1987) and average slope, visibility (*considered to be null in forested areas; see Benoist et al., 2013 for details) and distance to areas of low perceived predation (steep slope, i.e. ≥30°). '+' for a high value, '–' for a low value, '0' for a neutral effect.

unsupervised classification) of a SPOT satellite image taken in July 2005 and field validation in a 25 × 25 m grid (Tronchot, 2008), and slope from a digital elevation model (Fig. 2, resolution = 25 m; source: BD ALTI data set from the Institut Géographique National, http://professionnels.ign.fr/bdalti). We characterized each pixel by the dominant habitat type.

GPS Locations and Head Motion Sensors

During the springs of 2003–2009, we trapped a total of 30 females and 15 males (adults ≥ 3 years old) that we fitted with Lotek GPS collars 3300S (revision 2; Lotek Engineering Inc., Carp, Ontario, Canada).

Only four of 30 GPS-collared females were not lactating when captured. The majority of GPS-collared females therefore had a lamb at heel during their monitoring.

We scheduled GPS collars to record animal locations at intervals of 20 min, for identical 48 h periods for each individual in a specific year (from day 1 at 0300 hours to day 3 at 0240 hours UTC), but only one to four times per month (mean ± SD = 1.8 ± 1.0 48 h recording period per month per individual) to preserve batteries. This scheduling procedure allowed us to collect location data at a high frequency over nearly 1 year (mean ± SD individual monitoring duration = 329 ± 122 days). We screened these data for erroneous locations (Bjørneraas, Van Moorter, Rolandsen, & Herfindal, 2010) and interpolated isolated missing locations (i.e. unsuccessful fixes and removed erroneous locations) as the middle of the straight line between the previous and next location (Cargnelutti et al., 2007; see Appendix for details of GPS row data processing). We restricted our analyses to 48 h recording periods for which a minimum of 80% of the expected locations (i.e. 115/144) were actually recorded by GPS collars (i.e. maximum of 20% unsuccessful or interpolated data; $N = 956$; Table A1).

GPS collars also included head motion sensors continuously recording head movements for each 5 min period. We summed the data for the four 5 min periods preceding the final location of a step to describe head motions during each 20 min movement step (the linear segment between two consecutive locations). We then combined 20 min head motions and step characteristics (step length and turning angles) to distinguish between active and inactive steps (see Appendix and Fig. A1 for details).

Home Range Selection

We derived home ranges used by each individual during each 48 h period from a utilization distribution (UD) computed using the Brownian bridge movement model (BBMM; Horne, Garton, Krone, & Lewis, 2007). BBMM is a continuous time stochastic model of movement that incorporates an animal's movement path and time between locations to calculate UD, the probability density function providing the likelihood of an animal occurring in each unit of a defined area. The locations recorded by immobile GPS collars in the field (lost GPS collars or from dead animals; number of collars = 9; number of locations = 7965; see Ethical note) were used to compute GPS location error δ from BBMM as the mean distance between the centroids of data recorded by a still GPS collar and each of these locations, i.e. 24.5 m. The Brownian motion variance was determined for each 48 h trajectory using the maximum likelihood approach developed by Horne et al. (2007). We thus defined home ranges for each 48 h period as the set of pixels including 90% of the space use estimated by BBMM, to avoid the inclusion of unused areas (Bjørneraas et al., 2012).

Previous studies revealed matching spatial and genetic structure in this population, suggesting the existence of several spatially segregated subpopulations (Kings & Brooks, 2003; Martins et al., 2002; Maublanc, Dubois, Bon, & Le Pendu, 1994) with specific available ranges. Sex-specific criteria for home range habitat selection and their annual variation at a large scale were hence assessed by comparing habitat use during each 48 h period with available subpopulation ranges. Each mouflon was assigned to one of the five subpopulations identified according to the site where it was captured and the area it commonly used (see Fig. 2 and Table A1 for details). Then, we defined the available subpopulation range as the area including all the 48 h home ranges from GPS-collared individuals of the corresponding subpopulation (Fig. 2).

To determine the criteria for habitat selection within subpopulation ranges and their sex-specific annual variations, we computed Manly–Chesson selection ratios for each home range. We divided the proportion of each habitat type in each home range by the proportion of that habitat type in the corresponding subpopulation range (Manly, McDonald, Thomas, McDonald, & Erickson, 2002). We obtained standardized selection ratios by scaling selection ratios between 0 and 1 for each home range. They could be interpreted as the estimated probability that, for any selection event, an animal would choose the focal habitat type over all others, assuming habitat types were all equally available (Manly et al., 2002).

We modelled the variations of the standardized selection ratios for each habitat type and for each sex according to day of the year (corresponding to recording day 2, see GPS locations and head motion sensors), using general additive mixed models (GAMMs; Wood, 2006). GAMMs are well suited to model both linear and nonlinear relationships in habitat selection studies (Aarts, MacKenzie, McConnell, Fedak, & Matthiopoulos, 2008). A cyclic cubic regression spline constrained model predictions for the first and last day of the year to match. We added mouflon identity and subpopulation as nested grouping factors (individual mouflon within subpopulation, given that movements of mouflon between subpopulations were unlikely) to account for dependency among repeated measurements (random intercept models). We used a Tweedie family distribution with a logit link because subpopulation ranges included habitat types that were not always included in home ranges, resulting in a large number of zeros in the response variable (Dunn & Smyth, 2005; Tweedie, 1984). We restricted the Tweedie index parameters to values between 1 and 2 and estimated them within this scale using the maximum likelihood method (Dunn & Smyth, 2005).

For a given sex, we considered a focal habitat type as selected or avoided when the Bayesian confidence interval (95% confidence interval, CI; Wood, 2006) did not overlap 1/7, i.e. the reference value indicating a random use of the seven habitat types if equally available in the subpopulation range. An estimated degree of freedom (edf) of the smooth function of 0 indicated a constant selection over the year whereas a nonlinear response was indicated by an edf >1.

Activity States and Fine-scale Selection

Based on changes in habitat selection at the home range scale, we defined sex-specific ecologically relevant seasons. We then estimated sex- and season-specific habitat selection for each activity state at the scale of an individual's movement step using step selection functions (SSF; Forester, Im, & Rathouz, 2009; Fortin et al., 2005; Thurfjell, Ciuti, & Boyce, 2014). We only included 20 min steps actually recorded by GPS collars (i.e. two consecutive non-interpolated locations; see Appendix for details) in these analyses.

We coupled each observed step with 10 random steps according to the area used by an individual at that time (Boyce, 2006). We sampled these 10 random steps from around the starting location of the observed step, using the step length and turning angle distributions from each sex for the corresponding activity state during a given season (Fortin et al., 2005; see Fig. A2 for details of these distributions). We compared habitat types at end locations of observed and random steps using conditional logistic regression and a matched case–control design (Hosmer & Lemeshow, 2000). When calculating robust standard errors (see Fortin et al., 2005 and Forester et al., 2009 for details), we assumed autocorrelation to be strong within each 48 h period but steps were considered as independent between two 48 h periods (minimum of 6 days between two periods). The coefficients provided by the regression model are the log odds ratios for a step in a specific habitat type being chosen during a specific activity state relative to a reference habitat type and to a reference activity state for which $\beta = 0$. We chose to use inactive steps in grass-rich areas on slopes (‘grass’, Table 1) as the reference, as they provided the most explicit representation of the results. For each sex in each relevant season previously defined, a specific SSF was computed including habitat type, activity state and all their interactions but one as explanatory variables. Indeed, as conditional logistic regression did not allow us to compute coefficients for all levels of the interaction between two factors, we did not include in our models the level ‘active − grass’ (i.e. grass-rich areas on slopes).

We considered that nonoverlapping 95% CIs (based on robust standard errors) within and between habitat types across activity states indicated significant differences in habitat selection, a method recognized as very conservative (e.g. Cumming & Finch, 2005).

Ethical Note

We followed the conditions detailed in the specific accreditations delivered to the Office National de la Chasse et de la Faune Sauvage by the Préfecture de l’Hérault (prefectorial decrees no. 2005-15-057, 2006-15-040, 2008-15-122, 2009-15-059) and the Préfecture de Paris (prefectorial decree no. 2009-014) in agreement with the French environmental code (Art. R421-15 to 421-31 and R422-92 to 422-94-1).

Mouflon were caught using two types of traps (2 × 0.9 m and 1.8 m high or 10 × 5 m and 2 m high) and two types of drop nets (23 × 23 m or 46 × 46 m) baited with salt licks. These traps and nets allowed us to capture a maximum [realized mean] of six [1.2], eight [2.4], six [3.2] and 11 [3.6] mouflon at the same time during the study period (for details, see Cugnasse, 1982; Dubray, 1993). Most captures in traps were at night. Traps were hence checked early every morning during the capture period to reduce the time spent between capture and handling and avoid possible heat stress. For the same reason, traps were generally positioned under tree cover. Captures with drop nets were triggered manually. Consequently, animals were processed immediately after the capture. No specific bedding, food or water were thus required for either trap or net captures. All the interventions were carried out by professionals from the Office National de la Chasse et de la Faune Sauvage trained in wild animal capture and handling. Subsequently, animals were removed from the trap/net and restrained with their eyes covered to reduce stress. After measurements were taken and the collar fitted (5–10 min handling), they were released on site. All efforts were made to minimize this handling period. The priority was furthermore given to the handling and release of lactating females when caught without their lamb. We did not record any adverse effect of mother–lamb separations that occasionally occurred as a result of captures.

GPS collars weighed 400 g, corresponding to 1.6% and 1.0% of the average body mass of GPS-collared females and males, and to 2.2% and 0.7% of the smallest and largest individual's body mass, respectively. When tying GPS collars around a mouflon's neck, we left a 3 cm gap between the collar and the animal's neck to allow seasonal variation in neck circumference while ensuring that the collar would not rotate. After data acquisition (around 1 year depending on the batteries' life), we manually triggered the collars to fall off the animals with a remote drop-off system. We did not record any adverse effects or behavioural modifications linked to the wearing of the collars during the study.

Among the nine collars used to determine GPS location error (see Home range selection section in Methods), five were carried by mouflon that died during the monitoring (four females and one male of the 34 and 16 monitored during the study period, respectively). These mortality rates (11.7% and 6.3% for females and males, respectively) were in the range of those observed in adults of our population (0.5–26.4%; Cransac, Hewison, Gaillard, Cugnasse, & Maublanc, 1997) and of other ungulate populations (2.2–21.3%; see Gaillard, Festa-Bianchet, & Yoccoz, 1998 for a review).

RESULTS

Home Range Selection

Most habitat types were not used in line with their availability in subpopulation ranges, with patterns varying through the year. Indeed, the standardized selection ratios showed marked nonlinear annual variation for all the habitat types in both sexes (all P values <0.05 and all edfs >1; Fig. 3).

Males and females displayed similar patterns of home range selection from the beginning of October to the end of February, i.e. during most of the hunting/food-restricted period. The similarity between the sexes was at its highest during the rutting period (i.e. November–mid-December) when all habitat-specific 95% CIs of males and females overlapped. Plateaux generally perceived as unsafe (coniferous forests and grass-rich areas) and broom moorlands were consistently avoided by both sexes, whereas rocky areas and deciduous forests (i.e. refuge and cover areas) were generally selected (at least until December). However, males concentrated on the steepest rocky areas (‘rock.sl’, i.e. with slope $\geq 30°$) whereas females selected the less steep areas (‘rock’, i.e. with slope $<30°$). From the beginning of January, which corresponded to the second half of the gestation, females started to select grass-rich areas situated on slopes, indicating food-related selection criteria.

By contrast, strong differences between the sexes appeared when hunting was mostly over and forage was abundant and of high quality, i.e. during March to September (spring and summer). Males strongly selected areas where food was abundant and of high quality (grass-rich areas on plateaux) and used cover areas perceived as safe less than they were available (deciduous forests and rocky areas situated on slopes). For females, two successive phases could be distinguished during the same period. From the beginning of March to the end of June, when lambs were particularly vulnerable, females selected areas perceived as safe (rocky areas with slope $<$ or $\geq 30°$) and grass-rich areas on slopes, whereas they avoided plateaux perceived as unsafe and broom moorlands. During July to September, when lambs had grown and started eating plants, females no longer selected rocky slopes (perceived as safe) and no longer avoided grass-rich areas.

Activity States and Fine-scale Selection

Given the seasonal variation in the sex-specific patterns of home range selection highlighted in the preceding section (Fig. 3), we distinguished between March to September (mostly hunting-free and food abundant) and October to February (hunting, food restricted) for males, and March to June (mostly hunting-free, food abundant and small lamb at heel), July to September (mostly

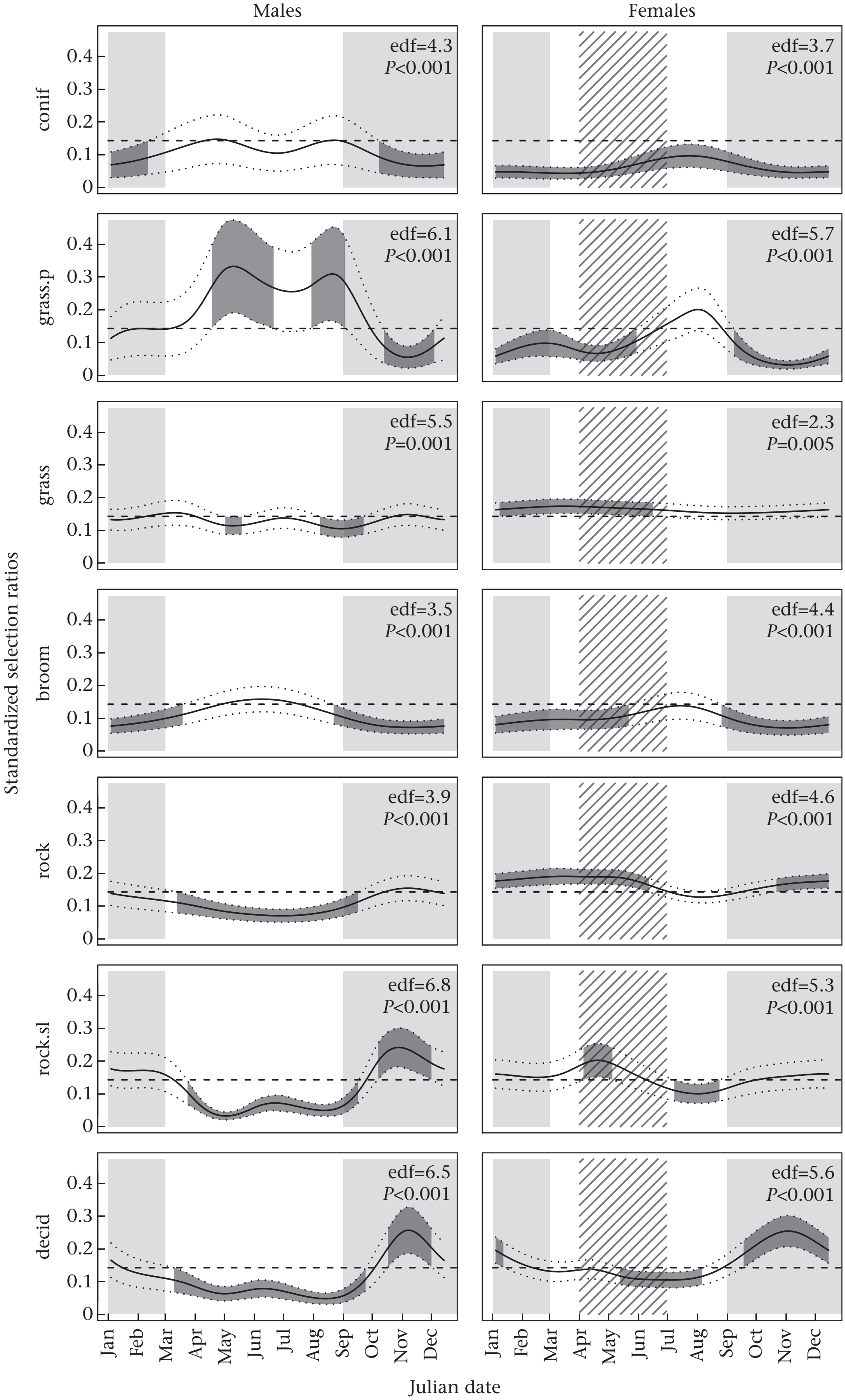

Figure 3. Seasonal variation in sex-specific habitat selection of Mediterranean mouflon. The relationships between the compositions of 48 h and subpopulation ranges (solid line) were modelled for each habitat type (see Table 1) and for both sexes using generalized additive mixed models including individual mouflon and subpopulation as nested grouping factors ($N = 956$ home ranges). Estimated degrees of freedom (edf) of the smooth functions and associated P value are shown. An edf of the smooth function of 0 indicates a constant selection over the year whereas an edf >1 indicates a nonlinear response. Dotted lines indicate 95% confidence intervals (95% CIs). A focal habitat type was considered as significantly selected or avoided (dark grey) when the 95% CI did not include 1/7; this reference value indicates that the proportion of the habitat used equalled the habitat-specific availability (dashed black line). The tick marks on the x-axis indicate the first day of each month. Light grey shading: hunting period; diagonal stripes: lambing period (females only).

hunting-free, food abundant and older lambs at heel) and October to February (hunting, food restricted) periods for females when analysing fine-scale selection. Inactive steps in grass-rich areas on slopes were fixed as the reference steps.

During March to September (mostly hunting-free and food abundant), step selection functions revealed changes in fine-scale habitat selection pattern of males as a function of activity states (Fig. 4a). Rocky areas with slope < or ≥30° (areas perceived as safe) were selected during inactive steps and avoided during active ones. By contrast, few significant differences between habitat types for a given activity state (only broom moorlands were avoided over the reference habitat type during inactive steps), and no differences between activity states for a given habitat type were found during October to February (hunting/food-restricted period; Fig. 4b).

During March to June (first half of the lambing season), when inactive, females preferentially used rocky areas (like males) and avoided broom moorlands and deciduous forests (unlike males; Fig. 4c). When active, females selected only deciduous patches. There was no avoidance of steep slopes, showing that females stayed close to those areas perceived as safe (i.e. rocky areas) during both active and inactive steps. During July to September (when lambs were older), steep rocky areas were no longer selected during inactive steps, whereas deciduous patches and broom moorlands were chosen over grass-rich areas on the plateaux (Fig. 4d). The selection for grass-rich areas on plateaux was highly contrasted between activity states. During October to February (hunting/food-restricted period), the different habitat types were used in line with their availability during female active steps and the only significant habitat selection contrast appeared for broom moorlands, which

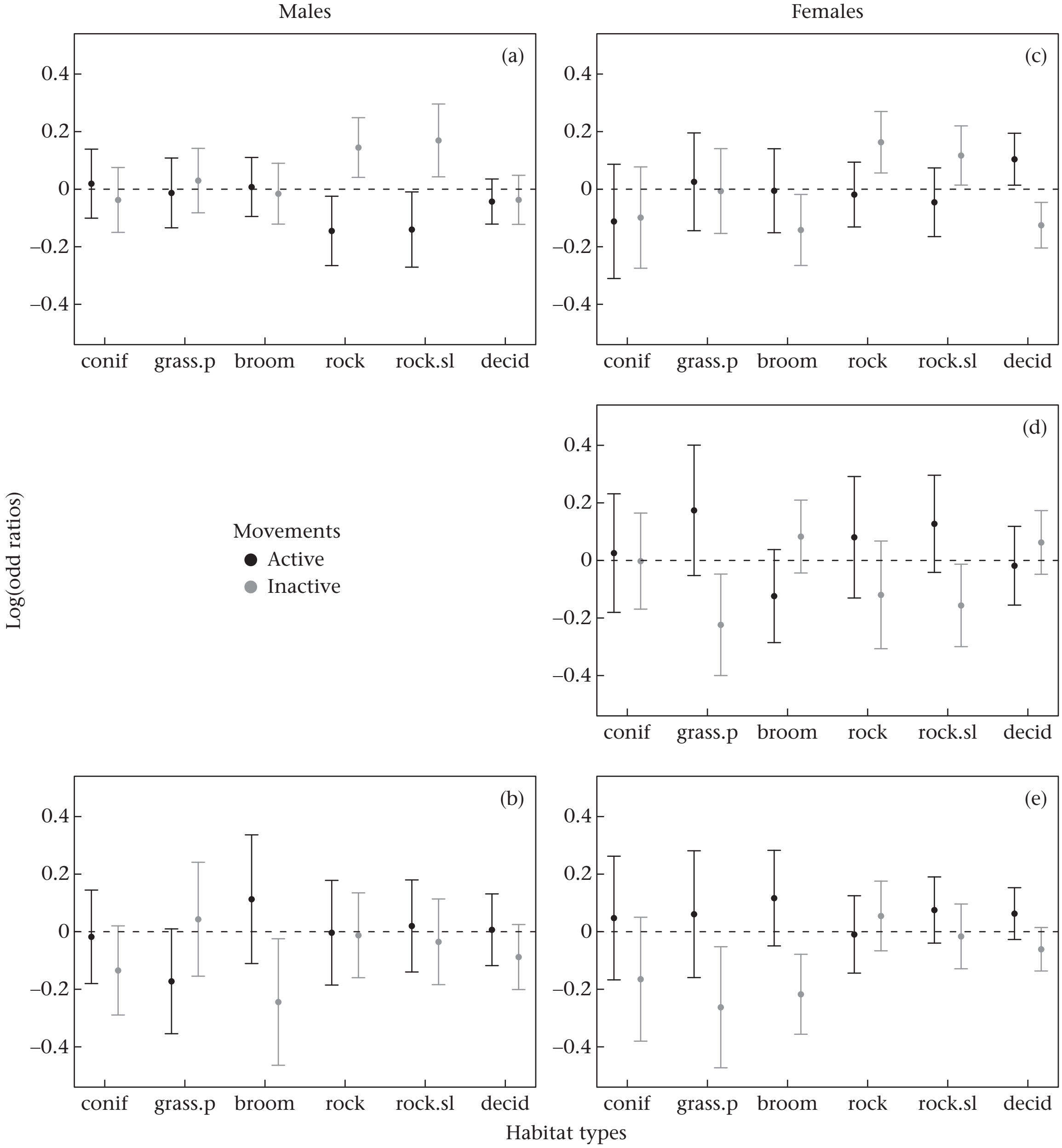

Figure 4. Results from sex- and season-specific step selection functions of Mediterranean mouflon during active (black) and inactive (light grey) movement steps (see Appendix for details of activity states). (a) Males in March–September; (b) males in October–February; (c) females in March–June; (d) females in July–September; (e) females in October–February. The reference steps for which β = 0 are inactive steps in grass-rich areas on slopes (grass; see Table 1 for details of habitat types).

were avoided during inactive steps and selected during active ones (Fig. 4e).

DISCUSSION

By investigating scale-dependent variation in habitat selection of Mediterranean mouflon, we revealed that the relative importance of external drivers of habitat selection (i.e. perceived predation risk and food resources) varied with season (1 in Fig. 1) and depended on sex (2 in Fig. 1). Temporal variation in availability of those habitat attributes important for fitness resulted in sex-specific adjustments in broad-scale habitat selection and cascading effects on decisions at a finer scale. We further showed how digestive features of ruminants, i.e. the necessary alternation of activity phases (foraging/ruminating–resting cycle) strongly influenced mouflon habitat selection (4 in Fig. 1). This latter factor, which operates at the within-day scale, has been overlooked so far, although these phases correspond to different levels of risk for most ruminants (e.g. Molinari-Jobin, Molinari, Loison, Gaillard, & Breitenmoser, 2004).

While sex and activity clearly determined habitat selection patterns in most cases, the magnitude of their effect was conditional on the overall level of actual risk and disturbance and on forage attributes. Accordingly, the largest differences between the sexes occurred when the actual risk and disturbance were highly contrasted between males and females with a lamb at heel (March to September period; Bon et al., 1993, 2 in Fig. 1). Males gave priority to foraging conditions (grasslands on plateaux; Baudière, 1970; Cazau et al., 2011) at a broad scale while avoiding cover areas of low perceived predation risk (deciduous forests and rocky areas). But within this overall pattern, they strongly selected these latter habitats at a finer scale during inactive steps. Females rather selected at a broad scale areas of low perceived predation risk (rocky areas) and suboptimal foraging conditions (moorlands on slopes, 3 in Fig. 1). At a fine scale, as in males, this pattern was reinforced by a selection for rocky areas and against deciduous patches and broom moorlands during inactive steps.

These results suggested that the past evolution of the species with natural predators has resulted in stronger behavioural consequences for females (Byers, 1997). They are consistent with findings in other wild sheep (bighorn sheep: Festa-Bianchet, 1988; Berger, 1991; Stone's sheep: Rachlow & Bowyer, 1998; Sardinian mouflon, *Ovis orientalis musimon*: Ciuti, Pipia, Grignolio, Ghiandai, & Apollonio, 2009) and more generally in mountain ungulates (mountain goats: Hamel & Côté, 2007; Alpine ibex: Grignolio et al., 2007). In species with young adopting the ‘follower’ neonatal behaviour (Ciuti et al., 2009; Pfeffer, 1967), females tend to select habitats perceived as safe at the expense of foraging resources, owing to the high vulnerability of their offspring during the first months of life. However, an optimal timing and activity-specific changes in female habitat selection may contribute to fulfilling the increased energetic requirements resulting from lactation and more generally lamb rearing (Clutton-Brock, Albon, & Guinness, 1989). Indeed, high proportions of grass-rich areas were selected at the home range scale during late gestation (January to March, on slopes) or as soon as lambs were weaned (early July, on plateaux). These habitats, providing favourable foraging conditions but of high perceived predation risk, and providing poor cover against hot summer conditions (a major driver of female activity and lamb survival in this population; Bourgoin et al., 2011; Garel et al., 2004), were, however, avoided during inactive bouts.

By contrast, the smallest differences between the sexes and activity states occurred during the hunting period, when the actual risk and disturbance were high and the food abundance low (October to February; 2 and 4 in Fig. 1). The actual risk imposed by hunting seemed to exceed all the other individual and environmental factors in the hierarchy of the drivers of habitat selection (Ciuti et al., 2012; Rettie & Messier, 2000), with all individuals selecting areas of low perceived predation risk. The absence of marked adjustments in habitat selection at a fine scale suggested that animals performed all their activities on steep rocky areas and in deciduous forests (Cransac & Hewison, 1997; Mysterud & Ostbye, 1999). Although fruits provided by deciduous forests may represent a significant part of the mouflon's diet during autumn (Cransac, Valet, et al., 1997; Faliu et al., 1990), the strong influence of hunting was also highlighted by the lower importance of protective cover in September, i.e. when hunting pressure was more limited (only 13% and 14% of male and female harvests whereas 16.5% would be expected under a constant pressure over the hunting period). Besides, the stronger selection of steep rocky areas by males compared with females before the rutting period (October to mid-November) could be the result of variable hunting pressures on both sexes (see Methods). Behavioural consequences of hunting with sex-specific responses have already been revealed in this population (Benoist et al., 2013; Marchand et al., 2014).

Sex differences in the balance between food resources and risk avoidance are at the heart of hypotheses explaining sexual segregation in space. Our results support the reproductive strategy hypothesis, also called the predation risk hypothesis, which considers habitat segregation to be the result of different strategies used by the sexes to maximize breeding success (Bowyer, 1984; Main, Weckerly, & Bleich, 1996; Ruckstuhl & Neuhaus, 2000). Indeed, differences in habitat selection peaked during the lambing period: males selected the best foraging conditions during this period, which benefit growth rate, the formation of energy reserves and horn development, all important in determining future male reproductive success (Coltman, Festa-Bianchet, Jorgenson, & Strobeck, 2002; Trivers, 1972). Females rather traded off conditions for both lamb survival and resources for lactation and lamb rearing. The forage selection hypothesis, or sexual dimorphism–body size hypothesis, which attempts to explain habitat segregation by contrasted foraging needs and predicts habitat segregation to occur year round except during the mating period (Beier, 1987; Ruckstuhl & Neuhaus, 2000, 2006), was less supported by our results. However, further research with more precise data on spatiotemporal variation in forage abundance/quality and an accurate assessment of the actual influence of human pressure on habitat segregation during the hunting period, are needed to confirm the underlying mechanism resulting in habitat segregation and more generally in sexual segregation. This latter is now often recognized as the consequence of multiple components (i.e. habitat, spatial and social; Loe et al., 2006; Ruckstuhl and Neuhaus 2006; Singh et al., 2010).

Recent advances in movement ecology and biologging have provided evidence in many animals and at multiple spatiotemporal scales for variable movement modes (see Owen-Smith, Fryxell, & Merrill, 2010 for a review in herbivores) and activity patterns (e.g. foraging/ruminating–resting cycle in ruminant herbivores, Gillingham et al., 1997; Hofmann, 1989). These movement/activity patterns may constitute the basic behavioural units explaining population distribution and dynamics (Morales et al., 2010). As in a few other studies on large herbivores (see e.g. Bjørneraas et al., 2011; Ewald et al., 2014; Godvik et al., 2009; Van Beest, Mysterud, Loe, & Milner, 2010), coupling movement/activity patterns and habitat selection in this study was decisive for revealing that decisions taken at a large spatiotemporal scale could be offset by fine-scale activity-specific habitat selection. This strategy could be interpreted as the way by which animals fulfil all their basic requirements in habitat types that rarely provide an adequate mix of food and protective cover (Bjørneraas et al., 2011; Godvik et al., 2009; Orians & Wittenberger, 1991). Further incorporating basic behavioural units in studies on habitat selection (see e.g. Wilson, Gilbert-Norton, & Gese, 2012; Zimmermann, Nelson, Wabakken, Sand, & Liberg, 2014 in carnivores), and more deeply investigating the extent to which temporal variation in the food/cover trade-off affects scale-specific decisions of individuals with ever-changing needs, may yield novel insights into links between spatial and temporal behaviours in many animal species.

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APPENDIX: DETERMINING ACTIVITY STATES

We relied on continuous recordings of spatial locations (20 min data) and head motions (5 min data from two sensors: X = side to side [horizontal] motions; HD = percentage of time the animal was head down [for more details, see Bourgoin et al., 2008, 2011]) over a 48 h period to determine activity state for each movement step of 45 GPS-collared individuals. Of the various methods available (see Body, Weladji, & Holand, 2012 for a review), we used that developed by Van Moorter et al. (2010). We expected the combination of data from sensors with trajectory characteristics recorded over a short timescale (20 min) to improve our ability to objectively disentangle activity states of large herbivores. Furthermore, complementary analyses revealed that this approach was consistent with the predictions from the discriminant model previously used to derive activity states of GPS-collared mouflon from our population based on data from sensors only (see Bourgoin et al., 2008; same predictions for 81% of the 102 459 data for which comparison was possible, i.e. 72% [61 221 data] and 93% [41 238 data] when the discriminant model predicted inactive or active 20 min periods, respectively).

GPS raw data processing

GPS locations were first screened for erroneous locations using the method developed by Bjørneraas et al. (2010) with the threshold determined based on knowledge of mouflon behaviour so that movements with higher values were unlikely (distance from median position of 10 fixes before and after the focal fix >1500 m; distance from mean position >1000 m; incoming and outgoing speed >1000 m/h; turning angle >166°; $N = 377$ errors; total percentage of screened fixes = 0.27%). Since the time between two fixes was short, isolated missing locations (i.e. unsuccessful fixes and removed erroneous locations) were interpolated as the middle of the straight line between the previous and the next location (Cargnelutti et al., 2007; $N = 4489$ unsuccessful fixes interpolated, i.e. 44% of unsuccessful fixes, 3.3% of the total number of fixes). However, we restricted our analyses to 48 h recording periods for which a minimum of 80% (115/144) of the data were actual records from GPS collars ($N = 956$; Table A1).

For each trajectory with three consecutive available fixes, step length and turning angle were derived (Turchin, 1998). We summed 5 min data from head motion sensors preceding a location to describe head motions for each 20 min movement recorded. These four characteristics of each 20 min step were then combined.

Methods

First, we used *k*-means clustering to identify a given number of groups in a set of observations characterized by the four variables (Steinley, 2006). As recommended, we first standardized all variable values on their range for each individual and transformed the standardized values to reduce skewness (log-transformation for X motion and step length, logit-transformation for percentage of time with head down). We then performed 10 *k*-means clustering procedures on the set of movements for which number of horizontal head motions (X), percentage of time head down (%HD), step length (SL) and turning angle (TA) were all available ($N = 93\,417$ movements), fixing successively the number of groups from 1 to 10.

The second step relied on the gap statistic which provided an objective criterion to determine without a priori assumptions the optimal number of groups in the set of observations (Tibshirani, Walther, & Hastie, 2001). It was based on a tolerance value, analogous to the α level of risk in the standard hypothesis-testing framework. The higher the tolerance value the higher was the strength of evidence for additional clusters. The gap statistic was calculated using tolerance values of 1 and 2 successively to reveal the optimal number of groups in this set of observations.

The previous clustering method was only applicable to steps with three consecutive locations (required to derive a turning angle) and was sometimes inconsistent within state series. We hence corrected the state of movement steps for which the previous and next cluster types were known and different from the state of the focal step. The states of both the previous and next movement steps were also attributed to the focal movement step ($N = 6232$, i.e. 6.7% of the data from the clustering procedure corrected).

Results

Four clusters were identified by combining *k*-means clustering and the gap statistic, for both tolerance values (Fig. A1a). The representation of the distribution of range-standardized and transformed clustering variables for each cluster (Fig. A1b) revealed that *k*-means opposed movements with intense head motions (1 and 4; high X and %HD values) with movements with fewer head motions (2–3; low X and %HD values). Each class was divided in two according to high (1–2) or low (3–4) turning angle (TA) values. Step length (SL) did not provide meaningful information for the clustering procedure. Van Moorter et al. (2010) obtained comparable clustering results in their illustration of the method with the data from one elk, *C. elaphus*, as did Owen-Smith, Goodall, and Fatti (2012) using another method in several ungulates. These four clusters were interpreted by these authors as movements between foraging patches (high activity and high directional persistence, corresponding to cluster 4), foraging movements (high activity and frequent direction changes, corresponding to cluster 1), and movements characterized by few head motions during which feeding was unlikely (corresponding to clusters 2 and 3). The variation of each cluster frequency according to time of the day (all individuals and 48 h periods pooled; Fig. A1c) confirmed this interpretation. The daily bimodal activity pattern of this species could be observed (Bourgoin et al., 2011; Ciuti et al., 2009), with two periods of high frequencies for clusters 1 and 4 and low frequencies for clusters 2 and 3, at dawn (0700–0900 hours UTC) and dusk (1800–2000 hours UTC). Two periods of lower frequencies for clusters 1 and 4 and higher frequencies for clusters 2 and 3 were also revealed during the second part of the night (0300–0600 hours UTC) and to a lesser extent during the afternoon (1300–0600 hours UTC).

It may also be noted that most of the time, the variation in the frequency of movements classified in clusters 4 or 2 preceded comparable variation in the frequency of movements classified in clusters 1 or 3, respectively. This result suggested a succession of the corresponding behaviours at the daily scale.

The interpretation of the differences between clusters 2 and 3 was not straightforward (Van Moorter et al., 2010), since the daily variation of the frequencies of clusters 1 and 4 on one side and of clusters 2 and 3 on the other were often comparable while consecutive. We therefore decided to only use two activity states, by distinguishing between active (clusters 1+4) and inactive (clusters 2+3) movement steps.

Table A1
Individual monitoring of 45 GPS-collared adult mouflon between 2003 and 2010 in five subpopulations of the Caroux-Espinouse massif, southern France

Sex	Subpopulation		ID	No. of 48 h periods	Season		
					March-June	July-September	October-February
Females	Caissenols		1035	1	1	0	0
			1356	31	**12**	**10**	**9**
			1375*	23	11	5	7
			1377*	37	15	13	9
			1398	4	0	**4**	0
			1857	35	**17**	**4**	**14**
			1867	25	**10**	1	**14**
			1888	34	**16**	**4**	**14**
			1890	37	**18**	**5**	**14**
			1892*	30	13	3	14
			1899	14	3	**4**	**7**
		Total	*N*=11	271	116	53	116
	Caroux West		1045	13	**7**	0	**6**
			1047	18	**7**	2	**9**
			1077	45	**18**	**13**	**14**
			1083*	17	8	0	9
			1098	6	**4**	0	2
			1179	24	**11**	**5**	**8**
			1188	27	**11**	**8**	**8**
			1210	17	**9**	2	**6**
			1211	26	**12**	**7**	**7**
			1229	11	3	**4**	4
			1303	29	**14**	**8**	**7**
		Total	*N*=11	233	104	49	80
	Caroux South		1048	5	0	**5**	0
			1050	13	**6**	2	**5**
			1091	4	1	1	2
			1321	19	**8**	**4**	**7**
		Total	*N*=4	41	15	12	14
	Pas de la Lauze		1230	30	**13**	**9**	**8**
			1381*	7	1	1	5
			1433	2	2	0	0
			1869	2	0	0	2
		Total	*N*=4	41	16	10	15
Males	Caissenols		974	17	**8**		**9**
			1100	19	**10**		**9**
			1298	7	5		2
			1304	41	**25**		**16**
			1452	21	**13**		**8**
			1455	10	1		**9**
			1551	39	**30**		**9**
			1585	8	**7**		1
			1632*	38	25		13
		Total	*N*=9	200	124		76
	Caroux West		1541	21	**14**		**7**
			1542	41	**31**		**10**
			1552	33	**26**		**7**
			1554	27	**17**		**10**
		Total	*N*=4	122	88		34
	Pas de la Lauze		1854*	13	2		11
			1859	35	**23**		**12**
		Total	*N*=2	48	25		23

The number of 48 h periods analysed per individual is given for males and females in total and per season. Data in bold type were included in within-season home range analyses (individuals with at least one 48 h period of data recording per month during a specific season).

[*] Individuals with activity sensor failure (excluded from corresponding analyses).

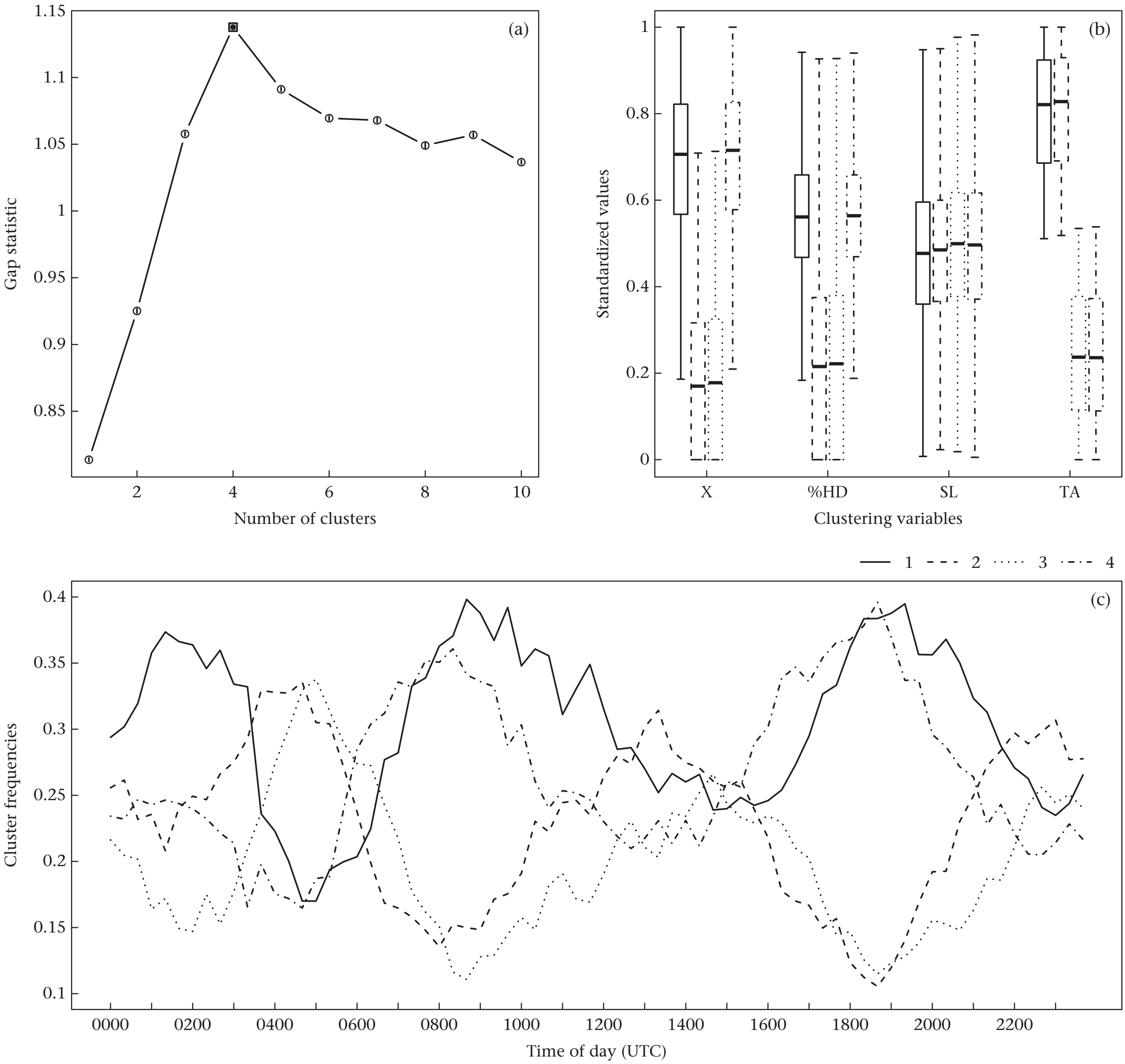

Figure A1. Identification of activity states in Mediterranean mouflon with similar head motions and movement characteristics by combining *k*-means clustering and the gap statistic (Van Moorter et al., 2010). (a) Gap statistic for different numbers of clusters. The selected number of clusters using a tolerance of 1 and 2 is marked with a black dot and a grey square, respectively. (b) Distribution of the standardized values of clustering variables for each cluster type revealed by the gap statistic. For each clustering variable values and each cluster type, box plots represent first, median and third quartile of the distributions. Vertical lines show either the maximum value or 1.5 times (roughly two SD) the interquartile range (i.e. the difference in the response variable between its first and third quartiles) of the data. X = horizontal head motions; %HD = percentage of time the animal was head down during a 20 min period; SL = step length between consecutive locations; TA = turning angle). Cluster 1 = solid line; cluster 2 = dashed line; cluster 3 = dotted line; cluster 4 = dot-dash line. (c) Frequencies of each cluster type (all individuals or 48 h periods pooled) according to time of day (UTC=Coordinated Universal Time).

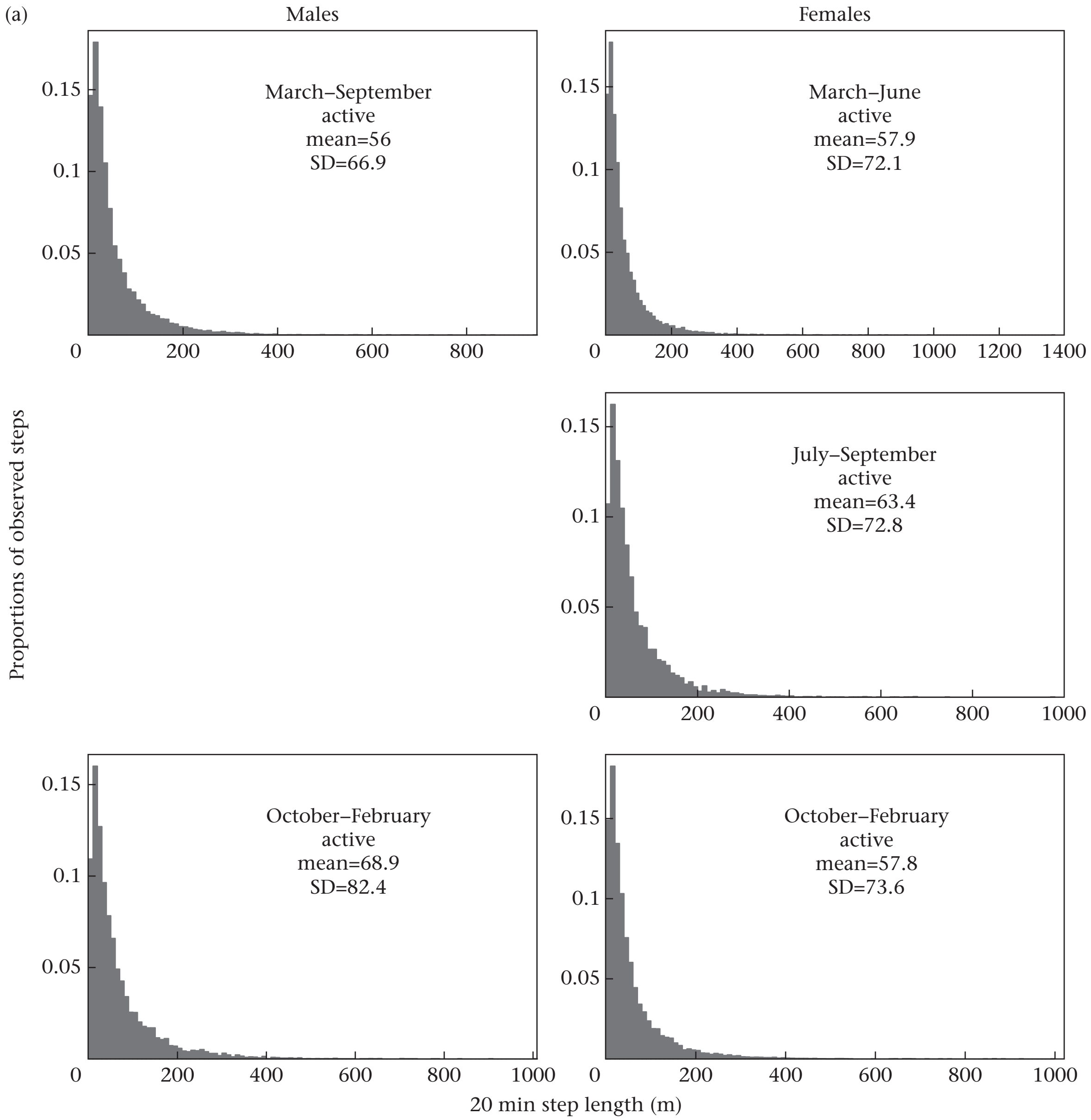

Figure A2. Sex-, season- and activity-specific distributions and summary statistics of movement characteristics of 45 GPS-collared adult mouflon. (a) Step length: active movements; (b) step length: inactive movements; (c) turning angles: active movements; (d) turning angles: inactive movements.

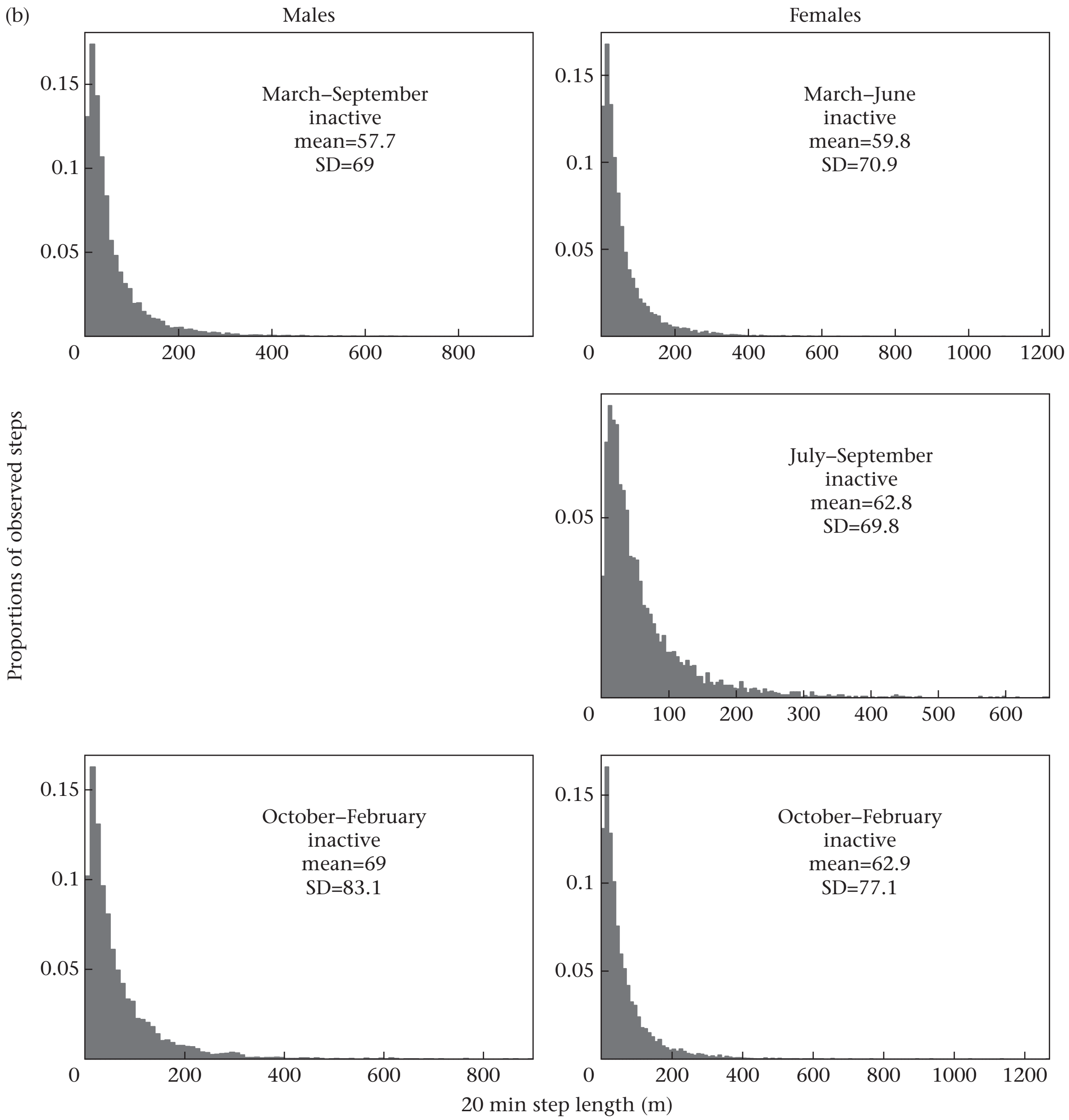

Figure A2. (*Continued*).

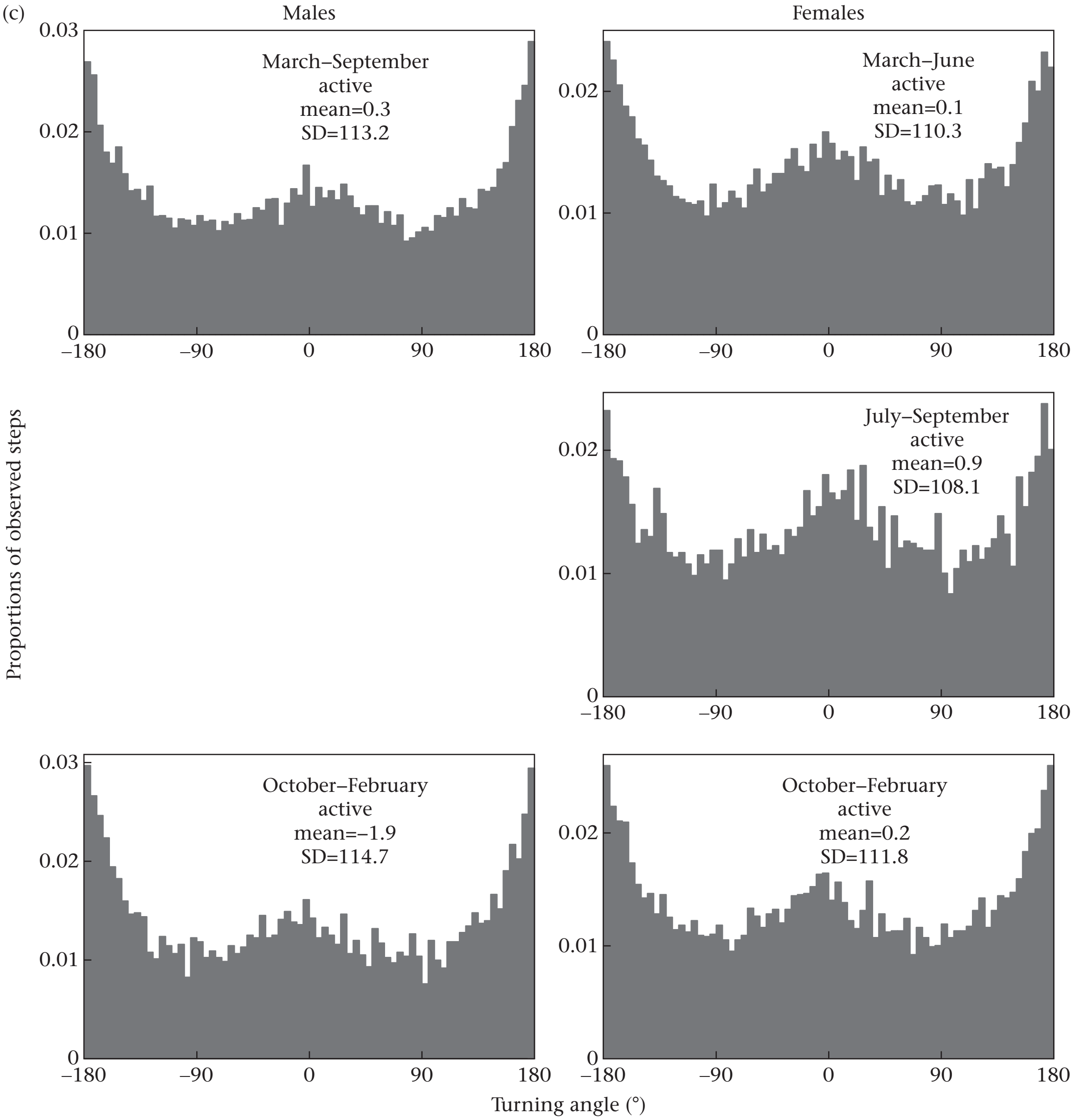

Figure A2. (*Continued*).

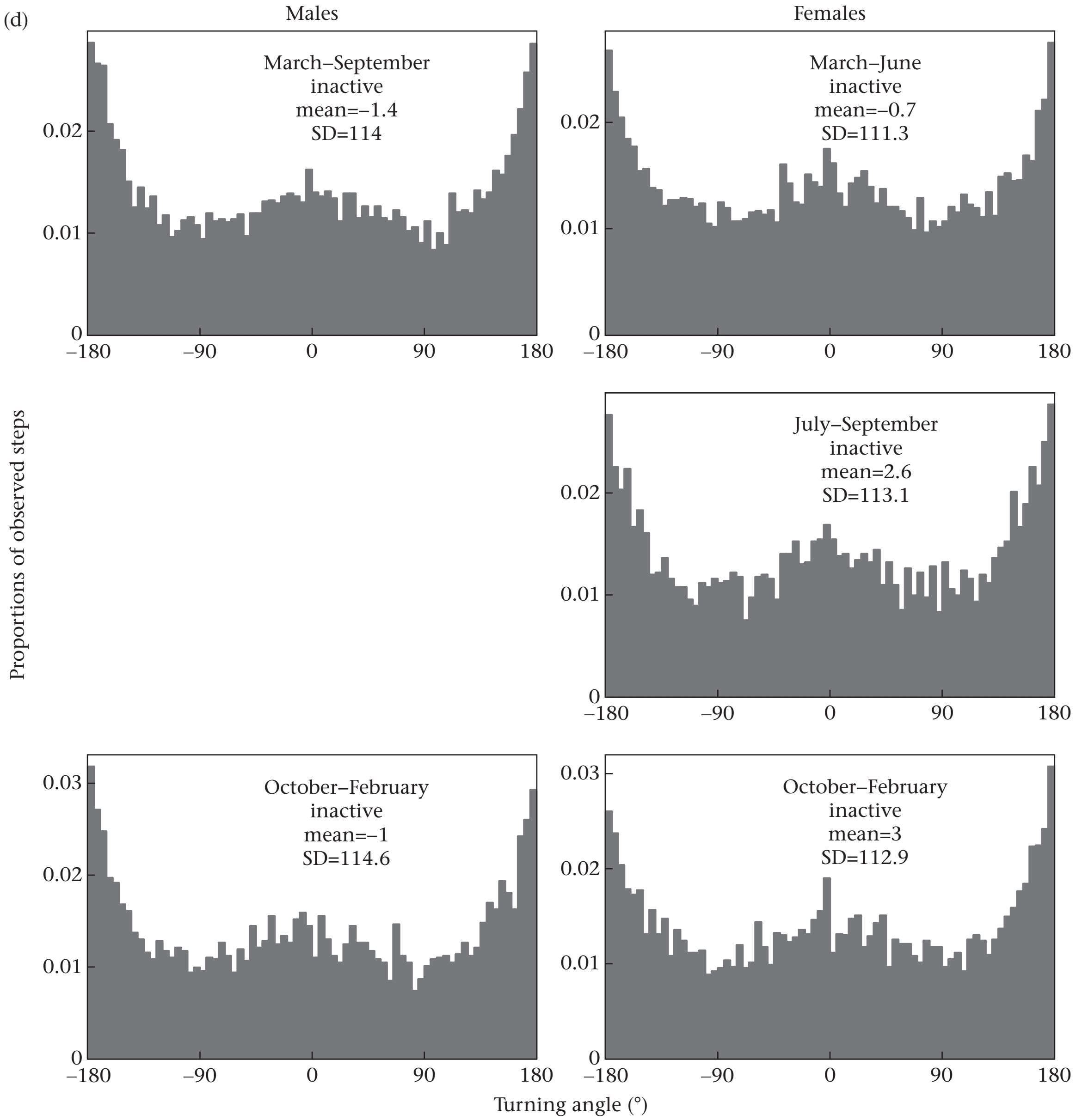

Figure A2. (*Continued*).