

MASTER 2  
EFCE



## Inter- and intraspecific variations in movements and space use of two large herbivores with contrasted life history traits

*MSc thesis*



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## INTRODUCTION

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In natural conditions, animals have to cope with landscapes composed with a matrix of patches characterized by variable abiotic and biotic conditions, providing more or less favourable resources ("substance consumed by an individual [e.g. food resources] or factors [e.g. thermic cover, nesting sites] that lead to an increase of the population when their quantity is increased"; Tilman 1980). These patches generally have variable size, shape, and are hierarchically distributed (Wiens 1976, Kotliar & Wiens 1990). In seasonal environments, this matrix also changes through time as circadian, seasonal and inter-annual changes in biotic and abiotic characteristics result in changes in patch characteristics and distribution. In order to fulfil their basic requirements, animals may perform non-random movements within this matrix, exploiting patches with favourable resources/conditions with slower/more sinuous movements, and moving quickly and straighter in less favourable areas (Pyke 2015). Hence, animal decisions result in typical movement characteristics that may vary in space, in time, and result in space use patterns at larger spatiotemporal scales (e.g. area-restricted space use patterns like territoriality or ranging behaviour; Van Moorter et al. 2016). Indeed, the plasticity of movement behaviour, at the individual and populations' levels, determine the ability of animal population to adopt adaptive responses and to cope more or less with environmental variability and changes (Berg et al. 2010, Chapman et al. 2011, Dall et al. 2012, Beever et al. 2017). This is why questions about the modalities, the determinants and the consequences of animal movement has become of high importance in ecology research owing the multiple threat posed by anthropogenic global changes (e.g. habitat fragmentation, global warming; Nathan et al. 2008, Tucker et al. 2018).

Recent advances in modern technologies, allowing now to monitor an increasing number of species of various sizes (e.g. from bees to elephants), at unrivalled spatiotemporal scales (from the meter to intercontinental displacement; from the second to the year), coupled with progress in computational and statistical treatment of tracking data, enables now to address questions about animal movement in the wild that could not be answered before in a recent past (Cagnacci et al. 2010, Demsar et al. 2015, Kays et al. 2015). Despite the emergence of the new paradigm proposed by Nathan et al. (2008) there is still no consensus in movement ecologists on how choices made by individuals are organized at different scales ("from movement steps to home range" *sensu* Tablado et al. 2015). On one side, Rettie & Messier (2000) suggested that the most limiting factors (i.e. those with the greatest potential to reduce

individuals' fitness) should be those which would be the most strongly selected at larger scales (i.e. typically home range's scale *sensu* Johnson 1980). Indeed by coping with limiting factors at larger scales, individuals may certainly cope with successive smaller scales (i.e. patch and within patch scales; Johnson 1980), and thus maximize their fitness (Rettie & Messier 2000). On the other side, Owen-Smith et al. (2010) suggested that decisions made at finer spatiotemporal scales mechanistically influence patterns at larger scales. In any case, this suggests that decisions made by animals occur at various spatial and temporal scales, and claim for multi-scale and multi-level approaches when studying animal movements and space use processes (MacGarigal et al. 2016). At the single-species levels, mechanistic processes linking movements and home range formation have for example already been explored (Fryxell et al. 2008, Rivrud et al. 2010). However little study for the moment have investigated these processes at inter-specific levels (but see Tablado et al. 2015).

Different species or different individuals from the same species living in the same area may not necessarily move in the same way and use the same patches, depending on (i) locomotion capacity (i.e. animal ability to move in its environment), (ii) navigation capacity (i.e. ability to know when and where to move), (iii) internal state (i.e. individual motivation to move; e.g. hunger, thirst, fear of predation, mate), and (iv) external factors that represent the influence of the environment (Nathan et al. 2008). Indeed, movements and space use patterns are the results from the interaction between the individual's characteristics (morphology, physiology, cognitive capacities), that determine individual needs, and the biotic and abiotic factors (e.g. climatic and weather conditions, landscape composition, spatiotemporal availability and distribution of resources) of the habitat it is living in (Kearney 2006). The perception of foraging resources ("foodscape" *sensu* Searle et al. 2007), and of risks imposed by predators and/or humans ("landscape of fear" *sensu* Laundré et al. 2001), i.e. both characteristics being generally negatively correlated and resulting in a "food-cover trade-off" for animals (Brown et al. 1999), may depend on species ecology and result in species-specific movement characteristics (Tablado et al. 2015). As an example, Valeix et al. (2009) showed that large herbivores' response to long-term predation risk was notably constrained by their diet. Especially, whereas browsers distributions in the landscapes were negatively correlated with predation risk, grazers were not affected because the most limiting factor for them was more the scarcity of open grasslands in a landscape mainly represented by woodland and bushland. Likewise, individual characteristics, that determine individual needs, may be of prime importance in determining how individuals perceive their environment and move. As an

example, males from polygynous species, which are selected by females during the mating season, invest a large part of their energy in the growth of sexual secondary traits whereas females rather invest in the survival of themselves and of their offspring (Trivers 1972, Andersson 1994, Ruckstuhl & Neuhaus 2002, 2006). As a result, a strong sexual dimorphism is often observed in these species, with physiological, morphological and behavioural differences between males and females (Andersson 1994). These inter-individual differences result in sex-specific needs and sex-specific motivations to move, resulting in sex-specific patterns of movement and space use (Barboza & Bowyer 2000, Bonenfant 2004, Ruckstuhl & Neuhaus 2002, 2006). Age may also be an important factor determining inter-individual differences in movements and space use, first because individuals do not have the same needs throughout their life, and different preferences in habitat characteristics (Kokurewicz et al. 2004, Ficetola et al. 2013). Secondly, as individuals get older, they may gain more experience about their environment, becoming more familiar with it and optimizing their space use (Sjöberg & Ball 2000, Wolf et al. 2009, Piper 2011, Marchand et al. 2017). Besides, learning may also allow individuals to be able to recognize and assess quality of habitats more easily (habitat-cuing hypothesis ; Davis & Stamps 2004) and to perform better in the use of those habitats (preference-performance hypothesis; Davis & Stamps 2004). Furthermore, senescence (i.e. the age-related decline in physiological performance, with consequences on survival probability and fertility) may also result in reduced movements and home ranges in the oldest individuals (Froy et al. 2018).

In this study, we considered the sex- and age-related differences in the movements and space use of two ungulate species with contrasted life history traits and facing contrasted landscapes: the roe deer (*Capreolus capreolus*) and the Mediterranean mouflon (*Ovis gmelini musimon* x *Ovis* sp.). Large herbivores are an ideal model to study because of their ubiquitous presence in all terrestrial ecosystems and the role they have in their functioning (Fritz & Loison 2006). Actually they are considered as ecosystems engineers as they directly affect the composition of plant communities and indirectly animal communities they live with (Smit et al. 2010, Boulanger et al. 2018). Large herbivores exert indeed a top-down regulation on vegetation, and their predators may also exert an indirect top-down regulation on vegetation through trophic cascades (Fortin et al. 2005, Winnie Jr & Creel 2017). As a consequence, in European countries where predators like wolves or lynx populations have been greatly reduced, along with hunting limitations measures and changes in human land use, wild ungulates populations have exploded (Côté et al. 2004, Apollonio et al. 2017). Then large

herbivores represent great social and economic stakes as they may cause damages to crops (Schley et al. 2008, Riga et al. 2009, Apollonio et al. 2017) and forests (Fratini et al. 2015, Nevřelová et Ružičková 2015, Apollonio et al. 2017), constitutes parasites and zoonotic diseases reservoirs that may affect domestic animals (Tampieri et al. 2008, Martin et al. 2011), be involved in traffic collisions (Bruinderink & Hazebroek 1996, Steiner et al. 2014) and affect biodiversity (Bernes et al. 2018). Their impact is all the more important as these species are highly flexible, with their ability to rapidly adapt and respond to their environment, and their important movement capacities. Nonetheless it is suspected that intrinsic characteristics may induce differences in movement patterns among species (e.g. due to differences in life history traits, Fritz & Loison 2006, Tablado et al. 2015) and among individuals of the same species (e.g. due to different needs between males and females, Ruckstuhl & Neuhaus 2006). Thus a comparative approach within a model group like large herbivores in contrasted landscapes may allow to better understand individual, species and environmental constraints that shapes movement capacities of animals.

The roe deer is the smallest widely distributed cervid in Europe, weighing between 20 and 25 with a maximum of 49 kg (Linnell et al. 1998). According to Hofman classification of herbivory (1989), roe deer are considered as browsers since they selectively feed on leaves, soft shoots and fruits from generally woody plants (e.g. shrubs, trees). Roe deer is slightly dimorphic as males only weight 10% more than females and grow a pair of antlers between December and March and cast them near mid-October (Sempéré et al. 1981). On another side, the Mediterranean mouflon is a medium size ungulate with a marked sexual dimorphism. Adult males weigh between 35-50 kg which is on average 30% heavier than females (25-30 kg), have large permanent horns that can reach 90 cm whereas females have small one or do not have any. Mouflon are generally classified as grazers (sensu Hoffman 1989) but a study by Marchand et al. (2013) suggested to use the term variable grazers as grass constitutes a high proportion of their diet (31% on average) but also forbs and shrublands (24% and 16%, respectively).

In this work we investigated sex- and age-related differences in movements and space use using the locations data of 231 roe deer and 93 mouflon equipped with GPS collars in two French study areas (roe deer: Aurignac [Haute-Garonne], mouflon: Caroux-Espinouse [Hérault]). First we estimated the cumulative daily distances travelled by animals to assess intraspecific variation of mobility at fine scale. Then we estimated monthly home range size to gain insight on intraspecific variation in space use related to sex and age of individuals

since the size of home range is directly linked to different needs like nutrition (Cederlund & Sand 1994, Tufto et al. 1996), lactation (Ciuti et al. 2009), reproduction (e.g. territoriality in roe deer males, Liberg et al. 1998).

Our first hypothesis was that intra-sexual competition in both species would induce differences between sex and among males according to their age by altering the movements and space use of those latter. Roe deer males actively defend a territory from March to August whose size is often reduced compared to the size of home ranges they occupy the rest of the year (Linnell et al 1994). Moreover Vanpé et al. (2009) showed that most males successfully reproduced for the first time at 3 years of age and that the few successful young males (i.e., 2 year olds) were likely fast-growing individuals that could successfully hold a territory. Differences in movements and space use between males and females and among males according to their age were therefore expected to occur only during the territoriality period and more especially during rutting period in July-August (Linnell et al. 1994, 1998). In contrast with roe deer, mouflon live most of the year in segregated monosex groups except during rutting season from mid-October to December where the proportion of mixed groups is at its highest (Dubois et al. 1993, 1996). During this period adult males (i.e.  $\geq 2$  years old) often leave their current home range to join their reproduction range which often corresponds to the areas they were reared. Therefore we predicted sex-related differences due to intra-sexual competition would occur only during the rutting period in Mediterranean mouflon, with no age-related differences as we only have adult males.

In the same time, our second hypothesis was that female would face reproductive constraints that would also induce sex- and age-related differences in movements and space use. Roe deer females reach sexual maturity at the age of one and give birth from the end of April to the very beginning of June with most of birth events occurring in May (Linnell et al. 1994, Plard et al. 2014). Due to the reproductive constraints they are confronted with, we predicted that movements and space use of reproductive females would be reduced during parturition period in May– June, when fawns are born and show reduced mobility and hiding behavior (Linnell et al. 1994, 1999; Tull et al. 2001, Van Moorter et al. 2009) compared to pre-parturition period and juvenile females not supposed to give birth. Inversely, mouflon's lambs follow their mothers (Lent 1974, Bon et al. 1991) very early after their birth that occurs in April-May in the Caroux-Espinouse Mountains (Bon 1991). Before parturition, females separate themselves from the group by reaching for isolated places safe from predation (e.g. in steep slopes, Ciuti et al. 2009, Marchand et al. 2014). Then we predicted that female mouflon



would also show a reduction of their movements and space use during parturition. However this decrease would be smaller than those expected in roe deer due to the highest mobility of lambs. Finally, as all mouflon were adults ( $\geq 2$  years old) and most females older than 1.5 years old reproduce ( $>80\%$ , Garel et al. 2005), we expected no age-related differences between them. We summarized all our predictions in Table 1.

Hypothesis	Species	Main assumptions	Period	Detailed predictions		Source
				Travelled distances	Home range size	
Intra-sexual competition will alter males' movements and space use	Roe deer	Differences between males and females and among males of different ages will be expected during territoriality period and especially during rut	Territoriality (March-August) and Rut (July-August)	Older males > younger males	Older males < younger males	Chapman et al. 1993; Wahlstrom 1994; Linell et al. 1998, Vanpé et al. 2009
			Non territoriality (September-February)	No differences expected among individuals	No differences expected among individuals	
	Mediterranean mouflon	Differences between males and females mainly during rutting season (Mid-October-November)	Rutting season	Males > Females	Males > Females	Dubois et al. 1993, 1996
Parturition and fawn mobility will affect breeding females movements and space use	Roe deer	Differences between males and females and among females of different reproductive status will be expected during parturition and post-parturition (June-July) periods	Parturition (late April-May) and post-parturition (June)	Older females < younger non-breeding females and males	Older females < younger non breeding females and males	Chapman et al. 1993, Linell et al. 1998; Van Moorter et al. 2009, Webb 2010
			Late post-parturition (July-August) and later	Increased fawn's mobility → Females ≈ adult males	Increased fawn's mobility → Females ≈ adult males	
	Mediterranean mouflon	Differences between pre-parturition and parturition periods will be expected in females	Parturition (April) and post-parturition (May-June)	No or little reduction females travelled distances No differences expected among females	No or little home range size No differences expected among females	Dubois et al. 1993, 1996

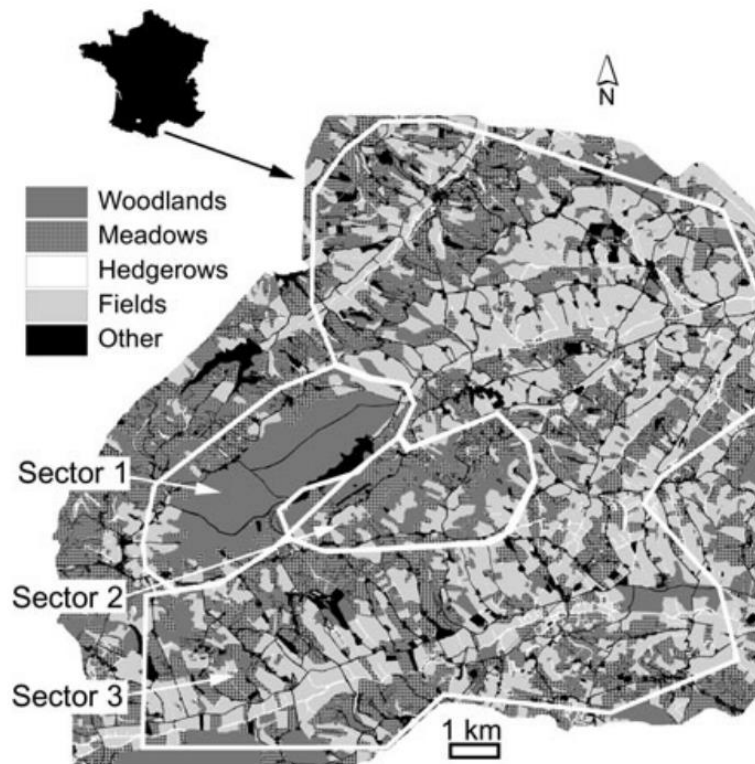
Table 1 : Summary of hypotheses and predictions tested in this study

## MATERIAL & METHODS

### Study areas and data collection

#### *Study areas*

Since 2003, 627 (822 with re-captures) roe deer have been captured by the CEFS laboratory during winter in the study site of “Vallons et Coteaux de Gascogne” near Aurignac, in the South West of France ( $43^{\circ}13'N$ ,  $0^{\circ}52'E$ , 260-380m a.s.l) using large-scale drives with 30-100 beaters and up to 4 km of long-nets. This area of more than 10,000 ha is a heterogeneous agricultural landscape with a fragmented forested cover that presents a large gradient of landscape opening (Figure 1).



*Figure 1 Description of the different habitat types of the Aurignac study site, southern France (Morellet et al. 2011)*

The sex and the age (juvenile = < 1 year; yearlings = 1-2 year(s); adults = >2 years) of each individual have been determined based on tooth eruption. Note that juveniles and yearlings change of age class during their monitoring and are referred to as yearlings and sub-adults from May to December. Among captured individuals, 142 females and 101 males were fitted with GPS collars (Lotek: 3300 GPS, GPS PLUS-C, Small WildCell GSM; Vectronic: GPS PLUS-1C), coupled with a drop-off system programmed to release the animal from its collar. GPS collars were scheduled to

record individual location every 10 min during 24 hours one to 4 days each month or every 6 hours otherwise.

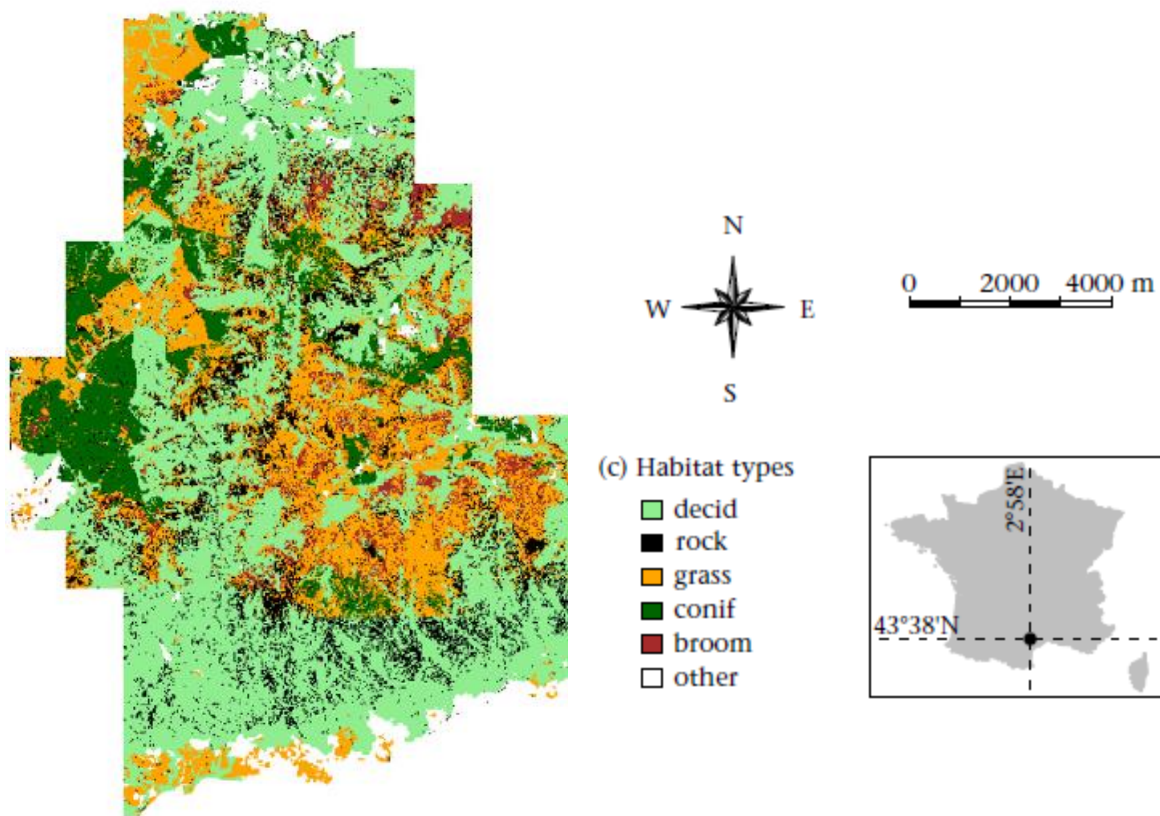


Figure 2 Description of the different habitat types of the Caroux-Espinouse massif, southern France (Marchand et al. 2015)

Mouflons' locations data were collected in the Caroux-Espinouse study area (43°38'N, 2°58'E, 3550 ha, 390–1124 m a.s.l.) in southern France by the Office National de la Chasse et de la Faune Sauvage (Figure 2), who annually performs captures between May and July, since 1974, using traps and drop nets baited with salt licks. Four age-classes were considered based on age at first capture, which is determined by tooth eruption pattern or horn growth annuli: 2-3 years old, 4-6 years old, 7-8 years old and > 8 years old. Between 2010-2016, 33 ewes and 60 rams were trapped and fitted with Lotek GPS collars 3300S, coupled with a drop-off system programmed to release the animal from its collar. GPS collars 3300S scheduled to record continuously animal locations at intervals of 2 hours during the monitoring period.

For both species, we first calculated all individuals trajectories with the function *as.ltraj* from the package *adehabitatLT* (Calenge 2015) for R software, GPS locations of both species were then screened for erroneous locations (i.e. fixes that would imply an unfeasible movement speed given the distance from the previous or to the next location), for each scheduling using a method inspired by Bjørneraas et al. (2010), with rules based on knowledge on mouflon and roe deer behaviour

(Figure 1). 85 fixes (0.02 % of total locations) and 165 fixes (0.04 % of total locations) were removed respectively from 10 minutes and 6 hours scheduling in roe deer, while 103 (i.e. 0.07% of total locations) were removed respectively from 2 hours scheduling in mouflon.

#### *Daily distances travelled*

We used 10-minutes (144 fixes scheduled per day) or 2 hours scheduled GPS data (12 fixes/day) in roe deer and mouflon, respectively, to compute the daily distance travelled by each individual, i.e. by summing the lengths of the straight lines between each pair of consecutive locations over 24h. As some scheduled locations were missing (due to satellites configuration regarding animal position or to the removal of aberrant fixes) we restricted our analyses to 24h periods for which a minimum of 130 (>90%; roe deer) and 10 (>83%; mouflon) scheduled locations were actually available, leading to n=2252 daily distances travelled in roe deer (94 males and 135 females retained) and n=15467 in mouflon (41 males and 26 females). Finally, as travelled distances originated from “incomplete” trajectories (i.e. trajectories with less than 12 or 144 fixes for mouflons and roe deer respectively) would underestimate the actual daily distance travelled, we divided these by the number of locations constituting the corresponding trajectories and then multiplied the result by 12 or 144 for mouflons and roe deer respectively.

*Table 2 : Sex and age classes effectives in roe deer for 10-minutes scheduling and in Mediterranean mouflon for 2-hours scheduling. The only female >8 years old was remove from our analyses. y.o.= years old*

	Roe deer			Mediterranean mouflon			
Sex	Juveniles	Yearlings	Adults	2-3 y.o.	4-6 y.o.	7-8 y.o.	>8 y.o.
Females	25	24	106	9	22	17	1
Males	19	17	66	21	25	24	14

#### *Home ranges*

We estimated monthly home range size for each individual using 6 hours locations in roe deer and 2h locations in mouflon. In contrast with mouflon that were only equipped with GPS collars when  $\geq 2$  years-old (i.e. after natal dispersal occurred; Dubois et al. 1994), some juvenile roe deer may disperse during their monitoring (34% of individuals in Aurignac study area, Debeffe et al. 2012). We chose to exclude from home range computation the locations recorded during dispersal period for individuals classified as dispersers and to estimate home range size the months before/after dispersal only if a sufficient number of locations was still available despite removal of these dispersal movements.

Indeed, home range area generally increases with increasing number of locations when this latter is low, and generally reaches a plateau when it is higher than a threshold value considered as the

minimum number of locations needed for home range size estimation. Hence, we restricted home range computation to individual-months for which a minimum of 120 locations ( $n = 1066$ , 80 % of initial data) in mouflon and 60 locations ( $n=2280$ , 95% of initial data) in roe deer, were truly known. For both species we used the function *kernelUD* from the package *adehabitatHR* (Calenge 2015) for R software to determine the best smoothing parameter to use as reference bandwidth for each individual-month. As differences in smoothing parameter may result in differences in home range size (Pellerin et al. 2006), we then set the smoothing parameter to the median value obtained in each species to derive utilization distributions and 90% kernel home range areas for each individual-month (Worton, 1989). Finally, as we expected home range size to be negatively correlated with home range quality (Saïd et al. 2005, Herfindal et al. 2005, Hanya et al. 2006), we included in analyses the percentage of woodland in roe deer and grass areas in mouflon derived from vegetation cover maps described in Morellet et al. 2011 (Figure 1) and Marchand et al. 2015 (Figure 2), respectively. These habitat types are key determinants of species-specific habitat selection and/or body condition (Morellet et al. 2011, Marchand et al. 2014, 2015), suggesting they can be used as index of home range quality.

*Table 3 : Sex and age classes effectives in roe deer for 6-hours scheduling and in Mediterranean mouflon for 2-hours scheduling. The only female >8 years old was remove from our analyses. Note that as an individual may be captured several times throughout its life, the effectives represented here are individual-years unit. y.o.= years old*

	Roe deer			Mediterranean mouflon			
Sex	Juveniles	Yearlings	Adults	2-3 y.o.	4-6 y.o.	7-8 y.o.	>8 y.o.
Females	32	27	115	9	22	17	1
Males	24	19	76	21	25	24	14

## Statistical analysis

### *Inter-individual difference in movements*

In order to assess for the effect of sex, age, month and their interactions on daily distance travelled (log-transformed) of each species, we fitted species-specific linear mixed models including individual identity as random factor to take into account individual variability and repeated measurements on the same individuals. We also added in the models the percentage of woodlands (roe deer) and of grass areas (mouflon) of every individual's monthly home range as an index of home range quality.

### *Inter-individual differences in space use*

We performed the same analyses as previously reported to evaluate temporal variation in inter-individual differences in monthly home range size (log-transformed) by both species.

### *Model selection*

We selected the best models with the lowest Akaike's information criterion (AIC) value, reflecting the best compromise between precision and complexity of the model (Burnham & Anderson 2002). We considered two competing models as different when the difference between AIC values was  $> 2$ . According to the rule of parsimony, when the AIC of two competing models was  $< 2$ , we retained the simplest one (*i.e.* the model with the lowest number of estimated parameters).

We performed all statistical analyses using R software version 3.2.1 (R Development Core Team 2015).

## **RESULTS**

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### **Daily distance travelled**

#### *Roe deer*

The two-way interactions between sex and age, between sex and month and between age and month were retained in the best model investigating the daily distance travelled (Table 3). The percentage of woodlands in monthly home ranges was also included in the best model, daily distances travelled increasing of 2149m (44%) between the minimum and maximum percentage of woodlands in monthly home range (3.5% (min. % observed) woodlands: 4887m [217], 99.5% woodlands (max. observed): 7036m [355], fixed parameters: daily distance travelled of adult males in May).

During territoriality, from March to August, adult males were the most mobile individuals travelling on average between 1500 to 4000 m (30 to 100%) more than females whatever their age, 1000 to 2500m (25 to 36%) more than juvenile males and 1000m (15 to 20 %) more than yearling males (Figure 3). A decrease 2200m (43%) in female mobility was also observed from March to June, however with weak differences among age classes (yearling females travelling 500m less than juvenile and adult females in May and June, juvenile females travelling 500 m less than older females during rut in July-August). Finally no sex- or age-related differences among individuals were observed from September to February (Figure 3).

Table 3 : AIC values for models explaining the log-transformed of daily distances travelled by roe deers and mouflons. The identity of individuals was set as a random factor. Underlined models represent the global model submitted to model selection procedure. The best models who were selected (AIC are typed in red.

		DL	AIC	$\Delta$ AIC	AIC weight
Roe Deer	<u>Log(distance) ~ Age*Sex*Month + % Woodlands</u>				
	Age + Month+ Sex + % Woodlands + Sex*Month + Age*Month + Sex*Age	53	1183.5	0.00	0.887
	Age + Month+ Sex + % Woodlands + Sex*Month + Age*Month	51	1187.6	4.17	0.110
	Age + Month+ Sex + % Woodlands + Sex*Month + Age*Month + Sex*Age + Sex*Age*Month	75	1195.3	11.80	0.002
	Age + Month+ Sex + % Woodlands + Sex*Month + Sex*Age	31	1200.0	16.57	0.000
Mediterranean mouflon	<u>Log(distance) ~ Age*Sex*Month + % Grasslands</u>				
	Age + Month + Sex + % Grasslands + Sex*Month + Age*Month + Sex*Age	65	19522.3	0.00	0.894
	Age + Month + Sex + % Grasslands + Sex*Month + Age*Month + Sex*Age + Sex*Age*Month	87	19526.6	4.27	0.106
	Age + Month + Sex + % Grasslands + Sex*Month + Age*Month + Sex*Age + Sex*Age*Month	63	19537.1	14.77	0.001
	Age + Month + Sex + Sex*Month + Sex*Age	64	19586.4	64.07	0.000

Daily distances travelled (m)

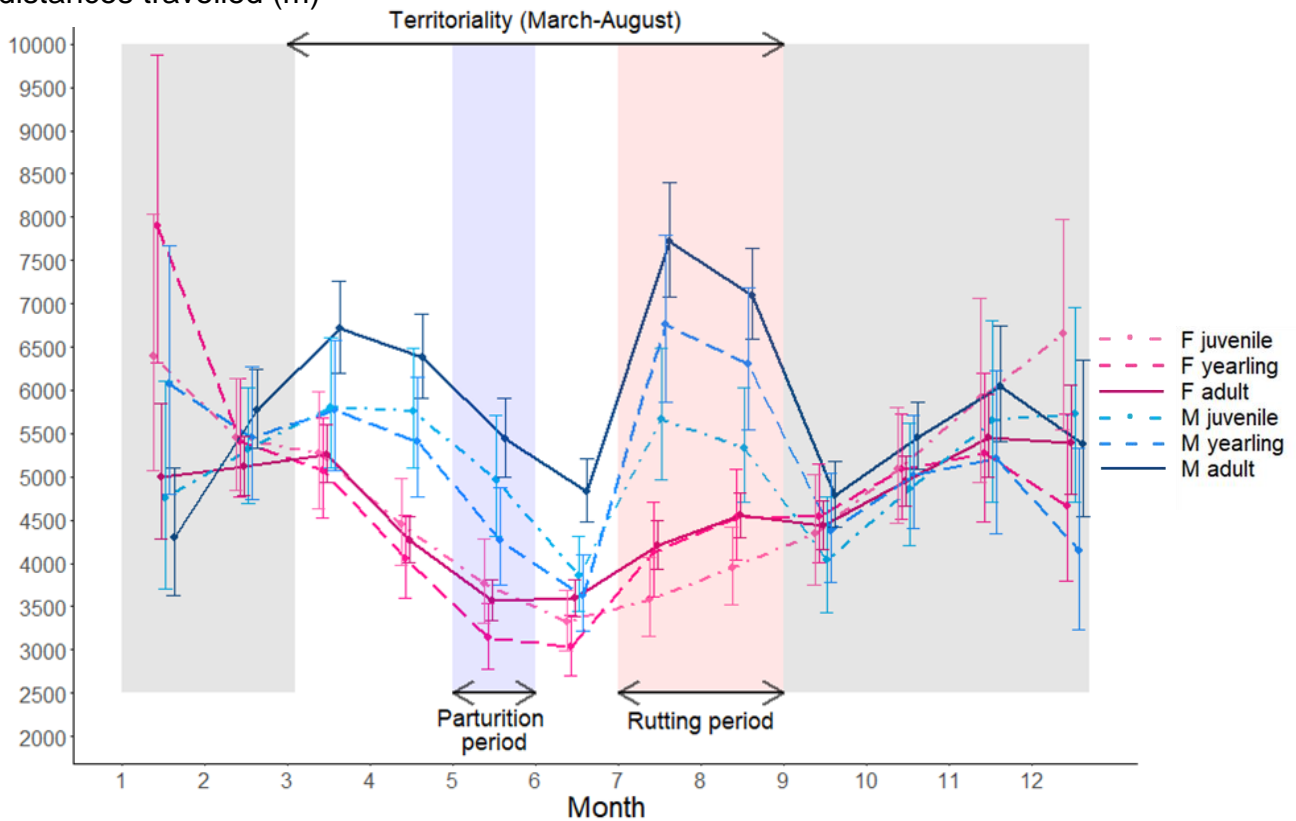
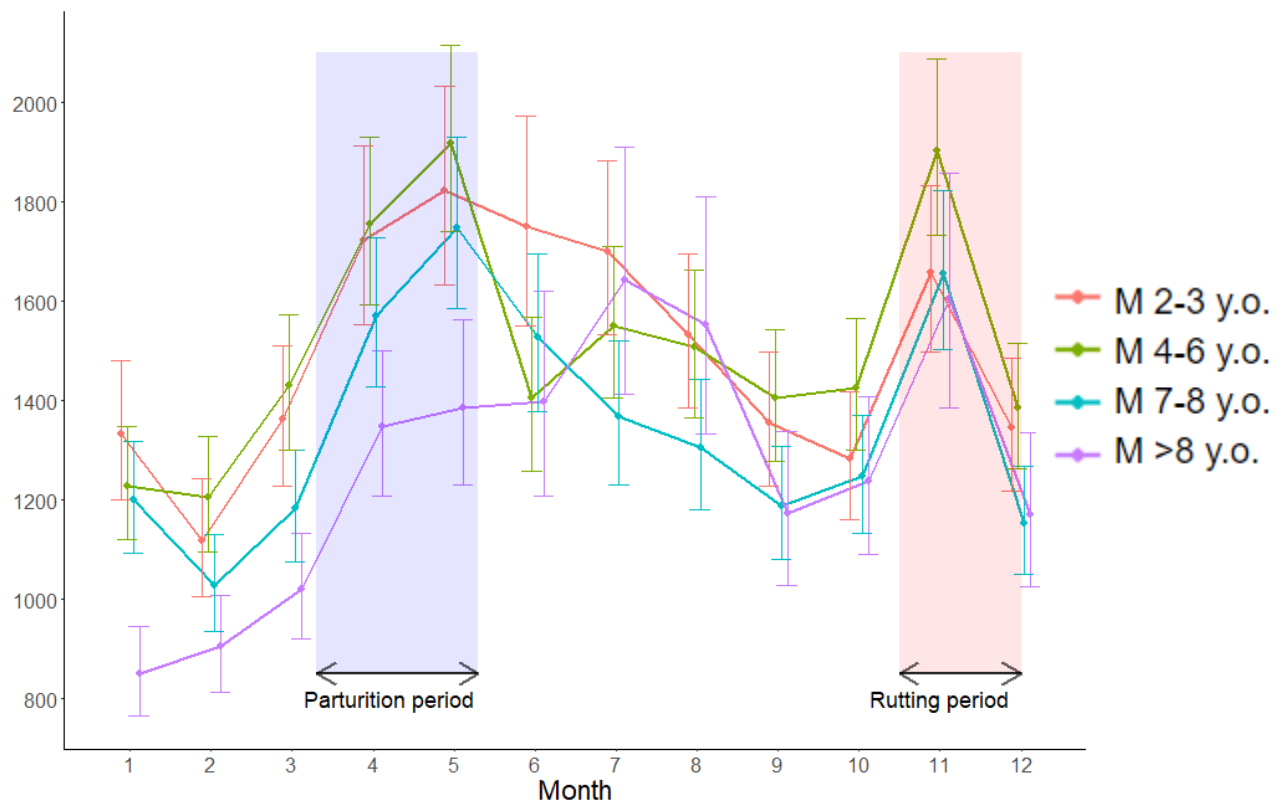


Figure 3 : Mean predicted *daily distance travelled in m* in roe deer throughout the year. Bars represent 95% CI.



Daily distances travelled (m)



**Figure 4:** Mean predicted *daily distance travelled in m* in male mouflon throughout the year. Bars represent 95% CI.

The two-way interactions between sex and age, between sex and month and between age and month were retained in the best model investigating the daily distance travelled (Table 3). The percentage of grass areas was also included in the best model with an increase of 817m (36%) between the minimum and the maximum (5% (min. % observed) grass: 2265m [127.6], 64% grass (max. observed): 1448m [86.7], fixed parameters: daily distance travelled of males 4-6 years old in May). In males we observed high age-related differences especially in winter where older males, especially those aged more than 8 years old, travelled between 200 and 500m less, that is to say on average 25% less than younger males between 2 and 6 years old (Figure 4). However these differences among age-classes were very reduced during the rutting period from October to December, where 4-6 year-old males travelled 200m (12.5 %) more than every other males (Figure 4).

## Daily distances travelled (m)

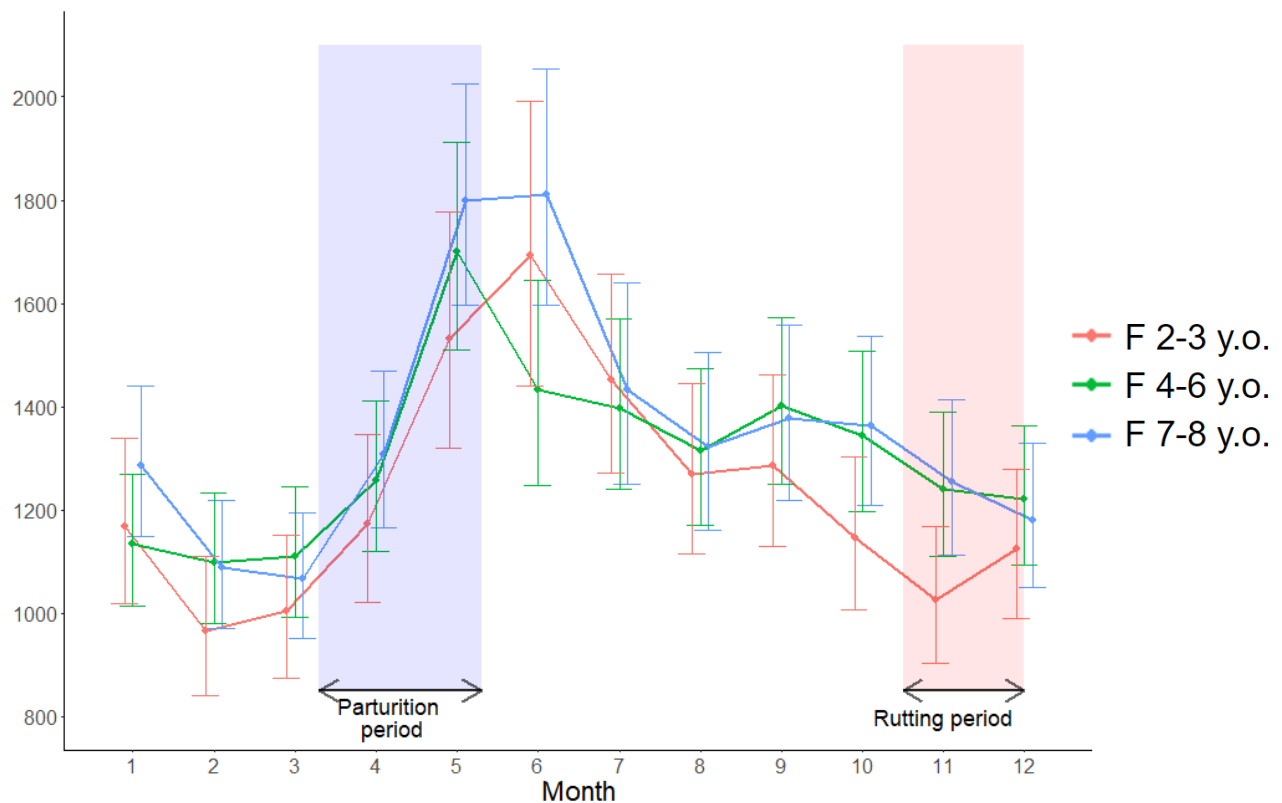


Figure 5: Mean predicted **daily distance travelled in m** in female mouflon throughout the year. Bars represent 95% CI.

In females, no differences related to age were observed except during rut period where 2-3 year-old females travelled 150-200m (15-20%) less than older females in October and November (Figure 5). Finally sex-related differences could be distinguished only during rutting period especially in November where males travelled between 600 (for 2-3, 7-8 and >8 year-old males) and 800m (for 2-3 year-old males), that is to say 60 to 80% higher distances than 2-3 year-old females and 400 to 600m more than 4-8 year-old females. Both sexes showed an increase in travelled daily distance travelled from the end of winter in February-March to late Spring in May-June, with increases ranging from 500m to 700m (58 to 63% augmentation), before a more or less continuous decrease from July to September with decreases ranging from 300 to 500m (18% to 30%).

## Home range size

### Roe deer

The two-way interactions between sex and month was retained in the best model investigating the home range size variation (Table 4). Besides, the proportion of woodlands habitat had also an effect, with an increase of 1% resulting in a decrease of 1.0 ha in home range size.

Sex-related differences were strong during territoriality period, males had home ranges on average 15 ha bigger (30%) than those of females (mean [SE]: males= 66.1 ha [3.4]; females = 51.4 ha [2.1], Figure 6). Age-related differences were also observed but only between adult males and younger males, whose home range size was on average 10 ha bigger (mean [SE]: yearlings= 71.1 ha [4.1]; juveniles = 68.9 ha [3.6]) than their elders (mean [SE]: adult= 58.4 ha [2.4])) and 25-30 ha bigger than females (Figure 6). No pronounced differences between females were observed, all females range decreasing from March to June (mean [SE]: 73.1 [2.9] to 38.3 ha, 40% decrease) before increasing again from July. A range contraction also occurred in males during territoriality, from March to July (from 85 ha and 70 ha in March to 60 and 50 ha in July for juveniles/yearlings and adult males respectively).

*Table 4 : AIC values for models explaining the log-transformed of monthly home range size by roe deers and mouflons. The identity of individuals was set as a random factor. Underlined models represent the global model submitted to model selection procedure. The best models who were selected (AIC are typed in red).*

	Models	DF	AIC	ΔAIC	AIC Weight
Roe Deer	<u>Log(HR size) ~ Age*Sex*Month + % Woodlands</u>				
	Sex + Age + Month + % Woodlands + Sex*Month + Sex*Age	31	1115.2	0.00	0.439
	Sex + Age + Month + % Woodlands + Sex*Month + Sex*Age + Age*Month	53	1116.5	1.22	0.239
	<b>Sex + Age + Month + % Woodlands + Sex*Month</b>	<b>29</b>	<b>1116.6</b>	<b>1.32</b>	<b>0.227</b>
	Sex + Age + Month + % Woodlands + Sex*Month + Age*Month	51	1118.3	3.09	0.094
Mediterranean mouflon	<u>Log(HR size) ~ Age*Sex*Month + % Grasslands</u>				
	<b>Sex + Month + % Grasslands + Sex*Month</b>	<b>27</b>	<b>498.5</b>	<b>0.00</b>	<b>0.904</b>
	Sex + Age + Month + % Grasslands + Sex*Month	30	504.5	5.98	0.045
	Sex + Age + Month + % Grasslands + Sex*Month + Sex*Age	32	504.7	6.12	0.042
	Sex + Age + Month + % Grasslands + Sex*Month + Age*Month	63	508.8	10.30	0.005

### Monthly home range size (ha)

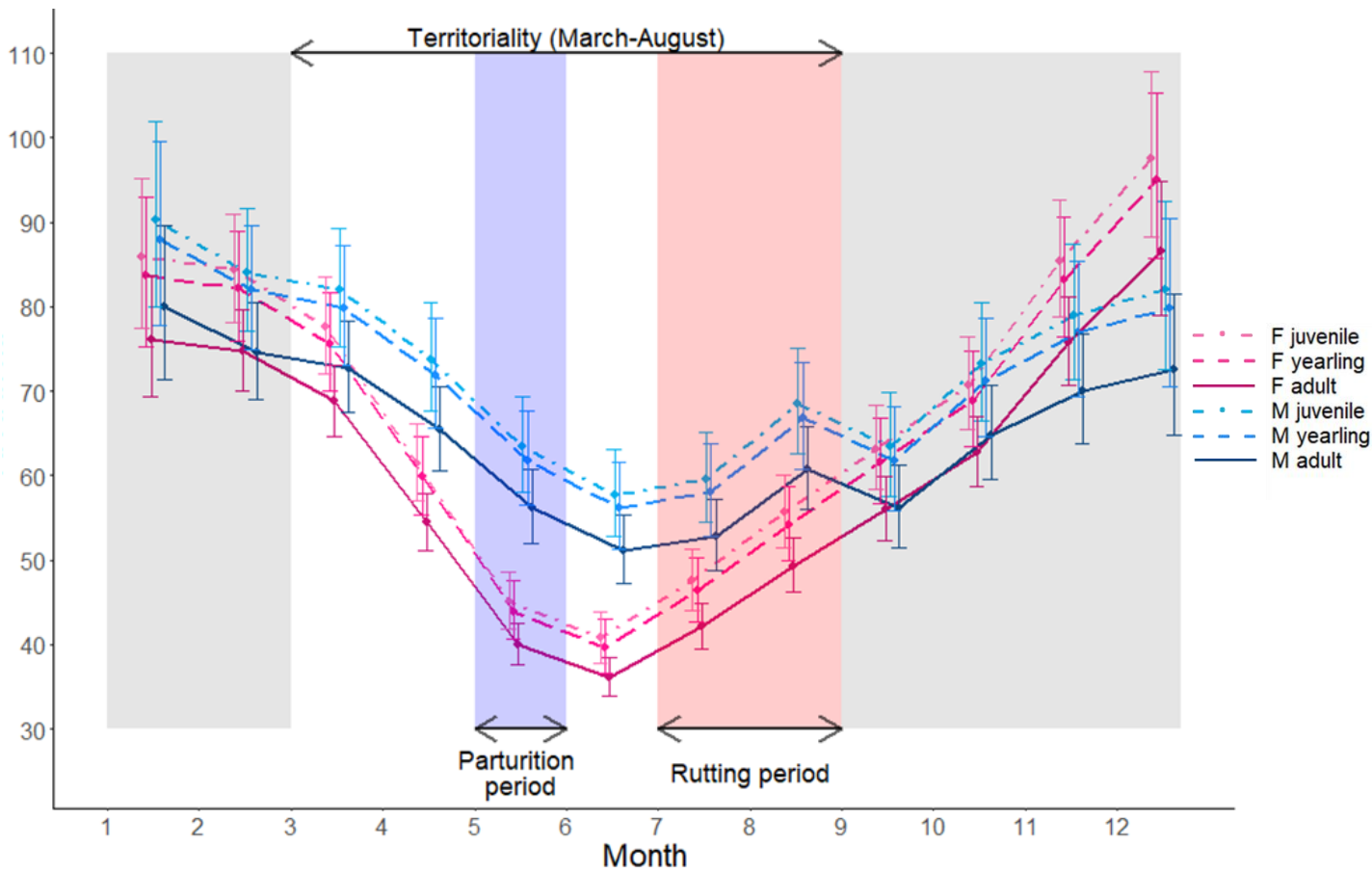


Figure 6: Mean predicted home range size in hectares in roe deer throughout the year. Bars represent 95% CI.

### Mediterranean mouflon

The two-way interaction between sex and month was retained in the best model investigating the home range size variation (Table 4). The percentage of grass areas in the monthly home range was also included in the best model, with an increase of 1% resulting in a decrease of 2.9 ha in home range size. Generally, we noticed that during summer, a drastic reduction in range size was observed especially in males, decreasing from 110 ha in May to 75 ha in June, (32% decrease) (Figure 7).

Sex-related differences were only pronounced during rutting period when males' range size more than doubled, from less than 100 ha in September to more than 210 ha in November whereas females range remained around 100 ha which is twice less than males (Figure 7).

### Monthly home range size (ha)

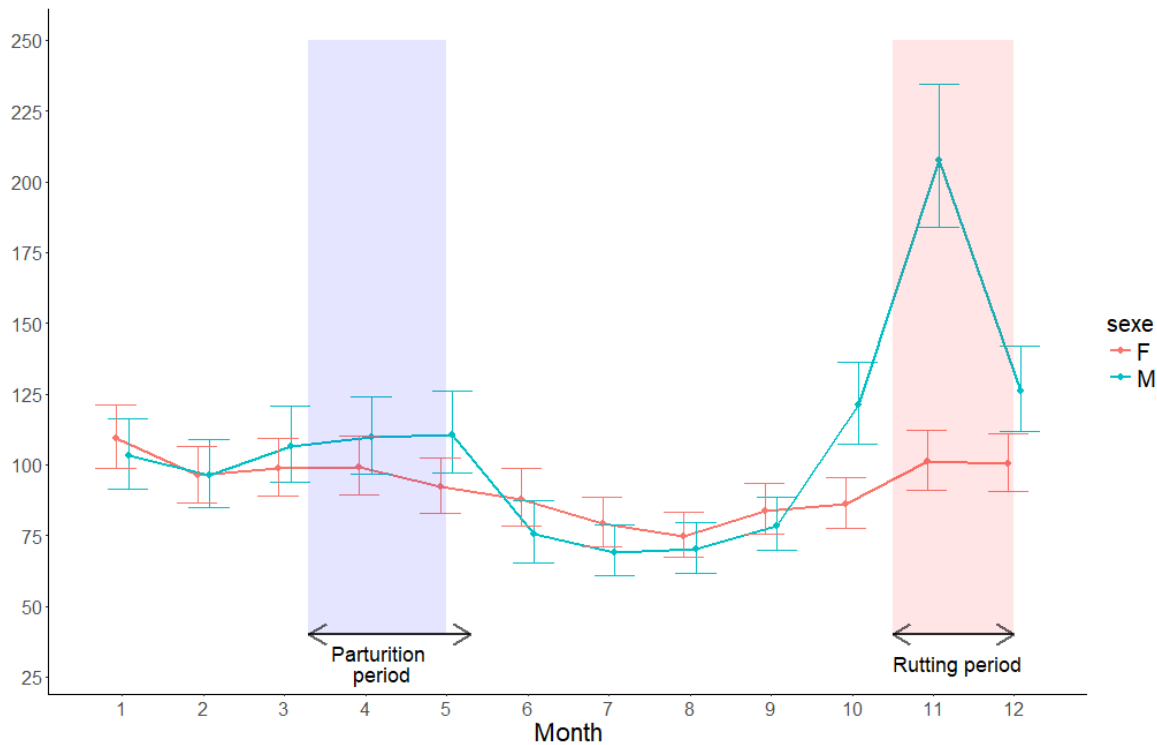


Figure 7 : Mean predicted home range size in mouflon in hectares throughout the year. Bars represent 95% CI.

## DISCUSSION

### Intra-sexual competition: territoriality vs gregariousness

As expected, in roe deer, adult males showed higher daily travelled distances than females and younger males and exhibited smaller territories than subadults (i.e. males captured as yearlings at the beginning of their monitoring) and yearlings (i.e. males captured as juveniles at the beginning of their monitoring) males. These results support then our hypothesis that territoriality would influence males movements and space use according to their age. Indeed monthly home range size contraction coupled with a great increase in mobility could indicate that adult males concentrated their movement during territoriality. First, the higher distances travelled in March-April may correspond to the establishment phase of the territory, during which agonistic interactions peak and overlaps between males' territory disappear (Johansson 1996). We may then suggest that during this phase that Johansson reported to last 6 weeks, males would likely chase each other to defend their territory, which could explain why they showed increased daily distances travelled at this period. Then the second peak of daily distances travelled in July-August could be attributed to the rutting

period during which males are known to patrol their territory in search of females, and chase intruder males off their territory (Liberg et al. 1998 ).

Even if differences in movements and space use among roe deer males according to their age were quite high, certainly due to the fact that adult males were supposed to be the most territorial individuals (Vanpé et al. 2009), younger males were also found to have a contracted range size associated with increased daily movements during rutting period. First this could be explained by the fact that subadults males (i.e. yearlings at the time of their capture) are known to adopt two types of spacing tactics: they either co-exist on an adult male territory and try regularly to court females there (“satellite” tactic) or to have their core areas in buffer zones between territories and made short raids into these in search of unattended females (“peripheral” tactic, Liberg et al. 1996). Finally yearling males (i.e. juveniles at the time of their capture) were found in a previous study to be the most subjected to aggression by older territorial males, (Wahlstrom 1994). Therefore, we could suggest that yearling males travelled higher daily distances than females during territoriality period because of harassments by adult males.

In contrast with roe deer, sex-related differences in movements and space use between males and females mouflon were mostly found during rutting period. These different patterns between roe deer and mouflon, could be explained by the fact that mouflons live most of the year in segregated monosex groups except in rutting period from mid-October to December where the proportion of mixed groups is at its highest (Dubois et al. 1993, Bourgouin et al. 2018). Whereas females’ mobility and home range size did not vary much between October and December, as predicted males range size and mobility increased a lot during the rutting period. During this period males leave their current home range to join their reproduction range which often corresponds to the areas they were reared and roam between females groups there (Dubois et al. 1996). The departure of males to join their rutting range and their search for females could then result for them in increased daily travelled distances and home range size during the mating season. The slight differences between 4-6 year-old males and other males in November could also be due to different mating strategy in males. Bon et al. (1992) reported that dominant males (i.e. >7 years old) most of the times tend females (i.e. impeding directly or indirectly other males’ attempts to mate with tended females), whereas younger subordinates males (<7 years old) are more prone to course females (i.e. breaching the defense of dominant males and chase after females, Hogg 1984). However, this might not explain entirely why 4-6 year-old individuals were the most mobile ones during rutting period because if this hypothesis was right, we would expect 2-3 year-old males to be as mobile as 4-6 year-old males which is not the case in our study.

Age-related differences in mobility were also recorded but only in males and mostly out of rutting period. Younger males between 2 to 6 year-old were indeed found to travel more than older males mostly in winter and late spring (December to June). Several reasons for such differences could be given. First, younger males often tend to revisit their rutting range during non-rutting period throughout the year (Dubois et al. 1993, 1996) whereas older males stick to their normal range outside of rutting period. On the other side, senescence in males, especially those older than 8 years old, may reduce their movement capacity, altering then their mobility and space use. Froy et al. (2018) for example reported in Soay sheep (*Ovis aries*) an age-related decline in annual home range core area associated with a decline in survival rates of individuals and an increase of home range quality (i.e. % of grasslands cover). Then these results were claimed to be consistent with the fact that older individuals may be more experienced and have a higher foraging efficiency than younger individuals while displaying reduced locomotor, cognitive, sensory function and resource acquisition. Even if we did not detect, at a monthly scale, a decline in home range size, at a finer spatial scale we did observe, during winter and late spring, a reduction of daily travelled distances in our study group of mouflon males, which we may suggest to be the results of experience and maybe of senescence. Effects of age related to senescence and familiarity in patterns of movement and space use have been poorly studied in the literature. Further investigations on age-related differences in survival rates and habitat selection would be needed to assess respectively the influence of senescence and experience in several ungulates species' movements and space use.

### **Parturition and offspring spacing tactic**

Roe deer females reach sexual maturity at the age of one and give birth from the end of April to the very beginning of June with most of birth events occurring in May. To minimize risk of predation, juveniles in large herbivores are known to adopt different tactics along a follower-hider continuum (Ralls et al. 1986) that may last for some days to several weeks after their birth (Lent 1974). Roe deer and white-tailed deer fawns (*Odocoileus virginianus*) for example typically hide in bed sites to avoid predators and get protection from adverse conditions while their mothers are foraging (Linnell et al. 1994, 1999, Tull et al. 2001, Van Moorter et al. 2009). As a consequence we hypothesized that roe deer females in age of reproducing (i.e. yearlings and adults) would have different movement patterns, due to their reproductive constraints. As an example, reduction in monthly home range size and movements in white-tailed deer females have been reported during parturition and post-parturition period compared to pre-parturition period (Bertand et al. 1996, D'Angelo et al. 2005). In pre-parturition period (April), roe deer adult and yearlings females were expected to travel higher daily distances and have larger home range than in May– June, when fawns are born and show reduced mobility and hiding behavior. Then fawns mobility increases

continuously and they switch from hiding to running after two months in roe deer (Linnell et al. 1994, 1998). Adult and yearlings females were then intended to have increased daily travelled distances and home range sizes back again in July-August. We did observe both patterns described as above, however in all females with no differences between juvenile and older females. Our results then did not support the hypothesis that the decrease in females' mobility during late April to June may be induced by parturition and reduced fawn's mobility and hiding tactic. Previous studies reported that home range size in roe deer females was mostly correlated with food and cover availability (Tufto et al. 1996, Saïd et al. 2005). Therefore, females appeared to be more influenced by seasonality than parturition, and we could then suggest that the reduction in their daily travelled distances and monthly home range sizes could be driven by the abundance of food resources and cover (Morellet et al. 2013), may be the two factors that are the most limiting at both fine and larger spatio-temporal scales.

Mouflon's lambs follow their mothers (Lent 1974, Bon et al. 1991) very early after their birth that occurs in April-May in the Caroux-Espinouse Mountains (Bon 1991). We then expected females to show little reduction in their daily travelled distances and monthly home range sizes during parturition period, and a rapid return to levels of mobility and space use similar to those before parturition. Actually, from April to May-June, a high increase in females travelled distances and home range size was observed, which was contrary to our predictions. However these patterns have already been observed by Ciuti et al. (2009), who showed that lactating female Sardinian mouflon during lambing season (April-May), used areas two to three times larger than those used by non-lactating ones. Consequently we could suggest that contrary to roe deer, increased needs to offset parturition and lactation requirements may explain why female mouflon exhibited an increase in daily travelled distances and home range size during the lambing period.

### **Seasonality and interspecific differences**

As expected for large herbivores, roe deer and mouflon movements and space use seemed to be mostly influenced by the availability of resources and its seasonal variation outside of mating season. Only roe deer males appeared to be less subject to seasonal variations in their movements and space use, certainly due to their territorial behavior. More generally we observed different movement patterns between the two species in response to seasonality. For example, while daily travelled distances and home range size of roe deer females (and males to a lesser degree) decreased, daily travelled distances of mouflon, whatever the sex and age, increased while their home range size did not vary much from February-March to May-June which correspond to the flush of vegetation period in both study sites. We may explain this by the difference of diet of those



two species and landscape composition. Roe deer are considered as selective feeders eating mostly on seeds, leaves, soft shoots and fruits of wood plants (e.g. shrubs and trees, Tixier & Duncan 1996). Moreover, when vegetation starts to regrow in Spring, roe deer also highly feeds on herbaceous plants as they are of high digestibility during this period. In the forested and agricultural landscape of Aurignac for example, Morellet et al. (2011) showed that roe deer use of meadows was increased during spring. As these habitats may provide high forage quantity and quality, roe deer may not have to travel much to gather resources which could explain the reduced daily travelled distances and home range size of roe deer females during Spring. On the other side, mouflon are grazers and mostly feed on herbaceous plants (Hoffman 1989) and they need to travel to find rich areas to fulfill their energetic needs. However in Caroux-Espinouse massif, grasslands distribution is relatively sparse into the landscape, then we could suppose that mouflon has to travel more than roe deer to reach the grass rich patches. Finally, our results are consistent with those of Mysterud et al. 2000 who reviewed the effect of season and feeding styles in temperate ruminants while accounting for body mass scaling. They found that for browsers weighing less than around 45 kg, winter range was larger than summer range whereas it was the contrary for grazers. This results are consistent support advocating for the need to account for the body mass, diet and environment of individuals while studying their movements and space use, as these variables are known to be of high influence (Du Toit 1990, Tucker et al. 2014).

Another explanation of the different movement patterns observed in both species could reside in their different breeding strategies. Roe deer is an income breeder, that is to say that it relies on continuous supply of forage to offset the costs of reproduction (Andersen et al. 2000). Income breeders, which stock few fat reserves, are then expected to adjust their movements to the availability of food resources. More precisely, when those are scarce, it is expected that they may need to travel more and have increased home range size to acquire them, and inversely to travel less and have decreased home range size when those are abundant. This could then explain why we observed a reduction of movements and space use in females (and males to a lesser degree) in spring when food availability is at its highest, followed by an augmentation of both travelled distances and home range size in both sexes in autumn-winter when food availability is reduced (Morellet et al. 2013). In contrast the Mediterranean mouflon is a capital breeder, that is to say a species that relies more on its energetic reserves accumulated mostly during the favourable season to offset the costs of reproduction (ref). Income breeders are then expected in general to move more and further during the season of food abundance as it represents the best period to accumulate the required resources, than during the food scarcity period during which they can rely on their fat reserves to meet their energetic requirements as observed in other capital breeders like red deer (*Cervus elaphus*, Geogii & Schröder 1983, Koubek & Hrabec 1996), moose (*Alces alces*, McCulley

et al. 2017) or bighorn sheep (*Ovis Canadensis*, Poole et al. 2016). Once again this could explain why we observed reduced mobility of mouflon in winter followed by an increase in distances travelled in spring in both sexes. Nonetheless a comparative study including a larger panel of large herbivore species differently distributed along several life history traits gradients (grazers vs browser, income vs capital breeders, low vs high sexual dimorphism) would be needed to clearly assess the determinants of inter-specific variations of movements and space use.

Finally the diminution of mouflon travelled distances and home range size in summer (July-September) could be due to thermic constraints. Indeed Marchand et al. (2014) demonstrated that mouflon, especially males, selected for forested areas during the hottest days of summer to buffer against high temperatures. Mouflon males are actually more sensitive than females to heat due to their larger body size. The drastic decrease of their home range size during the hottest month of the year, compared to females, could then be due to the need for males to stay more often in forest and move less. In roe deer on the contrary females showed increased daily distances and home range size during summer. However, this period coincides with the rutting period and this strong mobility during this period is probably largely influenced by the reproductive behaviour in roe deer (Liberg et al. 1998). Indeed in summer, every female in our study was supposed to participate to rut (i.e. juveniles at the capture have their first mating period in July-August), yet females are known to make reproductive expedition during this period and to visit several males' territories (Linnell et al. 1998, Debeffe et al. 2014). This could explain then the increase in both daily travelled distances and home range size of females during rutting period.

## CONCLUSION

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Our results showed that movements and space of two wild large herbivores species were both determined by intrinsic and extrinsic factors at various spatio-temporal scales. Intra-specific sex- and age-related differences in mobility and monthly home range size were observed in both species but with some inter-specific variations in regards of their contrasted life history traits. Concentration of movements and space use in roe deer males during rutting period and the previous month were likely due to their territorial behavior, and contrasted with mouflon spacing tactics that were more diffusive with increased travelled distances and range area during this time. The age-dependency of territorial status was also suspected to be at the origin of age-related differences in roe deer during territoriality period males whereas gregariousness in Mediterranean mouflon could explain the little differences among males (essentially in summer and rutting period) but also among females most of the year. Moreover age-related differences distinguished in winter and spring in mouflon males

may originate also from both familiarity and/or senescence. If the effects of sex-related differences have been well documented, however little studies until now have focused on the potential effects of age on movements and space use of ungulates and animals in general. This advocate for the need to perform longitudinal studies as monitoring individuals on a large part of their life may grant us access to their life history track and determine how individuals move throughout their life. Finally a comparative study including a higher number of ungulate species differently distributed along several life history traits and landscape gradients (grazers vs browser, income vs capital breeders, low vs high sexual dimorphism, body mass) and featuring large data about individual characteristics (sex, age, body mass, reproductive status, personality) would represent a great opportunity to clearly assess the different sources of intra- and inter-specific variations in patterns of movement and space use.

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# ANNEXES

## Daily distances travelled

Avant toute chose j'aimerais vous préciser que je n'ai choisi de ne détailler que mes scripts utilisés pour le mouflon par souci d'utilité. En effet les scripts utilisés pour le chevreuil ressemblent à peu de choses près exactement à ceux utilisés pour le mouflon, je me suis donc dit qu'il n'était pas nécessaire de détailler ceux-ci car cela serait une redite.

```
library(adehabitatHR)

load("mouf2h.RData")

### fichier de coordonnées GPS à 2h des individus après correction pour
les points aberrants

traject=as.ltraj(mouf2h[,c("OX.Lambert.2", "OY.Lambert.2")], id=mouf2h$Fichier,
date = mouf2h$dateR)
### on crée un objet as.ltraj qui va contenir les distances parcourues
entre chaque localisations successives que l'on va sommer plus tard pour
obtenir les distances parcourues journalières

trjmouf=ld(traject)

### on convertit l'objet as.ltraj en data frame pour l'utiliser dans la
boucle

test=merge(trjmouf,mouf2h, by.x= c("id", "date"),
by.y=c("Fichier", "dateR"), all.x=T)
### on a fusionné avec le fichier gps "mouf2h" du début car celui-ci
contient aussi des infos sur le sexe, l'âge des individus ainsi qu'un
identifiant jour-individu ("day") qui va nous servir dans le calcul des
distances journalières pour chaque individu

trjmouf=test
save(trjmouf, file="trjmouf.RData")

load(file="trjmouf.RData")
```

```
> head(trjmouf[c(2,3,4,7,8,14,34,17,54,53,69)])
  date           x           y      dist  dt day id_mouf sexe  classe_age poids_kg Freqxy
1 2012-07-01 00:00:53 649838.6 1847675  67.156749 7195  9    1019  F 7 ans et plus      26      10
2 2012-07-01 02:00:48 649781.8 1847711  27.172746 7218  9    1019  F 7 ans et plus      26      10
3 2012-07-01 04:01:06 649764.1 1847732  80.052034 7166  9    1019  F 7 ans et plus      26      10
4 2012-07-01 06:00:32 649707.7 1847789 118.342543 7235  9    1019  F 7 ans et plus      26      10
5 2012-07-01 08:01:07 649769.8 1847688 200.343964 7246  9    1019  F 7 ans et plus      26      10
6 2012-07-01 10:01:53 649616.5 1847559   9.156692 7151  9    1019  F 7 ans et plus      26      10
```

Date : date à laquelle le point GPS a été enregistré  
X et Y : coordonnées en Lambert 93 de chaque point GPS  
dist : distance entre le point GPS considéré et celui d'après, par exemple

ici la distance entre le point pris à 2012-07-01 00:00:53 et le point suivant pris à 2012-07-01 02:00:48 est de 67m.  
 dt : durée séparant le point GPS considéré du suivant  
 day : identifiant jour, chaque trajectoire a un identifiant jour unique et chaque individu peuvent avoir plusieurs trajectoires journalières qui leurs sont propres. Ici il s'agit de la trajectoire numéro 9 sur l'ensemble des trajectoires et celle-ci est associée à l'individu 1019  
 id\_mouf : identifiant de l'individu  
 sexe : F pour femelles et M pour mâles  
 classe\_age : classe d'âge à laquelle appartient l'individu à la capture  
 poids\_kg : poids de l'individu à la capture  
 Freqxy : nombre de points constituant la trajectoire. Ici la trajectoire journalière numéro 9 contient en tout 10 points.

```
dptot=NULL
```

```
### objet final qui va contenir les distances parcourues journalières des individus et leurs informations relatives comme le sexe, l'âge, le poids des individus, etc
```

```
### boucle qui va calculer pour chaque individu ses distances journalières parcourues
```

```
for (i in 1:length(levels(trjmouf$day))){
  gpsday<- droplevels(subset(trjmouf,
trjmouf$day==levels(trjmouf$day)[i])) # données gps et distances entre
chaque point associées à l'identifiant jour i
  gpsday= as.data.frame(gpsday)
```

```
> head(gpsday[c(2,3,4,7,8,14,34,17,54,53,69)])
```

	date	x	y	dist	dt	day	id_mouf	sexe	classe_age	poids_kg	Freqxy
1	2012-07-01 00:00:53	649838.6	1847675	67.156749	7195	9	1019	F	7 ans et plus	26	10
2	2012-07-01 02:00:48	649781.8	1847711	27.172746	7218	9	1019	F	7 ans et plus	26	10
3	2012-07-01 04:01:06	649764.1	1847732	80.052034	7166	9	1019	F	7 ans et plus	26	10
4	2012-07-01 06:00:32	649707.7	1847789	118.342543	7235	9	1019	F	7 ans et plus	26	10
5	2012-07-01 08:01:07	649769.8	1847688	200.343964	7246	9	1019	F	7 ans et plus	26	10
6	2012-07-01 10:01:53	649616.5	1847559	9.156692	7151	9	1019	F	7 ans et plus	26	10

```
#On va calculer la somme des distances parcourues pour chaque trajectoire,
ci-dessous on crée les objets qui vont contenir les informations
d'intérêts
```

```
datedeb=NULL
datefin=NULL
distparc=NULL
anid=NULL
sexe=NULL
age_cohorte=NULL
classe_age=NULL
poids_kg=NULL
day=NULL
cohortes=NULL
pose=NULL
age_estime=NULL
Freqxy=NULL
```

```

sumdis=sum(gpsday$dist, na.rm=TRUE)
# objet qui contient la somme des distances entre chaque point
successif, bref c'est la distance journalière totaler parcourue par
l'animal 1019 lors de la journée numéro 9

day=c(day,levels(gpsday$day))
sexe=c(sexe,levels(gpsday$sexe))
datedeb=c(datedeb,gpsday$date[1])
datefin=c(datefin,gpsday$date[nrow(gpsday)])
Freqxy=c(Freqxy,unique(gpsday$Freqxy))
poids_kg=c(poids_kg,gpsday$poids_kg[1])
id_mouf=c(anid,levels(gpsday$id_mouf))

distparc=c(distparc,sumdis)
#objet qui va stocker les distances parcourues journalières de chaque
individu

#Transformation des objets en vecteurs pour pouvoir les assembler en
colonnes dans un data frame appelé dp
distparc=as.vector(distparc) pose=as.vector(pose)
poids_kg=as.vector(poids_kg)
day=as.vector(day)
sexe=as.vector(sexe)
classe_age=as.vector(classe_age)
datedeb=as.vector(datedeb)
datefin=as.vector(datefin)
id_mouf=as.vector(id_mouf)

dp=as.data.frame(cbind(day,id_mouf,Freqxy,sexe,cohorte,age_cohorte,age_est
ime,poids_kg,distparc,datedeb,datefin,pose))
dptot=rbind(dptot,dp)
}
#tableau qui répertorie toutes les distances journalières parcourues par
tous les individus
dpmouf2h=dptot
dpmouf2h$distparc2=dpmouf2h$distparc/dpmouf2h$Freqxy*12
### on a calculé une 2nde distance qui correspondrait à celle mesurée si
normalement tous les points GPS de la trajectoire journalière avaient été
enregistrés

> head(dpmouf2h)
  id_mouf day sexe classe_age poids_kg distparc distparc2      datedeb      datefin
1    1019   9   F    >8 ans      26  679.5132  815.4158 2012-07-01 00:00:53 2012-07-01 22:00:47
2    1019  10   F    >8 ans      26 1255.9159 1507.0991 2012-07-02 00:01:21 2012-07-02 22:00:59
3    1019  12   F    >8 ans      26 1695.5710 2034.6852 2012-07-04 00:01:18 2012-07-04 22:01:19
4    1019  14   F    >8 ans      26 1580.5067 1724.1891 2012-07-06 00:00:49 2012-07-06 22:00:54
5    1019  20   F    >8 ans      26 2271.3426 2477.8283 2012-07-12 01:01:21 2012-07-12 23:01:20
6    1019  37   F    >8 ans      26  913.5923 1096.3108 2012-07-29 00:00:49 2012-07-29 22:01:09

save(dpmouf2h,file="dpmouf2h.RData")

```

## Monthly home range size

```
#####
##### Calcul des domaines vitaux mensuels #####
#####
load("mouf2h.RData")
library(adehabitatHR)

library(rgdal)
### Création identifiant ani_id_YM qui comprend l'id de l'individu et mois et
l'année de chacun de ses points GPS, par exemple "1019 2012-07" renvoie à tous les
points GPS de l'individu 1019 enregistré au mois de juillet 2012
mouf2h$ani_id_YM=paste(as.character(mouf2h$id_mouf),as.character(format(mouf2h$dateR,"%Y-%m", tz="GMT"))))

### On va faire un subset des points GPS sans NA
DVxymouf=mouf2h[,c("ani_id_YM","posx","posy")]
DVxymouf=droplevels(subset(DVxymouf,is.na(posx)==F))

### pour chaque ani_id_YM, on va compter le nombre de points GPS connus qu'on va
appeler freq
freq=as.data.frame(table(DVxymouf$ani_id_YM))
names(freq)=c("ani_id_YM","freq")
toto=merge(DVxymouf,freq,by="ani_id_YM", all=T)
quantile(toto$freq,c(.025,.05,.1,.15,.2,.25,.3))

xy=droplevels(subset(toto,freq>=120)) ### on ne retient que les mois des individus
où il y a au moins 120 points GPS connus, ce qui correspond à peu près à au moins
10 jours de suivi dans un mois

### Création d'un objet SpatialPoints DataFrame nécessaire pour calcul des kernels
idsp=droplevels(subset(xy,select=c("posx","posy","ani_id_YM")))
coordinates(idsp) <- ~posx+posy
proj4string(idsp) = CRS("+init=epsg:27572") ### projection des points en Lambert
II étendu
> head(idsp)
      coordinates      ani_id_YM
74 (649817, 1847390) 1019 2012-08
75 (649681, 1847350) 1019 2012-08
76 (649642, 1847440) 1019 2012-08
77 (649577, 1847490) 1019 2012-08
78 (649813, 1847730) 1019 2012-08
79 (649807, 1847720) 1019 2012-08
Coordinate Reference System (CRS) arguments: +init=epsg:27572 +proj=lcc
+lat_1=46.8 +lat_0=46.8 +lon_0=0
+k_0=0.99987742 +x_0=600000 +y_0=2200000 +a=6378249.2 +b=6356515 +towgs84=-
168,-60,320,0,0,0,0 +pm=paris+units=m +no_defs

kud= kernelUD(idsp, h="href",grid=300, extent=1) ### calcul
préliminaire des kernels avec comme paramètre de lissage la bande
de référence "href"

vert<-getverticeshr(kud,90) ### Extraction des polygones des kernels
```

```

à 90%
dfvert=as.data.frame(vert)

### On extraie pour chaque kernel la bande de référence href
href=NULL
for (i in 1:length(kud)){
  h=unlist(kud[[i]]@h[1],use.names=F)
  href=c(href,h)
}

### On recalcule les kernels avec la mediane des hrefs car Pellerin
et al. (2008) ont démontré qu'il s'agissait d'un bon compromis entre
puissance et précision dans l'estimation des domaines vitaux chez le
chevreuil
kud2= kernelUD(idsp, h=median(href),grid=300, extent=1)
vert2mouf_2h<-getverticeshr(kud2,90)
save(vert2mouf_2h, file="vert2mouf_2h.RData")
dfvertmouf_2h=as.data.frame(vert2mouf_2h)

> head(dfvertmouf_2h)
      id      area
1019 2012-08  54.41130
1019 2012-09  45.95561
1171 2011-08  71.74160
1171 2011-09  76.72104
1171 2011-10  74.86276
1171 2011-11 111.06646

save(dfvertmouf_2h,file="dfvertmouf_2h.RData")

### Fonction pour faire une sous-chaîne de caractère en partant de la
droite et pas la gauche
load("dfvertmouf_2h.RData")
substrRight <- function(x, n){
  substr(x, nchar(x)-n+1, nchar(x))
}

### On extraie l'année et le mois associé à chaque DV à partir de l'id qui n'est
autre que l'ani_id_YM vu précédemment
dfvertmouf_2h$annee=substrRight(as.character(dfvertmouf_2h$id),7)
dfvertmouf_2h$annee=substr(dfvertmouf_2h$annee,1,4)
dfvertmouf_2h$mois=substrRight(as.character(dfvertmouf_2h$id),2)
dfvertmouf_2h$id_mouf=ifelse(nchar(as.character(dfvertmouf_2h$id))==12,substr(dfve
rtmouf_2h$id,1,4),

ifelse(nchar(as.character(dfvertmouf_2h$id))==11,substr(dfvertmouf_2h$id,1,3),

ifelse(nchar(as.character(dfvertmouf_2h$id))==10,substr(dfvertmouf_2h$id,1,2),"ERR
OR"))))

### ajout de l'âge et du sexe
tata=merge(dfvertmouf_2h,mouf2h[,c("sexe","classe_age","ani_id_YM")],by.x="id",by.
y="ani_id_YM", all=F)
tata=tata[!duplicated(tata),]

```

```

DVmouf2h=tata

save(DVmouf2h,file="DVmouf2h.RData")

#####
##### ajout habitats liés aux DV #####
load("DVmouf2h.RData")
load("vert2mouf_2h.RData")
library(raster)
library(adehabitatHR)
library(adehabitatMA)
library(SDMTools)

t=read.asc(file="hab_8cat.asc") #importation du fichier ascii d'habitats

titi=raster(t) #création du raster des différents types d'habitats

proj4string(titi) = CRS("+init=epsg:27572") ### on met les coordonnées du raster
en LAMBERT II étendu

toto=extract(titi,vert2mouf_2h) ### on intersecte le raster avec les DV calculés
précédemment pour obtenir la composition du paysage au sein de ces derniers

DVmouf2h_extract=toto
save(DVmouf2h_extract,file="DVmouf2h_extract.RData")
dfvert2=as.data.frame(vert2mouf_2h)

plot(titi)
plot(vert2mouf_2h,add=T)
plot(xy,add=T)
plot(idsp)

### Proportion des différents types d'occupation du sol
h <- sapply(DVmouf2h_extract, function(x) tabulate(x, 8)) ### calcul du nombre de
pixels de chaque type d'habitats contenus dans chaque DV
h=t(h)
h=as.data.frame(h)

h$total=apply(h, 1, sum) ### total des pixels de 25*25m du raster compris dans
chaque DV

h$id=dfvert2$id
names(h)[1:8]=c("foret_feuillus","rocher_pente<30°","rocher_pente>=30°","landes_br
uyeres_HP","landes_bruyeres_P","foret_coniferes","landes_genet","autres")
h$p_landes=(h$landes_bruyeres_HP+h$landes_bruyeres_P)/h$total

toto=merge(DVmouf2h,h[,c("landes_bruyeres_HP","landes_bruyeres_P","total","p_landes",
"id")],by="id",all.x=F)
DVmouf2h=toto

# * 1 = forêts de feuillus (surtout dans les versants, pentu) = hêtre,
châtaigniers, chênes vert principalement
# * 2 = rochers avec pente < 30°
#
# * 3 = rochers avec pente >=30° (refuges pour mouflon car très pentu et

```

```
visibilité ++)
#
# * 4 = landes à bruyère/callune hors plateaux, riches en herbacées (+ pour
alimentation mouflon)
# * 5 = landes à bruyère/callune sur plateaux = pente < 10° et alti > 900m, très
riches en herbacées (+++ pour alimentation mouflon) mais risquées...
#
# * 6 = forêts de conifères (surtout sur les plateaux)
#
# * 7 = landes à genêts/fougères, ouvert mais moins favorables pour alim mouflon
# * 8 = autres
```

```
> head(DVmouf2h)
```

```
      id      area annee mois anid sexe classe_age p_landes
1 1019 2012-08  54.41130 2012  08 1019      F      >8 ans 0.1747126
2 1019 2012-09  45.95561 2012  09 1019      F      >8 ans 0.1718539
3 1171 2011-08  71.74160 2011  08 1171      F      7-8ans 0.2121739
4 1171 2011-09  76.72104 2011  09 1171      F      7-8ans 0.1781937
5 1171 2011-10  74.86276 2011 10 1171      F      7-8ans 0.1861436
6 1171 2011-11 111.06646 2011 11 1171      F      7-8ans 0.2056180
```

```
save(DVmouf2h, file="DVmouf2h.RData")
```

```
Global model call: lmer(formula = log(distparc2) ~ sexe * classe_age * mois + p_landes +
(1 | id_mouf), data = tyty, REML = F)
```

```
---
Model selection table
```

(Int)	cls_age	mos	p_lnd	sex	cls_age:mos	cls_age:sex	mos:sex	cls_age:mos:sex	df	logLik	AIC
128	7.021	+	+	-0.7583	+		+	+	65	-9428.511	18987.0
0.00	0.981										
256	7.011	+	+	-0.7558	+		+	+	+ 87	-9410.538	18995.1
8.05	0.018										
96	6.962	+	+	-0.7397	+			+	63	-9437.323	19000.6
13.62	0.001										
124	6.799	+	+		+		+	+	64	-9472.832	19073.7
86.64	0.000										
252	6.789	+	+		+		+	+	+ 86	-9453.414	19078.8
91.81	0.000										
92	6.751	+	+		+			+	62	-9479.773	19083.5
96.52	0.000										

```
Models ranked by AIC(x)
Random terms (all models):
'1 | id_mouf
```

## Analyse Home range mouflon

Notez que je ne détaillerai que l'analyse des domaines vitaux chez le mouflon car c'est à peu de chose près exactement la même chose côté script pour l'analyse des distances parcourues, seules les noms des objets et des variables changent.

```
#####
### Modeles linéaires mixtes ###
#####
load("DVmouf2h.RData")
library(nlme)
library(lme4)
library(MuMIn)
library(AICcmodavg)
library(ggplot2)
```



```

DVmouf2h$sexage=as.factor(paste(DVmouf2h$sexe,DVmouf2h$classe_age))

DVmouf2h=droplevels(subset(tata,sexage!="F >8 ans"))
### on enlève la femelle de >8 ans car on en a qu'une seule dans les effectifs

### Modèle linéaire global
lmech=lmer(log(area)~sexe*classe_age*mois+p_landes + (1|anid),
REML=F,data=DVmouf2h)

options(na.action = "na.fail")
msmod=dredge(lmech,rank="AIC") ### sélection de modèle sur critère d'AIC
head(msmod)

```

```

Global model call: lmer(formula = log(area) ~ sexe * classe_age * mois + p_landes +
(1 | anid), data = tata, REML = F)
---
Model selection table
(Int) cls_age mos p_lnd sex cls_age:mos cls_age:sex mos:sex df logLik AIC delta
weight
79 5.067 + -1.1610 + + 27 -115.522 285.0 0.00
0.854
80 5.098 + + -1.1540 + + 30 -114.595 289.2 4.15
0.107
112 5.128 + + -1.1600 + + 32 -113.626 291.3 6.21
0.038
96 4.947 + + -0.9905 + + 63 -88.096 302.2 17.15
0.000
128 4.976 + + -0.9960 + + 65 -87.106 304.2 19.17
0.000
75 4.771 + + + + 26 -132.605 317.2Global
model call: lmer(formula = log(area) ~ sexe * classe_age * mois + p_landes +
(1 | anid), data = tata, REML = F)

```

```

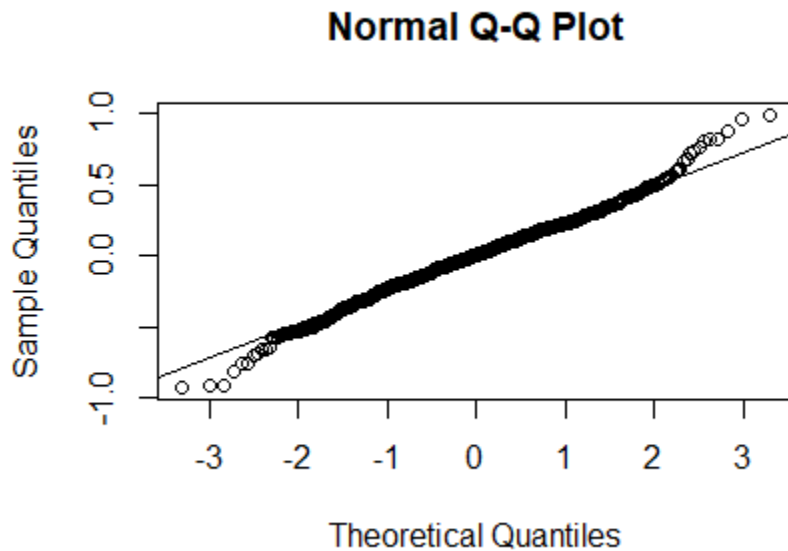
mod=(get.models(msmod, 1)[[1]]) #sélection du modèle le plus parcimonieux

```

```

### Vérification de la normalité des résidus
qqnorm(resid(mod))
qqline(resid(mod))

```



```
new2 <- list( sexe = levels(DVmouf2h$sexe), mois=levels(DVmouf2h$mois),
p_landes=mean(DVmouf2h$p_landes))

new2 <- expand.grid(new2)

### Prédictions du modèle
pred=predictSE(mod,new2,type="response",se.fit=T,level=0)

new2$fit=pred$fit
new2$max=pred$fit+1.96*pred$se.fit
new2$min=pred$fit-1.96*pred$se.fit

new2$aire=exp(new2$fit)
new2$airemax=exp(new2$max) ## on repasse les log à l'exp pour avoir les
distances en m
new2$airemin=exp(new2$min)

PrDVmouf2h_sex_mois_landes=new2
save(PrDVmouf2h_sex_mois_landes,file="PrDVmouf2h_sex_mois_landes.RData")

new2$sexage=as.factor(paste(new2$sexe,new2$classe_age2, sep=" "))

#### Plot en fonction du sexe et du mois
new2$dateplot=as.numeric(new2$mois)

k<- ggplot(new2, aes(x=dateplot, y=aire, colour=sexe))+

geom_point(aes(color=sexe),stat="identity",size=2.5,position=position_dodge
e(.3))+
```

```

    geom_line(data=new2,aes(x=dateplot, y=aire,
colour=sexe),stat="identity",size=1,position=position_dodge(.3))+
    geom_errorbar(aes(ymin=new2$airemin, ymax=new2$airemax, colour=sexe),
width=1,
                    position=position_dodge(.3))+
    scale_x_continuous(breaks=seq(1,12,1))
# guides(fill=F)+

print(k)
k+ggtitle("Home range size in mouflon ")+
  xlab("Month")+ylab("Area
(ha)")+scale_y_continuous(breaks=seq(0,250,25))+
  theme_classic()+
  theme(legend.title=element_text(size = rel(1.8)),
        legend.text = element_text(size = rel(1.8)))+
  #legend.position = c(1,1),legend.justification = c(1,1))+
  theme(plot.title = element_text(hjust=0.5,size = rel(2)))+
  theme(axis.title.x=element_text(size=rel(2)),
        axis.text.x=element_text(size=rel(1.8)))+
  theme(axis.title.y=element_text(size=rel(2)),
        axis.text.y=element_text(size=rel(1.8)))+
  annotate("text", x=11.3,y=30, label="Rutting period", size=6.5)+
  annotate("text", x=4.2,y=30, label="Calving \nperiod", size=6.5,
lineheight=.8)+
  annotate("rect", xmin=3.3, xmax = 5, ymin = 40, ymax=250, alpha=.1,
fill="blue")+
  annotate("rect", xmin=10.5, xmax = 12, ymin = 40, ymax=250, alpha=.1,
fill="red")+
  theme(legend.position="none")

#####
### Plot en fonction % landes
new2=list( sexe = levels(DVmouf2h$sexe)[2], mois=levels(DVmouf2h$mois)[9],
p_landes=seq(min(DVmouf2h$p_landes),max(DVmouf2h$p_landes),0.01))

new2 <- expand.grid(new2)

pred=predictSE(mod,new2,type="response",se.fit=T,level=0)

new2$fit=pred$fit
new2$max=pred$fit+1.96*pred$se.fit
new2$min=pred$fit-1.96*pred$se.fit

new2$aire=exp(new2$fit)
new2$airemax=exp(new2$max) ### on repasse les log à l'exp pour avoir les
distances en m
new2$airemin=exp(new2$min)

new2$dateplot=as.numeric(new2$mois)
k<- ggplot(new2, aes(x=p_landes, y=aire,colour=sexe))+
  geom_point(aes(color=sexe),stat="identity",size=2.5)+
  geom_errorbar(new2,aes(ymin=airemin, ymax=airemax,color=sexe),

```

```
stat="identity",width=1,)  
# guides(fill=F)+  
print
```



## DIFFERENCES INDIVIDUELLES DANS LES MOUVEMENTS ET L'UTILISATION DE L'ESPACE CHEZ DEUX GRANDS HERBIVORES AUX TRAITS D'HISTOIRES DE VIE CONTRASTES

---

Nous avons estimé les distances journalières parcourues et les domaines vitaux mensuels à partir des données GPS de 231 chevreuils (*Capreolus capreolus*) et de 93 mouflons méditerranéens (*Ovis gmelini musimon* x *Ovis* sp) durant toute la durée de leur suivi. Nous avons ensuite étudié la contribution relative du sexe et de l'âge des individus afin de déterminer les variations mensuelles de chacune de ces deux caractéristiques d'utilisation de l'espace. Nous avons alors émis les hypothèses selon lesquelles la compétition intra-sexuelle et les contraintes reproductives liées à la parturition allaient affecter les distances journalières parcourues et la taille des domaines vitaux mensuels respectivement chez les mâles et les femelles. Des différences liées à l'âge des individus étaient aussi attendues chez le chevreuil, à cause de la dépendance à l'âge de la territorialité chez les mâles et du statut reproducteur chez les femelles. Aucune différences liées à l'âge chez les mouflons étaient attendus car tous les individus étaient adultes et censé faire face aux mêmes contraintes dans leurs mouvements liées à leur âge. Nos résultats supportent notre première hypothèse car les patrons de mouvements chez les mâles des deux espèces ont été modifiés pendant la période de rut. Notre seconde hypothèse est partiellement confortée car des différences ont été observées chez les femelles des deux espèces mais pas de différences liés à l'âge chez les femelles chevreuils comme attendue. Enfin de fortes variations saisonnières dans la mobilité et l'utilisation de l'espace ont été détectées. Nous discutons nos résultats à la lumière des connaissances sur l'importance relative des déterminants individuels et des traits d'histoires de vie dans les variations intra-et interspécifiques dans le mouvement des animaux et leur utilisation de l'espace.

**MOTS-CLES-** *Ongulés- écologie du mouvement- distances parcourues- taille du domaine vital- différences interindividuelles*

## INTER- AND INTRASPECIFIC VARIATIONS IN MOVEMENTS AND SPACE USE OF TWO LARGE HERBIVORES WITH CONTRASTED LIFE HISTORY TRAITS

---

Using the locations data of 231 roe deer (*Capreolus capreolus*) and 93 Mediterranean mouflon (*Ovis gmelini musimon* x *Ovis* sp) equipped with GPS collars in two study areas in southern France, we estimated the cumulative daily distances travelled and monthly home range's size of each individual during all its monitoring period. Then, we assessed the relative contribution of sex and age classes in determining monthly variation of both space use characteristics. We hypothesized that intra-sexual competition and reproductive constraints linked to parturition will affect respectively males and females' distances travelled and monthly home range size, inducing sex-related differences. Age-related differences were also expected in roe deer first because of the age-dependancy of both territorial status in males, and reproductive status in females. No age-related differences in mouflon were expected as all individuals in our analyses were adults and suspected to face the same movement constraints related to their age. Our results showed support for our first hypothesis, as in both species mobility and space use of males were altered during the rutting period, and also the territoriality period in roe deer. Our second hypothesis had partial support as movements and space use of females were indeed affected during parturition period, but no age-related differences in roe deer were detected. Finally, strong seasonal variations in movements and space use of both species were observed. We discussed our results in the light of current knowledge about the relative importance of individual determinants and life history traits into intra- and interspecific variations in animal movements and space use.

**KEY WORDS-** *Ungulates- movement ecology- travelled distances- home range size- interindividual differences*