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Combining familiarity and landscape features helps break down the barriers between movements and home ranges in a non-territorial large herbivore

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Summary

1. Recent advances in animal ecology have enabled identification of certain mechanisms that lead to the emergence of territories and home ranges from movements considered as unbounded. Among them, memory and familiarity have been identified as key parameters in cognitive maps driving animal navigation, but have been only recently used in empirical analyses of animal movements.

2. At the same time, the influence of landscape features on movements of numerous species and on space division in territorial animals has been highlighted. Despite their potential as exocentric information in cognitive maps and as boundaries for home ranges, few studies have investigated their role in the design of home ranges of non-territorial species.

3. Using step selection analyses, we assessed the relative contribution of habitat characteristics, familiarity preferences and linear landscape features in movement step selection of 60 GPS-collared Mediterranean mouflon *Ovis gmelini musimon* × *Ovis* sp. monitored in southern France. Then, we evaluated the influence of these movement-impeding landscape features on the design of home ranges by testing for a non-random distribution of these behavioural barriers within sections of space differentially used by mouflon.

4. We reveal that familiarity and landscape features are key determinants of movements, relegating to a lower level certain habitat constraints (e.g. food/cover trade-off) that we had previously identified as important for this species. Mouflon generally avoid crossing both anthropogenic (i.e. roads, tracks and hiking trails) and natural landscape features (i.e. ridges, talwegs and forest edges) while moving in the opposite direction, preferentially toward familiar areas. These specific behaviours largely depend on the relative position of each movement step regarding distance to the landscape features or level of familiarity in the surroundings. We also revealed cascading consequences on the design of home ranges in which most landscape features were excluded from cores and relegated to the peripheral areas.

5. These results provide crucial information on landscape connectivity in a context of marked habitat fragmentation. They also call for more research on the role of landscape features in the emergence of home ranges in non-territorial species using recent methodological developments bridging the gap between movements and space use patterns.

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Introduction

Animal space use, distribution patterns and their consequences for individual performance and population dynamics have become key issues in ecology during the past decades owing to the challenging consequences of global changes on wildlife habitats (Gaillard *et al.* 2010; Morales *et al.* 2010). Analysing space use, resources and habitat selection is a first step in identifying the determinants of animal distribution and the multiple spatio-temporal scales at which decisions are made by individuals (Pulliam & Danielson 1991). Studying movements allows one to spot the underlying behavioural units by which animals mediate trade-offs in life-history requirements arising from heterogeneous and dynamic habitats (Johnson *et al.* 1992). Hence, assessing landscape connectivity, i.e. the degree to which landscape characteristics favour/impede movements among resource patches, and how they in turn influence ecological processes at broader scales, has become a major concern in movement ecology (Nathan 2008). This is also a critical issue for management and conservation purposes and the definitions of corridors, i.e. regions of the landscape that facilitate the flow or movement of individuals, genes and ecological processes (Chetkiewicz, St. Clair & Boyce 2006) and barriers, i.e. areas that impede such flow (Panzacchi *et al.* 2015), in a context of marked habitat fragmentation (Fahrig 2003; Hilty, Lidicker & Merenlender, 2006).

One puzzling question for movement ecologists concerns the mechanisms that lead to the emergence and maintenance of restricted space use patterns (home ranges and actively defended territories) from movement paths generally considered as unbounded (Börger, Dalziel & Fryxell 2008; Powell & Mitchell 2012; Potts & Lewis 2014). A consensus has been reached to recognize animal capacities to gather and memorize spatially explicit information in cognitive maps on which navigation relies (Benhamou 1997; Collett & Graham 2004; Gautestad 2011; Fagan *et al.* 2013). Decisions concerning movements would rely on both short-term memory associated with recent events and spatial information collected during navigation (i.e. working memory), and on long-term memory related to experiences far in the past and regularly reinforced (reference memory; Howery, Bailey & Laca 1999; Oliveira-Santos *et al.* 2016). Research on territorial species in particular, boosted by the development of statistical methods allowing to bridge the gap between the characteristics of movements and the consequences on space use patterns (e.g. mechanistic home range analyses, Moorcroft & Lewis 2006), has revealed the major role played by the memory of scent marks and aggressive interactions between neighbouring individuals in territory formation (Briscoe, Lewis & Parrish 2002; Moorcroft, Lewis & Crabtree 2006; Giuggioli, Potts & Harris 2011; Potts & Lewis 2014). Furthermore, territorial boundaries often take the form of conspicuous features in the landscape, motivating research exploring the role of the landscape in the division of space between territorial individuals (see Heap, Byrne & Stuart-Fox 2012 for a review).

In non-territorial species, these methodological improvements and their developments (e.g. Avgar, Deardon & Fryxell 2013; Schlägel & Lewis 2014) recently confirmed that the memory of resources distribution and of encounters with predators also plays a major role in movements and in the emergence of home ranges (Van Moorter *et al.* 2009; Gautestad, Loe & Mysterud 2013; Merkle, Fortin & Morales 2014; Avgar *et al.* 2015; Bastille-Rousseau *et al.* 2015; Polansky, Kilian & Wittemyer 2015). Up to now, however, only few empirical studies have accounted for memory and familiarity preferences in analyses of habitat/resources selection (Wolf *et al.* 2009; Piper 2011) as methods enabling incorporation of these parameters only recently started to develop (e.g. Oliveira-Santos *et al.* 2016). In addition, the format of cognitive maps, i.e. egocentric (i.e. structured relative to one's own position) and/or exocentric (i.e. structured relative to landmarks; Benhamou 1997), remains largely unknown in non-territorial species (Fagan *et al.* 2013). Yet, a growing body of literature has highlighted that natural and anthropogenic landscape features can favour or impede animals' movements (e.g. Ehrlich 1961 in insects, Harris & Reed 2002 in non-migratory birds, Seidler *et al.* 2014 in migratory herbivores, Zimmermann *et al.* 2014 in large carnivores). Even some features that animals are physically able to cross can act as behavioural barriers (Harris & Reed 2002; Beyer *et al.* 2013), involving modifications of movements characteristics and space use with proximity to the features (crossing and proximity effects; Fortin *et al.* 2013; Beyer *et al.* 2016). These results stress the major influence of landscape features and habitat edges on many ecological processes at broader scales, e.g. natal dispersal (Long *et al.* 2010), migration and invasion processes (Elton 2000; Long *et al.* 2010), disease spread (Sattenspiel 2009), gene flow and genetic structure (Coulon *et al.* 2006; Pérez-Espona *et al.* 2008; Robinson *et al.* 2012).

Despite the similar scheme with the adoption of landmarks for territorial boundaries (Heap, Byrne & Stuart-Fox 2012), few studies have investigated the role of landscape features in the emergence and the design of individual home ranges in non-territorial species (e.g.

Long *et al.* 2010; Bevanda *et al.* 2015). Indeed, while preferentially moving toward areas they are familiar with, animals may avoid being close to or crossing these features to reduce the costs they involve in terms of stress and/or perceived risks (Beyer *et al.* 2016). At a broader scale, impediments to movements could be less abundant in home range cores and more abundant in their peripheries where they could represent landmarks by which animals distinguish home range boundaries. Surprisingly, examining this potential influence of natural and anthropogenic features in shaping individual home ranges remains a challenging task that has received much attention for territorial animals but little for non-territorial species (Heap, Byrne & Stuart-Fox 2012) despite recent statistical developments making it possible to take boundaries into account in home range computation (Benhamou & Cornélis 2010).

Our goal here was to determine (i) whether movements of 60 GPS-collared Mediterranean mouflon *Ovis gmelini musimon* × *Ovis* sp. in a mountainous area of southern France (Caroux-Espinouse massif) were influenced by memory and familiarity preferences, and whether landscape features (ii) acted as behavioural barriers by impeding movements and (iii) were involved in the design of individual home ranges in this non-territorial species. We first assessed the influence of natural (i.e. ridges, talwegs and forest edges) and anthropogenic (i.e. roads, tracks and hiking trails) linear landscape features on movement step selection of both sexes, while accounting for habitat characteristics (Marchand *et al.* 2014, 2015a, b for this population), and for the too often neglected memory effects and familiarity preferences (Wolf *et al.* 2009; Piper 2011; Oliveira-Santos *et al.* 2016). We expected mouflon to preferentially move toward familiar areas and in the opposite direction of landscape features (e.g. in other ungulates: Coulon *et al.* 2008 in roe deer *Capreolus capreolus*, Seidler *et al.* 2014 in pronghorn *Antilocapra americana*, Thurfjell *et al.* 2015 in wild boar *Sus scrofa*). Such propensity should increase with decreasing distance to the landscape features and level of familiarity in the surroundings (Van Moorter *et al.* 2009; Gautestad 2011; Fagan *et al.* 2013). Second, we evaluated the influence of these movement-impeding landscape features on the design of home ranges by testing for a non-random distribution of these behavioural barriers within sections of space differentially used by mouflon (i.e. home range cores and peripheries).

Materials and methods

STUDY AREA

We collected data in the Caroux-Espinouse study area (43°38′ N, 2°58′ E, 17 000 ha, 130–1124 m a.s.l.), in southern France (Appendix S1, Supporting Information). The topography of this low mountain area is characterized by deep valleys indenting plateaux and resulting in a network of ridges (274 km) and talwegs (130 km). Plateaux are mostly exploited for conifer forestry (*Pinus sylvestris*, *Pinus nigra* and *Picea abies*) and crossed by numerous logging tracks (164 km). The bottoms of slopes have been colonized by broad-leaf trees (mainly beech *Fagus sylvatica*, chestnut trees *Castanea sativa* and evergreen oak *Quercus ilex*). Between the forested areas on plateaux and slopes occur rocky areas and open moorlands (either grass-rich heather *Erica cinerea* and *Calluna vulgaris*, or broom *Cytisus oromediterraneus* and *Cytisus scoparius*) delineating an important network of forest edges (255 km). This area is sparsely populated (39 inhabitants km^{-2}) and crossed by few roads (80 km). It is very much appreciated by recreationists (>200 000 per year, Dérioz & Grillo 2006) who can hike on numerous trails (84 km), mostly during spring and summer (Marchand *et al.* 2014). Conversely, human activities are strictly regulated in the central National Hunting and Wildlife Reserve (1658 ha) where we collected most of the data: hunting is forbidden and recreational activities are restricted to hiking on a few main trails (see Marchand *et al.* 2014 for details). In surrounding unprotected areas, hunting occurs from 1 September to the end of February, with around 500 mouflons harvested per year during the study period (2010–2013).

MOUFLON POPULATION, GPS DATA, HOME RANGE AND FAMILIARITY

The population of Mediterranean mouflon inhabiting this area is monitored by the Office National de la Chasse et de la Faune Sauvage according to the ethical conditions detailed in the specific accreditations delivered by the Préfecture de Paris (prefectorial decree n°2009-014) in agreement with the French environmental code (Art. R421-15 to 421-31 and R422-92 to 422-94-1). Mouflon are caught and marked annually between May and July using traps and drop nets baited with salt licks. Most traps and nets were located in the National Reserve, so that human disturbance for the monitored mouflon was limited (Benoist *et al.* 2013; Marchand *et al.* 2014).

Between 2010 and 2013, we equipped 34 adult females and 26 adult males (≥2 years old) with Lotek 3300S GPS collars (revision 2; Lotek Engineering Inc., Carp, ON, Canada). We programmed GPS collars to record animal locations (i) on even hours (2010: 11 females and 5 males), or (ii) even hours on 1 day (from 0 to 22 h UTC) and odd hours the following day (from 1 to 23 h UTC, hence including one 3 h and one 1 h step in each 48-h period; 2011–2012: 23 females and 21 males), for nearly 1 year [on average (SD) 387·5 (56·2) days, range = (307; 522) days]. We screened GPS data for positional outliers (n = 1212; 0·46% of the full data set) based on unlikely movement characteristics (Bjørneraas *et al.* 2010; $\Delta = 1500$ m, $\mu = 1000$ m, α = 80% quantile of movement speeds from a focal individual, $\theta = -0{\cdot}95$).

To determine the intensity of space use by each mouflon and the level of familiarity in the surroundings for each individual location, we computed individual utilization distribution using the Brownian bridge movement model (BBMM; Horne *et al.* 2007). BBMM is a continuous time stochastic model of movement that incorporates the animal's movement path and time between locations to calculate the probability density function providing likelihood of an animal occurring in each unit of a defined area during the monitoring period. The GPS location error δ from BBMM was fixed to 24·5 m (Marchand *et al.* 2015a). The Brownian motion variance σ_m^2 was determined for each annual trajectory of an individual using the maximum likelihood approach developed by Horne *et al.* (2007). Individual utilization distribution was then scaled between 0 and 100 and used as a familiarity index within individual home ranges (0 = unfamiliar, 100 = familiar; Appendix S2). We found consistent results when we analysed the step selection of an individual within the same year as its familiarity index (see results section; see Oliveira-Santos *et al.* 2016 for a similar approach), or during the previous/next year of monitoring (Appendix S2), suggesting that the space use and home ranges of mouflon from this population were stable from year to year. In addition, this familiarity index was computed with data collected during nearly one year with strong seasonal variation in habitat selection of mouflon (Marchand *et al.* 2015a). This led to low correlation coefficients ($r < 0{\cdot}34$) between this index (computed for the year) and distances to each habitat type (computed for each 2-h step). By contrast, this familiarity index was largely correlated with time since last visit to locations chosen by each individual mouflon ($r = 0{\cdot}87$), a variable recently used to detect the effects of dynamic information collected during movements (spatial memory) and shown to shape movement processes (see Schlägel & Lewis 2014 for details). All these results suggested our familiarity index could be interpreted as an intermediate memory index integrating both short-term dynamic information gathered during daily navigation (i.e. working memory) and long-term memory related to experiences further in the past and regularly reinforced (i.e. reference memory; Howery, Bailey & Laca 1999).

INFLUENCE OF HABITAT CHARACTERISTICS, FAMILIARITY AND LANDSCAPE FEATURES ON MOVEMENTS

We performed sex- and season-specific analyses to account for sex-specific seasonal patterns in habitat selection (Marchand *et al.* 2015a), which could be expected to result in divergent influences of landscape features. We distinguished spring (March–June, late gestation and lambing period for females), summer (July–September), autumn (October to 15 December, including rutting period) and winter (15 December to February; see Marchand *et al.* 2015a for details). For each individual, we also defined excursions as movement steps that started outside the area including 95% of space use computed using BBMM (on average 4·2% and 2·9% of males' and females' steps respectively) and excluded them from analyses to focus on the landscape features included in individual home ranges or located in close proximity to them.

We assessed the influence of natural and anthropogenic landscape features on movements of mouflon on a fine scale using Step Selection Functions (SSFs, Fortin *et al.* 2005). We coupled each observed 2-h movement step with 10 random steps (Appendix S3a) according to the area used by an individual at that time. We sampled random steps from around observed locations using the observed step length and turning angle distributions from each sex, for the corresponding season and day period (±1 h around the hour of the focal step, to account for sex-specific daily and seasonal variations in movement characteristics while obtaining sufficient sample size; Appendix S4; Fortin *et al.* 2005; Thurfjell, Ciuti & Boyce 2014).

We then compared observed step characteristics with control step characteristics using conditional logistic regression models and a matched case-control design (Hosmer & Lemeshow 2000), of the form:

$$\hat{w}(x) = \sum_{i=1}^{n} \beta_i x_i, \qquad \text{eqn 1}$$

β_1 to β_n are the coefficients estimated by a conditional logistic regression associated with the step characteristics x_1 to x_n respectively. Steps with higher SSF scores $\hat{w}[x]$ have higher odds of being chosen by an animal. We developed seven candidate SSF models testing for the influence of landscape features and of the level of familiarity within individual home ranges while accounting for other variables identified as key determinants of movements and habitat selection of large herbivores, namely foraging conditions, protection against perceived predation risk and thermal cover (see Table 1). We controlled for these three variables by including in SSF models the minimum distances to the same eight habitat types previously used to study habitat selection in this population ('habitat', Table 1; see Marchand *et al.* 2014, 2015a, b for details on these habitat characteristics and their computation).

We tested for the influence of familiarity by including in SSF models ('familiarity', Table 1), the difference in our familiarity index between ending and starting locations of each step (hereafter called Δfamiliarity; see Appendix S2). As we expected the selection of familiar areas to increase with the decreasing level of familiarity in the surroundings of each step, we also included in this model the average value of the familiarity index at the ending locations of the 10 random steps (hereafter called $\text{familiarity}_{10\,random}$).

Finally, we considered six natural or anthropogenic landscape features that could constitute impediments to movements of mouflon while being physically traversable by them. Roads, tracks and hiking trails were extracted from the BD CARTO© data set from the Institut Géographique National (http://professionnels.ign.fr/bdcarto). Ridges and talwegs were derived from the digital elevation model previously described using the *r.param.scale* tool in GRASS GIS 6.4.4 (Neteler *et al.* 2012). Forest edges were extracted from the BD FORÊT© data set from the Institut Géographique National (http://professionnels.ign.fr/bdforet). We tested for the influence of these potential impediments by including a factor in SSF models ('impediments', Table 1) that summarizes the crossing of a feature for each observed and random step ('crossing effect' sensu Beyer *et al.* 2016, coded 1 when mouflon crossed the focal feature and 0 otherwise). Similarly, we distinguished steps when mouflon move away in the opposite direction from each landscape feature, i.e. steps with a negative difference between distances at starting and ending locations of each step from focal feature (coded 1) from steps when they did not (coded 0). As we expected the behaviour of mouflon to vary with distance to these features ('proximity effect' sensu Beyer *et al.* 2016) and with the level of familiarity in the surroundings ($\text{familiarity}_{10\,random}$), we also included in models the interaction between each of the two factors along with their additive effects. Besides, as the permeability of forest edges could also depend on the origin and destination of an individual, i.e. from open habitat to forest or from forest to open habitat, we distinguished these two types of forest edges when considering crossing effect (hereafter called 'forest edge_{of}' and 'forest edge_{fo}' respectively).

For each sex and season, we compared the seven models fitted to investigate the influence of landscape features, familiarity and habitat characteristics on movements of mouflon (Table 1) using the Quasi-likelihood under Independence Criterion (QIC, Pan 2001). The QIC penalizes overcomplexity by adding a penalty term for the number of parameters, thus allowing for a compromise between parsimony and adjustment capacities, and hence preventing from

Table 1. Set of models fitted to investigate the respective influences of landscape features, familiarity and habitat types on movements of Mediterranean mouflon *Ovis gmelini musimon* × *Ovis* sp. during the 2010–2013 period in the Caroux-Espinouse massif (southern France). '+' corresponds to additive effects and '×' to the interaction between two variables

Model	Name	Description	Step characteristics included in the model (x_i in equation 1)
1	Habitat	Minimum distance to each of the 8 habitat types	$\text{Distance}_{conif} + \text{distance}_{grass.p} + \text{distance}_{grass} + \text{distance}_{rock} + \text{distance}_{rock.sl} + \text{distance}_{broom} + \text{distance}_{decid} + \text{distance}_{other}$
2	Familiarity	Difference in the level of familiarity between ending and starting locations, average level of familiarity in the surroundings	$\Delta\text{familiarity} + \Delta\text{familiarity} \times \text{familiarity}_{10\,random}$
3	Impediments	Crossing (crossing = 1; no crossing = 0), opposite direction (opposite = 1; neither opposite nor crossing = 0), distance to each of the 6 potential impediments, average level of familiarity in the surroundings	$\text{Crossing} + \text{opposite} + \text{crossing} \times \text{distance}_{impediment} + \text{crossing} \times \text{familiarity}_{10\,random} + \text{opposite} \times \text{distance}_{impediment} + \text{opposite} \times \text{familiarity}_{10\,random}$ Impediment = roads, tracks, hiking trails, ridges, talwegs, forest edges
4	Habitat + familiarity		1 + 2
5	Habitat + impediments		1 + 3
6	Familiarity + impediments		2 + 3
7	Habitat + familiarity + impediments		1 + 2 + 3

overadjustment. It also accounts for non-independence between autocorrelated movement steps from the same individual by being calculated while also taking independent step clusters into account (Craiu, Duchesne & Fortin 2008). These clusters were determined using the procedure proposed by Forester, Im & Rathouz (2009) and used to compute robust standard errors of the coefficients provided by the models. They contained between one (no autocorrelation) and 37 steps (74 h) depending on individuals/seasons. We ranked the seven candidate models for each sex and season using the difference in QIC between each model and the best model (hereafter called ΔQIC) and considered a focal model and the best one as different when their difference in QIC was >2. We also computed QIC weights (w_i) that can be interpreted as the probability that a model is the best model, given the data and the set of candidate models (Burnham & Anderson 2002). Finally, we assessed the robustness of the best models using a *k*-fold cross validation procedure for case–control design (Fortin *et al.* 2009). Using a random sample representing 80% of the available strata (i.e. one observed and 10 control steps), we built a new SSF model including the same explanatory variables as the best model and used the resulting parameter estimates to predict SSF scores for the observed and control steps in the remaining 20% strata. Based on these scores, we ranked observed and control steps from 1 to 11, and tallied the ranks of observed steps into 11 potential bins. We then performed Spearman rank correlation between the bin's ranking and its associated frequency. We reported the mean and 95% confidence intervals (95% CI) of r_s derived from the 100 repetitions of this process (hereafter called r_{s-obs}).

INFLUENCE OF LANDSCAPE FEATURES ON THE DESIGN OF HOME RANGE

We investigated the relative densities of landscape features within 19 sections of individual home ranges, each representing 5% of space use estimated from BBMM [(0−5%), (5−10%), …, (90−95%)]. For each landscape feature, we then computed its relative density in each section as the density of the focal feature observed in a specific section of the home range (i.e. total length in the section divided by the area of the section) divided by the density observed in the whole home range (i.e. total length in the home range divided by the home range area). If randomly distributed within individual home ranges, we hence expected relative densities of 1, whereas relative densities < or > 1 respectively indicated landscape features were included less or more than expected in the focal home range section. The variation in the relative densities of each landscape feature were modelled for both sexes according to utilization distribution values using general additive mixed models (GAMMs) including individual identity as a random factor to account for repeated measurements on the same individuals. We used a Tweedie family distribution with a log link to account for the large number of zeros in the response variable (Tweedie 1984; Dunn & Smyth 2005). 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 each sex, we then used 95% Bayesian confidence interval (95% CI; Wood 2006) of GAMMs to determine whether mouflon included each landscape feature evenly in the different sections of their home ranges (95% CI including 1), or less (95% CI < 1) or more (95% CI > 1) than expected with a random distribution.

Results

INFLUENCE OF HABITAT CHARACTERISTICS, FAMILIARITY AND LANDSCAPE FEATURES ON MOVEMENTS

For both sexes and in all seasons, the best model to explain mouflon step selection included the influence of landscape features and familiarity in addition to those from habitat types (Table 2). The strength of evidence in favour of this model over the others (QIC weight w_i >0.98) and its robustness to the *k*-fold cross-validations ($r_{s-obs} > 0.78$) were both very high (Table 2). Interestingly, while the model including the influence of habitat characteristics alone received much less support (last model in the QIC_c classification with $\Delta QIC_c > 1823$), the model accounting for familiarity and landscape features without habitat constraints systematically had the second best rank in the model selection procedure (Table 2). The full list of SSF coefficients is given in Tables S5.1, S5.2 and S5.3 from Appendix S5.

In addition to moving toward or away from habitat characteristics already known as important in this population (Marchand *et al.* 2014, 2015a, b; Table S5.1 in Appendix S5), females consistently oriented their movements toward familiar areas (all SSF coefficients Δfamiliarity were highly significant and negative) and these familiarity preferences increased with decreasing level of familiarity in the surroundings (all SSF coefficients Δfamiliarity × $\text{familiarity}_{10\,random}$ were highly significant and positive; Table S5.2 in Appendix S5). Males followed the same pattern during spring and summer, but were more prone to move toward unfamiliar areas during the rutting period (i.e. autumn) and were less influenced by familiarity preferences during winter (Table S5.2 in Appendix S5).

Mouflon also systematically avoided crossing most of the landscape features tested (all significant SSF coefficients were negative; Figure 1a; Table S5.3), and this behaviour was particularly consistent over seasons and sexes for ridges. All the landscape features tested in both sexes were crossed less often than expected during at least one season, and especially in spring (females), autumn and winter (both sexes). No clear pattern was observed concerning the influence of the level of familiarity on the probability of crossing landscape features (Fig. 1c). By contrast, the probability of crossing systematically increased with decreasing distance to the landscape features (all significant SSF coefficients were negative; Fig. 1b) except for males and tracks during winter. This pattern was particularly consistent for ridges and talwegs in both sexes (Fig. 2a), with odds ratios most often <1 except when movement steps started in their close proximity where crossing events were more probable (odds ratio around or slightly >1 for distances <100 m; Fig. 2a). However, it must be noted that such movement steps constitute rare events due to the pervasive behavioural pattern consisting in moving away in the opposite direction from the landscape features (all significant SSF coefficients were positive; Fig. 1d), especially at very short distances from them (odds ratios >1.5 for distances <100 m, Fig. 2b). This repulsive effect generally decreased with increasing distance to the landscape features (all significant SSF coefficients were negative; Fig. 1e; see also Fig. 2b) and with increasing familiarity in the surroundings for some features and seasons (all significant SSF coefficients were negative; Fig. 1f).

INFLUENCE OF LANDSCAPE FEATURES ON HOME RANGE SELECTION

None of the landscape features, except forest edges, were randomly distributed within individual home ranges of both sexes (95% confidence intervals significantly lower or higher than 1, Fig. 3). The dominant pattern consisted in lower relative densities of landscape features within the sections of home ranges highly used by mouflon (UD < 60–80%) than expected under a random distribution, and conversely, higher densities than expected in the less-used sections of home ranges (UD >85%). This pattern was observed in both sexes for roads, hiking trails and talwegs, and also for tracks in females (Fig. 3). Only ridges detracted from this general scheme by being included more than expected in highly-used sections of home ranges (both sexes) and less than expected in the less-used ones (females only).

Discussion

While providing a new empirical contribution highlighting the role of memory and familiarity preferences on animal movements (Merkle, Fortin & Morales 2014; Avgar *et al.* 2015; Bastille-Rousseau *et al.* 2015; Polansky, Kilian & Wittemyer 2015; Oliveira-Santos *et al.* 2016), our analyses also revealed the overwhelming influence of landscape features on the spatial ecology of a non-territorial herbivore and relegated other habitat characteristics previously identified as important to a lower level. Although most previous studies focused on the influence of a restricted number of landscape features, generally anthropogenic, that we also found as important for movements of mouflon (i.e. roads, and also tracks and hiking trails in our study; Fig. 1), our findings further support a pre-eminent role of natural features that mouflon can cross easily (i.e. ridges and talwegs). In general, both sexes moved towards familiar areas (Briscoe, Lewis & Parrish 2002; Van Moorter *et al.* 2009; Gautestad 2011; Fagan *et al.* 2013) but avoided crossing most of the landscape features we tested (see e.g. McDonald & Cassady St Clair 2004; Shepard *et al.* 2008; Seidler *et al.* 2014 for examples in other species) by moving away in the opposite direction when too close. However, landscape features not only acted as behavioural barriers for movements (Harris & Reed 2002) but also had cascading consequences on the design of home ranges. These results provide crucial information on landscape connectivity in a context of marked habitat fragmentation and could help identify the mechanisms underlying the emergence and maintenance of home ranges in non-territorial animals (Börger, Dalziel & Fryxell 2008; Powell & Mitchell 2012; Potts & Lewis 2014).

Table 2. Model selection table summarizing the respective influences of landscape features, habitat types and familiarity (see Table 1 for variable description) on movement step selection in Mediterranean mouflon *Ovis gmelini musimon* × *Ovis* sp. during 2010–2013 period in the Caroux-Espinouse massif (southern France). The selected models (lowest Quasi-likelihood under Independence Criterion = QIC) are in bold type. ΔQIC is the difference in QIC between the focal model and the selected one, w_i is the QIC weight. r_{s-obs} and 95% CI are the means and 95% confidence intervals of the Spearman rank correlation coefficients derived from the *k*-fold cross-validations of the best models (100 iterations)

Sex	Season	Models	k	QIC	ΔQIC	w_i	r_{s-obs} [95% CI]
M	Spring	**Habitat+familiarity+impediments**	**49**	**43 933·1**	**0·0**	**1**	**0·853 [0·804; 0·900]**
		Familiarity+impediments	41	43 988·2	55·1	0	
		Habitat+familiarity	10	45 325·1	1392·0	0	
		Familiarity	2	45 410·2	1477·1	0	
		Habitat+impediments	47	45 596·9	1663·8	0	
		Impediments	39	45 787·1	1854·0	0	
		Habitat	8	47 763·1	3829·9	0	
	Summer	**Habitat+familiarity+impediments**	**49**	**27 727·3**	**0·0**	**0·99**	**0·874 [0·827; 0·918]**
		Familiarity+impediments	41	27 735·8	8·5	0·01	
		Habitat+familiarity	10	28 381·5	654·1	0	
		Familiarity	2	28 392·3	665·0	0	
		Habitat+impediments	47	29 340·0	1612·7	0	
		Impediments	39	29 399·0	1671·7	0	
		Habitat	8	30 735·9	3008·6	0	
	Autumn	**Habitat+familiarity+impediments**	**49**	**27 359·5**	**0·0**	**1**	**0·802 [0·735; 0·862]**
		Familiarity+impediments	41	27 405·5	46·0	0	
		Habitat+impediments	47	27 946·0	586·4	0	
		Impediments	39	27 980·1	620·5	0	
		Habitat+familiarity	10	28 271·6	912·0	0	
		Familiarity	2	28 382·5	1023·0	0	
		Habitat	8	29 183·0	1823·4	0	
	Winter	**Habitat+familiarity+impediments**	**49**	**33 524·6**	**0·0**	**1**	**0·815 [0·755; 0·851]**
		Familiarity+impediments	41	33 560·1	35·5	0	
		Habitat+familiarity	10	34 477·5	952·9	0	
		Habitat+impediments	47	34 485·7	961·1	0	
		Impediments	39	34 535·7	1011·1	0	
		Familiarity	2	34 545·5	1020·9	0	
		Habitat	8	36 007·0	2482·4	0	
F	Spring	**Habitat+familiarity+impediments**	**49**	**54 436·8**	**0·0**	**1**	**0·816 [0·777; 0·878]**
		Familiarity+impediments	41	54 528·6	91·7	0	
		Habitat+impediments	47	55 879·1	1442·2	0	
		Habitat+familiarity	10	55 912·2	1475·4	0	
		Familiarity	2	56 030·2	1593·4	0	
		Impediments	39	56 147·6	1710·8	0	
		Habitat	8	58 107·4	3670·6	0	
	Summer	**Habitat+familiarity+impediments**	**49**	**31 623·0**	**0·0**	**1**	**0·852 [0·790; 0·904]**
		Familiarity+impediments	41	31 644·6	21·6	0	
		Habitat+familiarity	10	32 530·7	907·7	0	
		Familiarity	2	32 607·3	984·3	0	
		Habitat+impediments	47	33 034·2	1411·3	0	
		Impediments	39	33 077·1	1454·2	0	
		Habitat	8	34 590·8	2967·8	0	
	Autumn	**Habitat+familiarity+impediments**	**49**	**33 861·1**	**0·0**	**1**	**0·789 [0·745; 0·841]**
		Familiarity+impediments	41	33 887·2	26·1	0	
		Habitat+impediments	47	34 729·2	868·1	0	
		Impediments	39	34 768·8	907·7	0	
		Habitat+familiarity	10	34 829·5	968·4	0	
		Familiarity	2	34 868·2	1007·1	0	
		Habitat	8	36 239·3	2378·2	0	
	Winter	**Habitat+familiarity+impediments**	**49**	**43 767·9**	**0·0**	**1**	**0·802 [0·745; 0·851]**
		Familiarity+impediments	41	43 783·1	15·2	0	
		Habitat+impediments	47	44 916·8	1148·9	0	
		Impediments	39	45 004·2	1236·3	0	
		Habitat+familiarity	10	45 014·0	1246·1	0	
		Familiarity	2	45 033·4	1265·5	0	
		Habitat	8	46 747·7	2979·7	0	

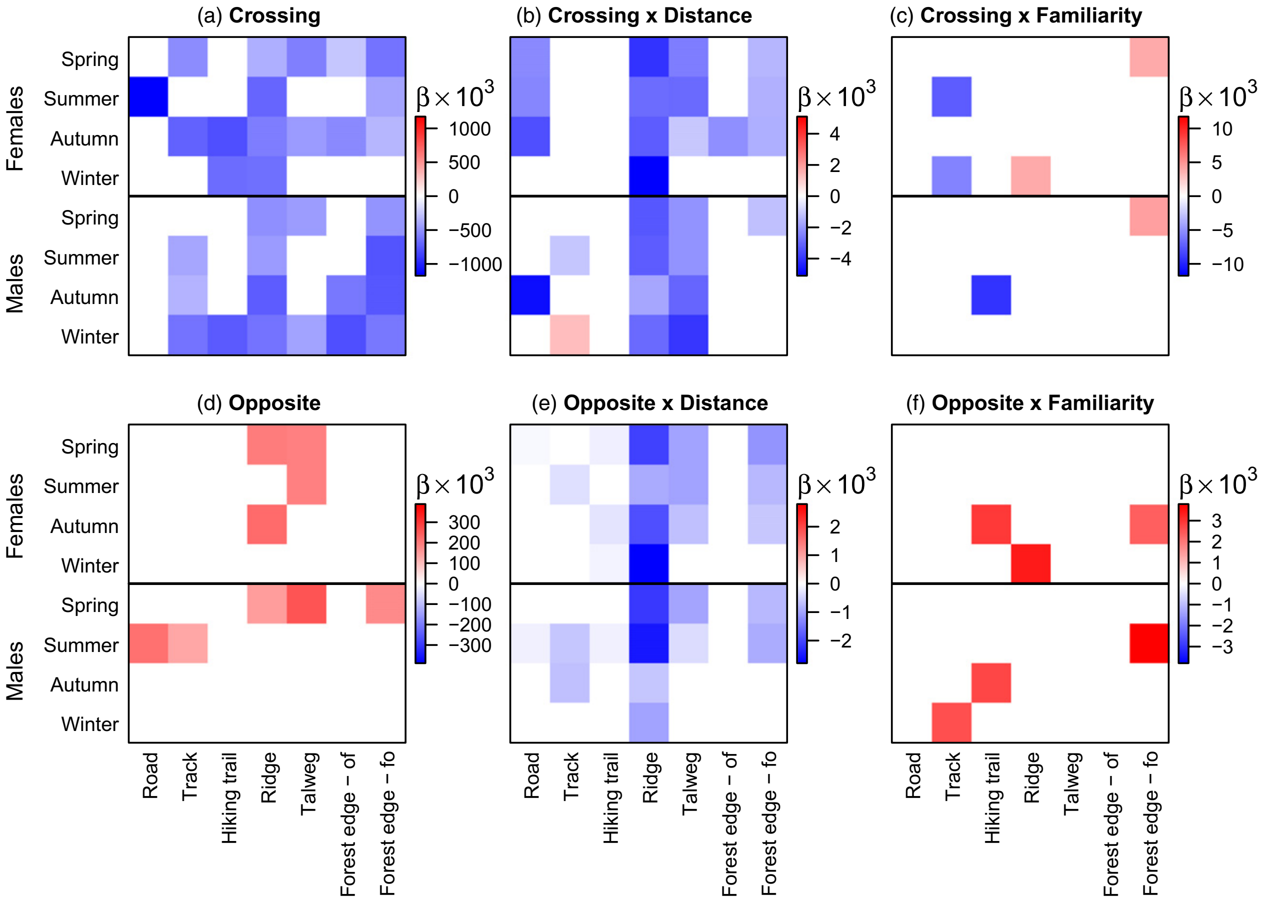
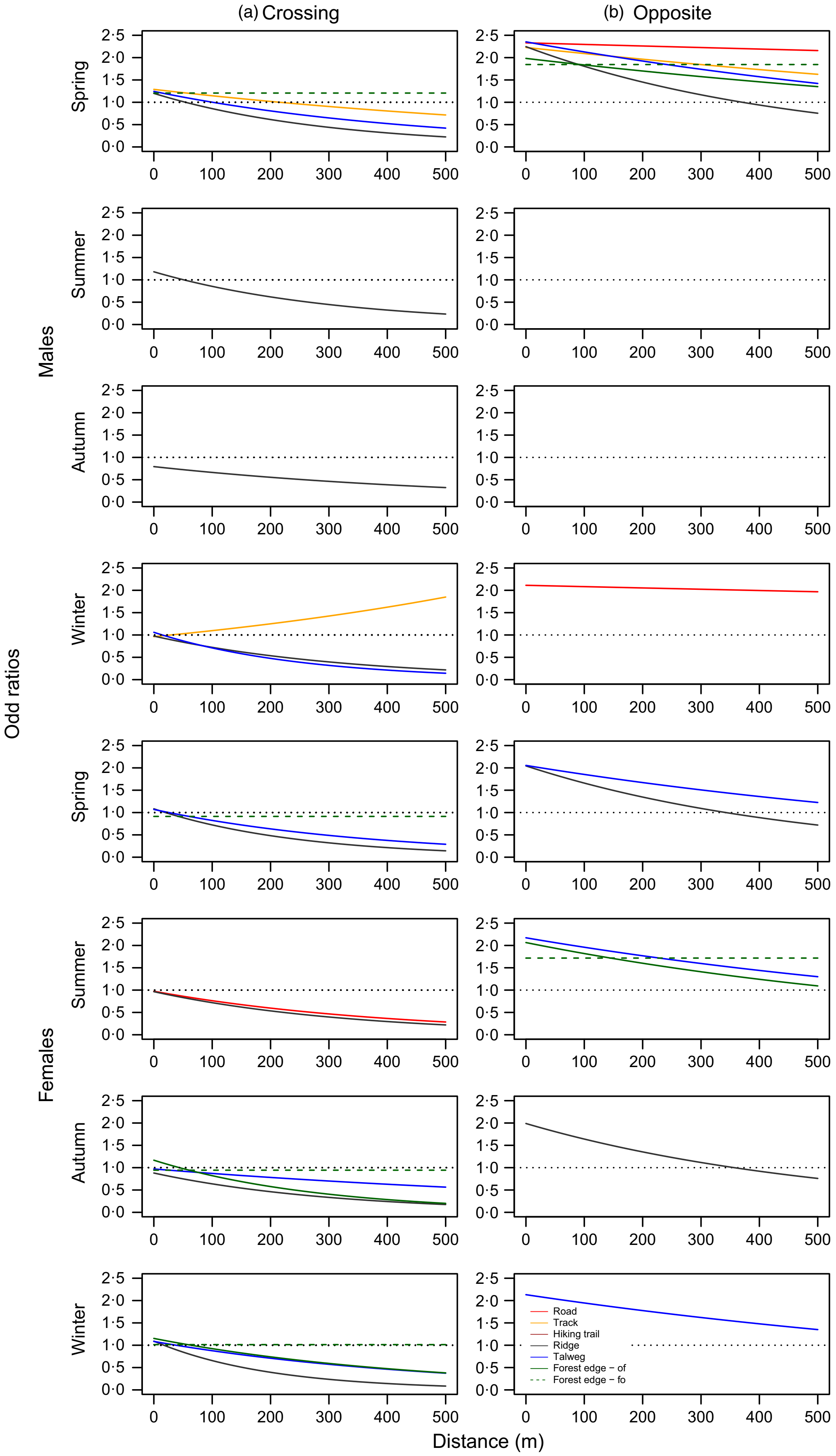


Fig. 1. Coefficients from the sex- and season-specific Step Selection Function (SSF) best models (see Tables 1 and 2 for details) representing the influence of landscape features on movements of Mediterranean mouflon *Ovis gmelini musimon* × *Ovis* sp. from the Caroux-Espinouse massif (southern France). These log(odds ratios) represent the logarithm of the increase (positive values: red cells) or decrease (negative values: blue cells) in the probability of observing a step with the corresponding characteristics compared to control steps: (a) probability that a movement step crossed the focal impediment; (b) variations in this probability to cross with distance to the impediment and (c) with the level of familiarity in the surroundings; (d) probability that a movement step is in the direction opposite the focal impediment; and (e) variations in this probability of moving away in the opposite direction with distance to the impediment and (f) with the level of familiarity in the surroundings. Non-significant log(odds ratios) (95% confidence intervals including 0) were given a value of 0 (white cells). For complete results of SSF best models, see Appendix S5. [Colour figure can be viewed at wileyonlinelibrary.com]

The occurrence and the intensity of these specific movements regarding landscape features and familiar areas differed slightly between sexes and seasons. These differences probably originate in the sex-specific reproductive and foraging strategies for space use related to sexual dimorphism in this species (Ruckstuhl & Neuhaus 2006). As an example, females in this population traded thermal cover for steep refuges where lambs had a better chance to survive during lambing period (spring–summer), whereas males not constrained by the need to protect young and more affected by hot conditions seek thermal cover on unsafe plateaux (Marchand *et al.* 2015a, b). This sex-specific use of habitats could expose both sexes differentially to each feature or involve contrasting responses as a result of different needs and perceptions of risk (Marchand, *et al.* 2015a, b). Likewise, males did not move preferentially toward familiar areas during the rutting period (i.e. autumn), when a large proportion of them returned to the birth range they had dispersed from, moving toward areas they knew but that they did not use at all as adults (hence

Fig. 2. Sex- and season-specific variation in odds ratios (OR) representing the variation in the relative probability that a mouflon *Ovis gmelini musimon* × *Ovis* sp. from the Caroux-Espinouse massif (southern France) (a) crossed or (b) moved away in the direction opposite the focal landscape feature depending on the distance to this feature. OR <1 or >1 indicated that observed steps crossing or going in the direction opposite a focal feature were, respectively, less or more probable than steps that do not, with the percentage of decrease (OR < 1) or increase (OR > 1) determined by the value of the odds ratio, e.g. OR = 0·6 indicating a decrease of 40%. These variations in OR were estimated for each landscape feature separately while maintaining the other variables included in the best SSF model at their mean observed value.The dotted line indicated OR = 1, i.e. when movement steps that crossed the focal landscape feature or went in the opposite direction were as probable as those that did neither. For clarity, only significant relationships were represented, without 95% CI around predictions. [Colour figure can be viewed at wileyonlinelibrary.com]


(a) Crossing
(b) Opposite
Males
Females
Spring
Summer
Autumn
Winter
Odd ratios
Distance (m)
0·0
0·5
1·0
1·5
2·0
2·5
0
100
200
300
400
500
Road
Track
Hiking trail
Ridge
Talweg
Forest edge − of
Forest edge − fo

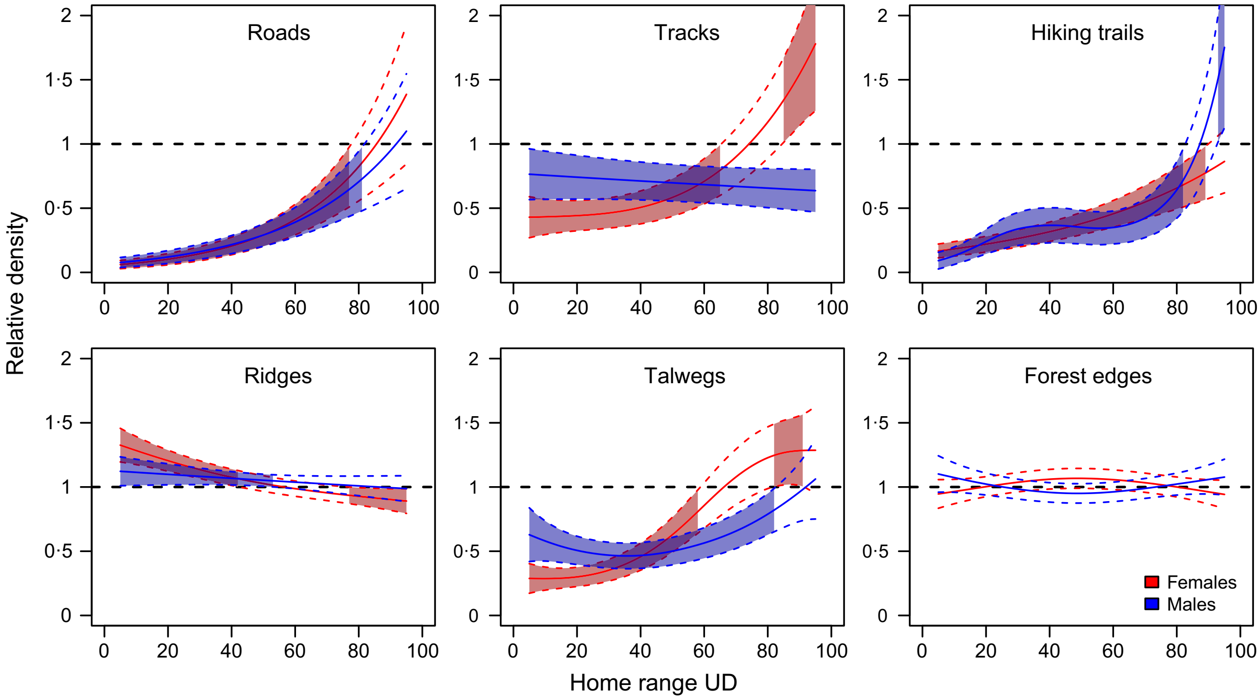


Fig. 3. Variations in the relative densities of landscape features in sections of space differentially used by Mediterranean mouflon *Ovis gmelini musimon* × *Ovis* sp. from the Caroux-Espinouse massif (southern France). Dotted lines indicate 95% confidence interval (95% CI). A focal landscape feature was considered included/rejected in the corresponding home range section of males (blue-shaded 95% CI) or females (red-shaded 95% CI) if it was more/less present than expected with respect to a random distribution of the focal feature within the home range (dashed black line representing this reference value) when the 95% CI did not include 0. [Colour figure can be viewed at wileyonlinelibrary.com]

less familiar; Dubois *et al.* 1996). In contrast, these specific behaviours largely depended on the relative position of each movement step with regard to familiar areas or landscape features. Familiarity preferences increased with decreasing level of familiarity in the surroundings, whereas the repulsive effect of landscape features generally decreased with increasing distance to them. This latter result explicitly exemplified the crossing and proximity effects, i.e. the modification of the probability of space use as a function of distance to physical or behavioural barriers that animals avoid crossing (Fortin *et al.* 2013; Beyer *et al.* 2016). It also challenges sampling and monitoring methods that often rely on the network of linear features for data collection, assuming that animals are homogeneously distributed within habitats (Chetkiewicz, St. Clair & Boyce 2006; Miller *et al.* 2013). Furthermore, it confirmed that landscape connectivity can be transient and depended on spatial contexts, motivation, internal state and the prior experiences of navigating animals (Bélisle 2005).

Interestingly, we also revealed that these modifications of movements resulting from anthropogenic and natural features had cascading consequences on the design of home ranges. These results are consistent with observations reported in other non-territorial species (see e.g. Long *et al.* 2010 in white-tailed deer *Odocoileus virginianus*) and studies that related landscape configuration with home range size and shape (e.g. Bevanda *et al.* 2015). The results suggest that, just as territorial species use landmarks for space division (Heap, Byrne & Stuart-Fox 2012), these easily-crossable landscape features might constitute exocentric information in cognitive maps and allow non-territorial animals to distinguish between inside/outside their home ranges (Benhamou 1997; Powell & Mitchell 2012; Spencer 2012). This would challenge the notion widespread in the community of movement ecologists that movements of non-territorial species are unbounded paths, calling into question the relevance of defining and measuring unbounded home ranges (e.g. Powell & Mitchell 2012: ‘We expect that non-territorial animals [...] do not envision distinct boundaries to their home ranges, making home-range area undefined and a nonentity. [...] Calculating an area for a home range that, in reality, has no biological boundary is irrelevant and misleading’).

However, some landscape features, i.e. ridges, detracted from this general pattern by being largely included in home range cores yet crossed by mouflon less frequently than expected. This result showed that the influence of landscape features on movements did not necessarily involved spill-over effects on the home range scale. Further research is hence needed to firmly conclude on the influence of landscape features in the emergence and maintenance of home ranges and their role as home range boundaries in non-territorial species. This task could be achieved by comparing observed home ranges with those generated by mechanistic movement models built using the outcome of our movement step selection analyses (Moorcroft & Lewis 2006; Potts, Mokross & Lewis 2014; Van Moorter *et al.* 2016). Indeed, this approach could provide a unifying framework for incorporating barrier effects (Beyer *et al.* 2016) in models accounting for the distributions of resources, conspecifics and predators (Potts, Mokross & Lewis 2014; Bastille-Rousseau *et al.* 2015), for memory (Merkle, Fortin & Morales 2014; Avgar *et al.* 2015; Polansky, Kilian & Wittemyer 2015) and for their temporal dynamics (Spencer 2012; Schlägel & Lewis 2014). However, an essential preliminary step consists in better characterizing memory, evaluating its temporal decrease, and determining the relationship between its short- and long-term components. Although the familiarity index we used was proposed by others as an indicator of long-term memory (Oliveira-Santos *et al.* 2016), we showed that it was also correlated to variables that integrate shorter term spatial memory (e.g. time since last visit to animal locations; Schlägel & Lewis 2014). Focusing on mechanistic movement models that rely on other memory indicators such as those gained from correlation present in animals' tracks (e.g. return delays, movement characteristics such as recursions and low navigational variance; see Fagan *et al.* 2013 for a review) and enabling comparison between observed and simulated paths may once again constitute a promising approach.

Finally, reporting the consequences of landscape configuration on several scales of the spatial ecology of a non-territorial herbivore provides crucial information for research, management, and conservation purposes in a context of marked habitat fragmentation. In addition to the availability of habitat resources that received most conservation efforts, connectivity among resource patches has been more recently recognized as a key parameter in controlling fitness, dynamics and distributional patterns in metapopulation biology (Hanski 1998; Fahrig 2003; Moilanen & Hanski 2006; Cattarino, McAlpine & Rhodes 2015). As movements and home ranges constitute the cornerstone connecting fundamental spatial processes in animal ecology (e.g. habitat selection, Van Moorter *et al.* 2016; dispersal and migration processes, Elton 2000; Long *et al.* 2010) and also gene flow, genetic structure and diversity in populations (Coulon *et al.* 2006; Pérez-Espona *et al.* 2008; Robinson *et al.* 2012), the relative position of landscape features could be of prime importance in modelling habitat suitability maps, planning reintroduction programmes and predicting adaptive potential and population viability in the long term (Fahrig 2003; Crooks & Sanjayan 2006; Hilty, Lidicker & Merenlender, 2006).

Authors' contributions

P.M., M.G., D.D., D.M. and A.L. conceived the ideas and designed methodology; P.M., M.G., G.B., D.D. and D.M. collected the data; P.M., M.G., G.B., A.D. and A.L. analysed the data; P.M. and M.G. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data accessibility

Most of the data we used in this manuscript were collected in a protected area where strict restrictions on human activities made it possible to control for human disturbance on mouflon behaviour. Many of our ongoing analyses of human disturbance and its consequences for mouflon (behaviour, physiology, reproduction, survival) rely on the persistence of a spatial contrast between this protected reference area and surrounding areas characterized by intense human activities. If all mouflon locations are made fully-accessible, we are concerned that human activities may be encouraged, creating disturbance in the protected area and consequently menacing the integrity of our ongoing research. In addition, these locations could be used by people locally involved in various recreational activities (e.g. hunting, hiking, photography) to determine the preferential routes used by mouflon to move out of this protected area. Hence, a minimum sample of data required for a third-party to be able to reasonably interpret those data correctly, and to allow each result in the published paper to be re-created, are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.q3670 (Marchand *et al.* 2016). They are also available upon request to anyone who wishes to collaborate with us or repeat our analyses.

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Supporting Information

Details of electronic Supporting Information are provided below.

Appendix S1. Location of the Caroux-Espinouse massif (southern France, topleft panel) and its habitats (center left panel), where the influence of anthropogenic and natural landscape features (three top right and three center right panels) on movements and home range selection of Mediterranean mouflon *Ovis gmelini musimon* × *Ovis* sp. (bottom panels) was the object of investigations between 2010 and 2013.

Appendix S2. Could the utilization distribution of a mouflon within its home range be used in Step Selection Function analyses as reliable information on the level of familiarity?

Appendix S3. Approaches used to study the influence of landscape features on movements and home range selection in Mediterranean mouflon *Ovis gmelini musimon* × *Ovis* sp. from the Caroux-Espinouse massif (southern France).

Appendix S4. Sex-specific variation in the movement characteristics of mouflon on both seasonal and daily scales.

Appendix S5. Coefficients ($\times 10^3$) of the best candidate SSF models explaining the sex- and season specific variation in movement step selection by Mediterranean mouflon *Ovis gmelini musimon* × *Ovis* sp. in the Caroux-Espinouse massif (southern France).