



## Do reproductive constraints or experience drive age-dependent space use in two large herbivores?

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Life histories are strongly age dependent, notably linked to the onset of reproductive maturity and subsequent senescence. Consequently, ageing is predicted to impact behaviour, through the expression of either mating tactics in males or neonatal antipredator tactics in females. However, the influence of ageing, and the associated reproductive activity, on spatial behaviour remains poorly investigated. In this regard, we quantified age- and sex-specific intra-annual variation in movement rates and space use of two large herbivores with contrasting life histories: the roe deer, *Capreolus capreolus*, an asocial species with a territorial male mating strategy and a hider neonatal tactic, and the Mediterranean mouflon, *Ovis gmelini musimon* × *Ovis* sp., a gregarious species with a roaming male mating strategy and a follower neonatal tactic. We expected age-related differences to be mostly related to (1) age-specific mating tactics during the rut for males and the presence/absence of offspring for females, and (2) experience and/or locomotory senescence otherwise. During the rutting period, older roe deer males travelled greater daily distances than younger males due to patrolling behaviours for territory defence, whereas older mouflon males travelled less than younger males, which often adopted coursing tactics to mate with females. During the birth period, reproductive females had smaller home ranges than nonreproductive females in roe deer, whereas no marked differences were observed in mouflon females. The most marked age-related variation in space use of mouflon occurred outside the reproductive periods; specifically, the oldest individuals travelled less far and had a smaller home range (females only) than younger individuals. Our findings illustrate how space use tactics vary within and between populations of large herbivores, providing strong evidence that age and reproductive activity are major determinants of their spatial behaviour.

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Animals living in heterogeneous and/or seasonal environments must cope with marked spatial and/or temporal variation in resource availability and predation risk, resulting in seasonal variation in space use (Nicholson, Bowyer, & Kie, 1997; Myrsetrud & Ims, 1998; Gunnarsson et al., 2005; Godvik et al., 2009; Gillies & Clair,

2010; Tucker et al., 2018). However, not all individuals respond in the same way to changes in environmental conditions. Indeed, individuals differ in their perception of resources and risks, their locomotor abilities and their energetic requirements (Harel, Horvitz, & Nathan, 2016; Laundré, Hernández, & Altendorf, 2001; Searle, Hobbs, & Gordon, 2007). For example, in dimorphic and polygynous vertebrates, sexual size dimorphism is associated with sex differences in resource requirements, activity patterns, sensitivity to adverse weather conditions and social preferences, often leading to sex-specific patterns of movement and space use (Bourgoin, Marchand, Hewison, Ruckstuhl, & Garel, 2018; Catry, Phillips,

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Croxall, Ruckstuhl, & Neuhaus, 2006; Ruckstuhl & Neuhaus, 2002, 2006).

In an analogous way to other life history traits, the sex-specific spatial ecology of a given species (Ruckstuhl & Neuhaus, 2006) is also expected to be strongly structured by age and life stage (Charlesworth, 1980; Stearns, 1992; Gaillard, Festa-Bianchet, Yoccoz, Loison, & Toigo, 2000). For instance, old individuals are reported to move less and use restricted home ranges compared to younger individuals, as a result of a decline in locomotor performance and/or greater experience, presumably through a better knowledge of the distribution of resources and predation risk in the local environment (birds: Catry et al., 2006; Harel et al., 2016; fish: Magnhagen et al., 2008; large herbivores: Froy et al., 2018; Montgomery, Vucetich, Peterson, Roloff, & Millenbah, 2013; Thurfjell, Ciuti, & Boyce, 2017; carnivores: MacNulty et al., 2009). Furthermore, allocation to reproduction varies markedly with age and/or life stage in numerous vertebrate taxa (Clutton-Brock, 1984; Forslund & Pärt, 1995; Lemaître et al., 2015; McBride et al., 2015). In most species, for instance, young males that are still growing are unable to compete for mates with older fully grown males and so often adopt alternative reproductive tactics, resulting in age-specific patterns of movement and space use during the rutting period (Cederlund & Hakan, 1994; Foley et al., 2015; Taylor et al., 2020). Likewise, during the critical perinatal period, female large herbivores are constrained to select those habitats that best compensate for the increased energetic requirements linked to pregnancy and lactation, while minimizing predation risk for their offspring (Bongi et al., 2008; Ciuti et al., 2006, 2009; Viejou et al., 2018). In contrast, immature and nonreproductive females are unconstrained by the presence of dependent young, resulting in age- and/or stage-specific space use patterns (Kie & Bowyer, 1999; Marchand et al., 2015; Oehlers, Bowyer, Huettmann, Person, & Kessler, 2011; Viejou et al., 2018; Villaret, Bon, & Rivet, 1997).

Surprisingly, age dependence is still often largely overlooked in studies of spatial behaviour, mostly because of the difficulty of accurately assessing the age of individuals in the field. The increasing number of long-term monitoring studies (Festa-Bianchet, Douhard, Gaillard, & Pelletier, 2017), in combination with the development of tracking technologies (e.g. GPS, Kays, Crofoot, Jetz, & Wikelski, 2015), offers new opportunities to assess the crucial role that age may play in determining an animal's movement behaviours. A better understanding of which individual attributes shape patterns of movement and, more specifically, locomotion, is of fundamental importance as locomotion makes up a substantial part of an animal's daily energy budget (Halsey, 2016). Moreover, the amount of energy that an animal expends while moving can significantly constrain the amount of energy available for growth and reproduction, resulting in long-term implications for individual fitness (Grémillet et al., 2018). Recent work on large herbivores has highlighted the importance of age-related differences in movements and space use (e.g. Eggeman, Hebblewhite, Bohm, Whittington, & Merrill, 2016), investigated the relative importance of locomotor senescence and experience (e.g. Froy et al., 2018; Thurfjell et al., 2017) and inferred relationships between these behavioural modifications and survival/reproduction (e.g. Froy et al., 2018; Taylor et al., 2020). However, there is a need to delve deeper into the effect of age on movement in both males and females in a larger number of species that differ in sexual dimorphism (which affects senescence patterns in ungulates) and sociability level.

In this study, we investigated the influence of sex and age on fine-scale movements and home range size over the annual cycle in two large herbivore species, the roe deer, *Capreolus capreolus*, and the Mediterranean mouflon, *Ovis gmelini musimon* × *Ovis sp.*

Home range size results from the different components of individual movements such as speed, sinuosity or recursion (Börger, Dalziel, & Fryxell, 2008; Péron, 2019; Van Moorter, Rolandsen, Basille, & Gaillard, 2016). Hence, differences in small-scale movements, when measured with simple statistics such as cumulated distance travelled in a day, do not always translate to a similar extent at a larger scale (Tablado et al., 2016). Therefore, we analysed two proxies of space use, the daily distance travelled (DDT) and the resulting monthly home range size (monthly HRS). We also accounted for the established influence of habitat type on the extent of individual movements, using species-specific proxies (i.e. % woodland for roe deer, Morellet et al., 2011; % grass-rich areas for mouflon, Garel et al., 2007; Marchand et al., 2014; see Methods and the Appendix), and evaluated the following hypotheses.

During the rutting period (July–August in roe deer, mid-October–December in mouflon), we expected reproductive males of both species to show a marked difference in DDT and monthly HRS compared to nonreproductive males, but with a species-specific signal related to their contrasting mating tactics. In the territorial roe deer, most males successfully reproduce for the first time when they have reached full physical maturity and are able to successfully hold a territory (in general at 3 years old; Vanpé et al., 2009). During the territorial period, and particularly during the rut, we predicted that adult bucks would have higher DDT due to patrolling behaviours within their territories (H1a), but should also have smaller monthly HRS (H1b) compared to younger nonreproductive males, most of which are expected to be nonterritorial, with less constrained movements. In the roaming mouflon, while males generally do not reproduce before 4 years old, alternative mating tactics have been reported. Whereas older males generally adopt a tending tactic, following receptive females and impeding attempts of other males to mate, young subordinate males often adopt a courting tactic, attempting to breach the defence of the tending males (Bon, Gonzales, Bosch, & Cugnasse, 1992). We therefore predicted that young subordinate males would have both higher DDT (H2a) and larger monthly HRS (H2b) during the rut than old dominant males and nonreproductive males.

Following parturition, the movements and home ranges of reproductive females should be constrained by the presence of offspring compared with nonreproductive females (Bongi et al., 2008; Ciuti, Bongi, Vassale, & Apollonio, 2006). This should be particularly apparent in the roe deer which adopts a hider anti-predator tactic (Linnell, Nijhuis, Teurlings, & Andersen, 1999), but much less so in mouflon where offspring are capable of following their mother shortly after birth (Langbein, Scheibe, & Eichhorn, 1998; Langbein, Streich, & Scheibe, 1998). Females give birth for the first time at 2 years old in roe deer, and 2 or 3 years old in mouflon, while the vast majority of females of both species subsequently reproduce every year (Gaillard et al., 2000; Garel et al., 2005). We therefore predicted that during parturition adult roe deer females ( $\geq 2$  years old) would have lower DDT (H3a) and smaller monthly HRS (H3b) than younger females ( $<2$  years old), while no age-related differences in DDT (H4a) or monthly HRS (H4b) were expected for female mouflon.

Outside of the reproduction periods, we expected age-specific variation in movement to be driven by experience, which is assumed to be higher in older individuals, and/or locomotor performance, which should decrease in senescent individuals (Froy et al., 2018). We therefore predicted that old individuals of both sexes and both species (H5: roe deer males; H6: mouflon males; H7: roe deer females; H8: mouflon females) would have (1) lower DDT and (2) smaller monthly HRS than young individuals outside the reproductive periods.

## METHODS

### Study Areas

The study on roe deer was carried out at Vallons et Coteaux de Gascogne (Zone Atelier PyGar) in the southwest of France (43°16'N, 0°52'E, 260–395 m above sea level; Fig. 1) in a 19 000 ha rural region. It is a hilly area composed of two large forests (672 and 463 ha, 6.0% of the study area), numerous small woodland patches (mean  $\pm$  SD = 2.4  $\pm$  11.5 ha, 18.8%), meadows (37.2%), crops (cereals, oilseed and fodder crops, 31.6%) and hedgerows (3.6%). The study area is typical of a modern agricultural landscape with human presence scattered throughout in small villages, farms and isolated houses. The roe deer is hunted by drive hunting from the second Sunday in September to the end of January (until 2008) or February (since 2009), mostly using dogs, and by stalking of males only from 1 June to the second Sunday in September.

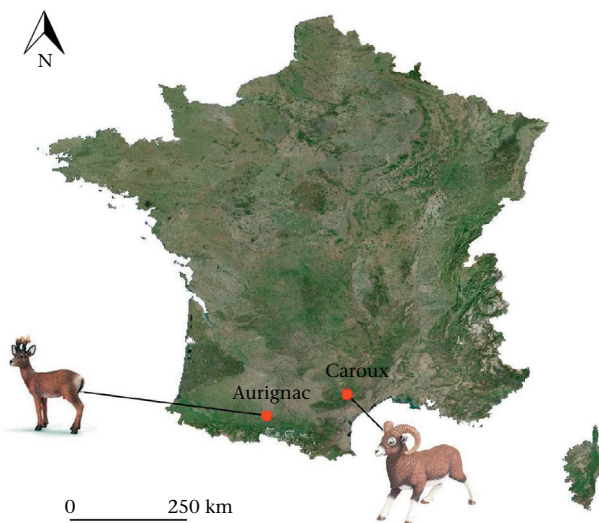
The study on mouflon was carried out in the Caroux-Espinouse massif in southern France (43°38'N, 2°58'E, 150–1124 m above sea level; Fig. 1) in a 17 000 ha low elevation mountain range. This area is characterized by deep valleys interspersed between plateaux which are mainly exploited for the timber of conifers (*Pinus sylvestris*, *Pinus nigra* and *Picea abies*). Slopes are covered by broadleaved trees (mainly beech, *Fagus sylvatica*, chestnut, *Castanea sativa*, and evergreen oak, *Quercus ilex*) or rocky areas and open moorlands (either grass-rich heather, *Erica cinerea* and *Calluna vulgaris*, or broom, *Cytisus oromediterraneus* and *Cytisus scoparius*). The area has a low human presence (39 inhabitants/km<sup>2</sup>) with limited human activities, particularly in the central National Hunting and Wildlife Reserve (1658 ha) where the hunting of mouflon is forbidden and activities are strictly regulated (see Marchand et al., 2015 for more details).

### Capture and Marking

Roe deer were caught in winter (from 16 November to 27 March) from 2005 to 2016 using drives with human beaters and 4 km of long-nets. Drives were carried out without dogs to reduce stress. When an animal was captured, it was immediately tranquilized with an intramuscular injection of acepromazine by a person

licensed to do so (Federation of European Laboratory Animal Science Associations category C accreditation). The animal remained conscious between capture and release, but this short-acting neuroleptic quickly attenuates the response to stress and prevents any adverse effects in deer (Montané et al., 2003). The drug dose (1.65 mg/injection) was calculated following Montané et al. (2003). To reduce stress and risk of injury, each tranquilized animal was then transferred to a wooden retention box until the end of catching operations. Then, it was removed from the box by three highly experienced animal handlers, with the eyes covered to minimize stress during handling procedures. We marked each individual with ear tags, weighed and sexed them. We classified the individuals into three age classes: juveniles (6–10 months old), yearlings (18–22 months old) and adults (more than 2.5 years of age). Juvenile roe deer were identified by the presence of a tricuspid third premolar milk tooth (Ratcliffe & Mayle, 1992), while we used tooth wear to distinguish yearlings from adults (Hewison et al., 1999). Finally, we equipped some of the animals ( $N = 287$ , Table 1) with a GPS collar (Lotek 3300 or Vectronic GPS PLUS-1C Store On Board). GPS collars weighed 400 g corresponding to no more than 3.5% and less than 2% of the lowest and highest individual body mass, respectively. For juveniles, which have not completed body growth (neck circumference about 2.5 cm less than that of yearlings), we accounted for a projected growth of about 10% by fitting the collar slightly looser. After 11 months of GPS monitoring, we used the preprogrammed remote drop-off system to retrieve the collars and download the recorded data. The animal capture and handling protocol was carried out in accordance with local and European animal welfare laws (prefectural order from the Toulouse Administrative Authority to capture and monitor wild roe deer and agreement no. A31113001 approved by the Departmental Authority of Population Protection).

Mediterranean mouflon were caught during spring and summer (from May to July), from 2010 to 2018, using collective or individual traps (enclosure with mesh walls and a guillotine door triggered when the animal pulls a wire while entering the trap) and 40  $\times$  40 m or 5  $\times$  5 m drop nets baited with salt licks. For fixed traps, to reduce the time between capture and handling and so avoid stress, as captures mostly occurred at night, traps were checked early every morning during the capture period. In addition, to further limit the risk of heat stress, traps were generally positioned under tree cover. Mouflon caught with drop nets triggered manually were processed immediately after the capture. These catch procedures do not require specific bedding, food or water. The capture and handling of mouflon were carried out by highly experienced animal handlers from the Office Français de la Biodiversité. As soon as an animal was handled, it was restrained with the eyes covered to reduce stress. We sexed each individual and determined age by tooth eruption patterns in females, with



**Figure 1.** Study sites in France. The study on roe deer was carried out at Vallons et Coteaux de Gascogne (here named Aurignac, i.e. the closest town to the study site) and the study on mouflon was carried out in the Caroux-Espinouse massif.

**Table 1**

Number of roe deer and mouflon per sex and age class at capture for the analyses of daily distance travelled (DDT) and monthly home range size (HRS)

Response variable	Sex	Roe deer			Mediterranean mouflon			
		Juveniles	Yearlings	Adults	2–3	4–6	7–8	>8
DDT	Females	25	24	93	9	17	8	3
	Males	20	17	65	25	17	12	6
HRS	Females	56	25	93	9	17	8	3
	Males	51	17	64	25	17	12	6

Note that an individual recaptured several times may occur in different age classes; hence the total number of individuals in this table differs from the total number of captured individuals. Juveniles: 0.5 year old; yearlings: 1.5 years old; adults: >2.5 years old. In Mediterranean mouflon, age is given as number of years old.



individuals classified as one of lamb, 1, 2, 3,  $\geq 4$  years old, and by horn growth annuli in males, with individuals classified as one of lamb, 1, 2, 3, 4, 5, 6,  $\geq 7$  years old (Garel, Cugnasse, Hewison, & Maillard, 2006). A random sample of individuals at least 2 years old was fitted with GPS collars (Lotek 3300). We only included GPS-collared individuals of known age ( $N = 90$ , i.e. first captured as lamb, 1, 2, 3 years old for females, or as lamb, 1, 2, 3, 4, 5, 6 years old for males) in the analyses, grouping them into four age classes (i.e. 2–3, 4–6, 7–8 and  $> 8$  years old, Table 1) to obtain balanced sample sizes. All efforts were made to minimize the handling time used to take measurements and adjust the collar, to release individuals on site as soon as possible. Mouflon were equipped with GPS collars weighing 400 g, a weight never exceeding 2.5% and less than 1% of the body mass of the smallest and largest individual, respectively. To allow for possible seasonal variation in neck circumference, we left a gap of 3 cm between the GPS collar and the animal's neck while making sure that the collar would not rotate. After 1 year of GPS monitoring (depending on the batteries' life), we retrieved the collar using a remote drop-off system (triggered manually) and downloaded the recorded data. The mouflon capture and handling protocol was carried out in accordance with local and European animal welfare laws (prefectural decree no. 2009-014 delivered to the Office National de la Chasse et de la Faune Sauvage by the Préfecture de Paris, in accordance with the French environmental code—Art. R421-15 to 421-31 and R422-92 to 422-94-1).

From repeated observations of GPS-collared individuals throughout the year as part of long-term capture–mark–recapture monitoring of both populations, we were able to ascertain that the GPS collars did not cause changes in behaviour (foraging, social behaviour) compared to other unmarked individuals in the population. In addition, we did not detect any adverse effects linked to the wearing of the collars in terms of injury or reproductive activity.

#### GPS Monitoring

We scheduled GPS collars to record locations of roe deer every 10 min over a 24 h period, once or twice each month, and every 6 h all year round otherwise. As the days sampled at 10 min intervals were selected randomly within the month, irrespective of environmental conditions, and the total monitoring period spanned 12 years (2005–2016), we can assume that these data provide a reliable representation of age-specific monthly space use at the population level. We scheduled GPS collars to record locations of mouflon every 2 h all year round, alternating between even hours on one day and odd hours on the following day.

To improve the accuracy of GPS locations for roe deer, we used differential correction (Adrados, Girard, Gendner, & Janeau, 2002). Moreover, in case capture and handling of roe deer temporarily altered their behaviour, we removed all locations recorded during the first 7 days after the release date of the animal (Morellet et al., 2009). For mouflon, GPS monitoring was programmed to begin only after a predetermined date which was several days or weeks after animal handling. A large percentage of juvenile roe deer dispersed during the monitoring period, around their first birthday (34%; Debeffe et al., 2012). Hence, we removed locations recorded during the dispersal period for individual roe deer classified as dispersers, following Ducros et al. (2020), to ensure that we only analysed habitual ranging behaviour. Note that no juvenile mouflon were monitored. Finally, we screened GPS locations of both species for erroneous locations (i.e. fixes that would imply an unfeasible movement speed given the distance from/to the previous/next location) using a method inspired by Bjørneraas, Van Moorter, Rolandsen, and Herfindal (2010), but adapted to our specific study models' behaviour. We removed 85 fixes (0.02% of all

locations) and 165 fixes (0.04% of all locations), respectively, from the 10 min and 6 h schedules in roe deer, and 1760 fixes (i.e. 0.03% of all locations) in mouflon.

#### Statistical Analysis

We analysed two proxies of space use: DDT and monthly HRS. Depending on species and sex, the correlation between average monthly DDT and monthly HRS ranged between 0.03 and 0.59, suggesting the two variables were partially related (as expected from the link between movements and home range emergence; e.g. Van Moorter et al., 2016), but also that they provided a degree of independent complementary biological information.

#### DDT

We used data from the 10 min GPS schedule for roe deer and the 2 h GPS schedule for mouflon to compute the DDT for each individual as the sum of the step lengths between each pair of consecutive locations over 24 h. As some scheduled locations were missing, we restricted our analyses to 24 h periods for which a minimum of 130 ( $>90\%$  for roe deer) and 10 ( $>83\%$  for mouflon) scheduled locations were available, generating 2151 DDT for roe deer and 20 549 DDT in mouflon. Then, to ensure that DDT was comparable among individuals despite a few missing fixes, we averaged observed values of DDT based on the 10 min or 2 h steps for each individual-day, and multiplied this by the number of steps scheduled per day (i.e. 143 10 min steps in roe deer; 11 2 h steps in mouflon). We used linear mixed models (LMMs) to investigate variation in log-transformed DDT in relation to age and month, including individual identity as a random effect on the intercept. We included the main effects and two-way interaction between age and month. As we were interested in investigating age-related differences in space use, rather than the differences between species and sexes, and because of marked a priori differences in both life history and GPS monitoring schedule, we ran separate models for each species and sex. Moreover, to control for the known influences of habitat type on ranging behaviour (roe deer: Morellet et al., 2011; mouflon: Garel et al., 2007; Marchand et al., 2014; Appendix), we included in all models the percentage of woodland (roe deer) or of grassland (mouflon) within the monthly HRS of each individual.

#### Monthly HRS

We estimated monthly HRS for each individual using data from the 6 h GPS schedule in roe deer ( $> 110$  scheduled fixes per month) and the 2 h GPS schedule in mouflon ( $> 330$  scheduled fixes per month). Only individual-months with data available on all days of a focal month were included in the analyses ( $N = 2403$  and 937 monthly HRS in roe deer and mouflon, respectively). We used the fixed-kernel method to estimate monthly HRS. Although other methods are available and may be more suited when fixes are collected at very frequent time intervals, the fixed-kernel method is the most commonly used method in the literature (Kie et al., 2010), and is well suited for comparing home range size among age classes and months (the shape and location of the home ranges are not under scrutiny here). As differences in smoothing parameter may result in differences in monthly HRS (Pellerin, Saïd, & Gaillard, 2008), we set the smoothing parameter  $h$  to the median value obtained for each species to recalculate monthly HRS for each individual. We estimated monthly HRS at the 90% isopleth, as recommended by Börger et al. (2006), to obtain an unbiased estimate. To investigate age-related variation in log-transformed monthly HRS, we fitted the same model structure as for DDT (see details above).

### Model selection

We fitted models using maximum likelihood and used Akaike's information criterion (AIC, Burnham & Anderson, 2002) and Akaike weights to select the model with the most support. When  $\Delta\text{AIC}$  was  $< 2$  between competing models, we retained and interpreted the model with the fewest parameters following the rule of parsimony. We also calculated the marginal and conditional  $R^2$  of the models, which can be interpreted as the proportion of variance explained by the fixed effects alone, or by both fixed and random effects, respectively (Nakagawa & Schielzeth, 2013). We performed all statistical analyses using R software version 3.6.1 (R Core Team, 2019) and 'lme4', 'adehabitatHR' and 'adehabitatLT' packages (Bates et al., 2015; Calenge, 2011). We performed the selection process on a model subset including the null model and all models that included the percentage of woodland (roe deer) or of grassland (mouflon).

## RESULTS

### Male Age-specific Space Use during the Mating Season

In both species, the best models for explaining variation in DDT among males included the two-way interaction between age and month (Table 2), while the best model for explaining variation in monthly HRS included an additive age effect only in roe deer, and no age effect in mouflon (Table 2).

In roe deer, in agreement with H1a, differences in DDT between age classes were detected during the territorial period, and more particularly during the rutting period: adult DDT was  $8.55 \pm 0.40$  km/day in July and  $7.54 \pm 0.29$  km/day in August, i.e. 51.5% and 44.1%, respectively, greater than juvenile DDT (July:  $5.64 \pm 0.48$  km/day; August:  $5.24 \pm 0.41$  km/day), and 33.9% and 9.4%, respectively, greater than yearling DDT (July:  $6.39 \pm 0.60$  km/day; August:  $6.90 \pm 0.60$  km/day; Fig. 2a). In contrast, the monthly HRS of adult males was consistently smaller than that of younger individuals throughout the year (average monthly HRS for adult males 14.7% and 18.4% smaller than juveniles and yearlings, respectively; Fig. 2c), providing only partial support for H1b.

In mouflon, during the rutting period, we observed higher DDT in nonreproductive males (2–3 years old:  $1.69 \pm 0.09$  km/day and  $1.44 \pm 0.08$  km/day in November and December, respectively; Fig. 2b) and younger adult males (4–6 years old:  $1.59 \pm 0.1$  km/day and  $1.25 \pm 0.07$  km/day in November and December, respectively) compared to older adult males (7–8 years old:  $1.27 \pm 0.07$  km/day and  $0.93 \pm 0.05$  km/day, 19.9–24.9% and 25.5–35.0% less in November and December, respectively; >8 years old:  $1.26 \pm 0.11$  km/day and  $0.85 \pm 0.07$  km/day, 20.8–25.8% and 31.7–40.4% less in November and December, respectively; Fig. 2b), in agreement with H2a. However, contrary to our prediction H2b, these age-related differences were not observed at the home range scale (Fig. 2d).

### Female Age-specific Space Use following Parturition

In roe deer females, the best model for explaining variation in DDT included month only, whereas for monthly HRS the best model included the two-way interaction between age and month (Table 3). These results did not support our prediction H3a that, following parturition, reproductive females should have lower DDT, but supported our prediction H3b that reproductive females should have lower monthly HRS than nonreproductive females (Fig. 3a, c). Indeed, during the peak of parturition in May, the monthly HRS of nonreproductive females was  $51.20 \pm 2.47$  ha, whereas it was  $39.62 \pm 2.66$  ha for yearlings and  $37.27 \pm 1.25$  ha for adults, i.e. 22.7% and 27.2% smaller, respectively. These differences persisted to the following month in June, when nonreproductive females had a monthly HRS of  $42.29 \pm 2.11$  ha, whereas those of yearling and adult females were  $35.87 \pm 2.51$  ha and  $34.70 \pm 1.18$  ha, respectively, i.e. 15.2% and 17.9% smaller.

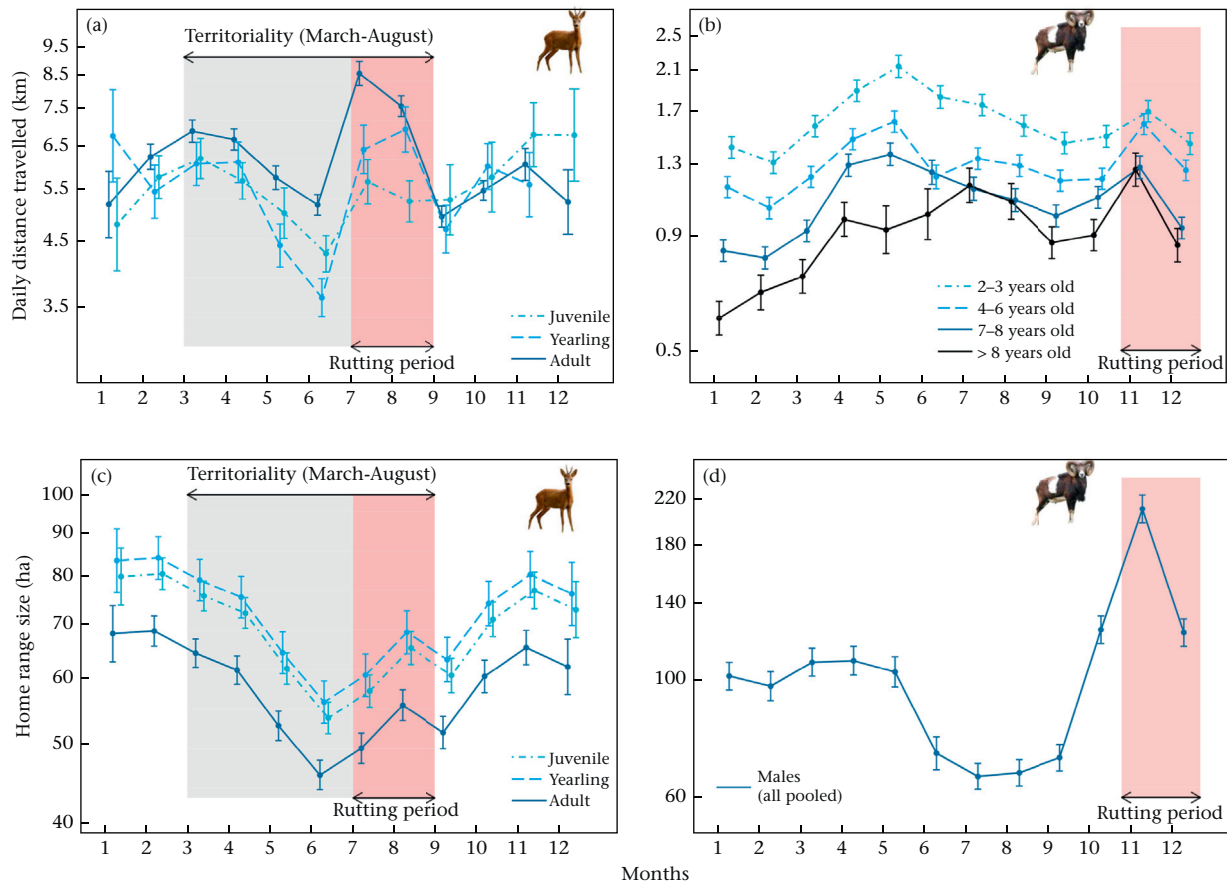
In mouflon females, the best model for explaining variation in DDT included the two-way interaction between age and month (Table 3). Our prediction H4a, that there would be no age-related variation in movement rates during the birth period linked to the lamb follower tactic, was partially supported as, although 2–3-year-old females had a DDT of  $1.15 \pm 0.08$  km/day in March, i.e. 2.5% higher than that of 4–6-year-old females (March:  $1.12 \pm 0.05$  km/day), 17.8% higher than that of 7–8-year-old

**Table 2**

Candidate linear mixed models to investigate variation in log-transformed daily distance travelled (DDT) and monthly home range size (HRS) in roe deer and mouflon males, with individual identity as a random effect on the intercept

Response variable	Species	Models	K	$\Delta\text{AIC}$	AIC weight	$R^2\text{m}$	$R^2\text{c}$
DDT	Roe deer	<b>Month + Age + % Woodlands + Month*Age</b>	<b>38</b>	<b>0.00</b>	<b>0.974</b>	<b>0.26</b>	<b>0.37</b>
		Month + Age + % Woodlands	17	7.25	0.026	0.22	0.33
		Month + % Woodlands	15	22.17	0.000	0.19	0.32
		% Woodlands	4	174.85	0.000	0.03	0.15
		Null model	3	184.91	0.000	0.00	0.14
	Mouflon	<b>Month + Age + % Grasslands + Month*Age</b>	<b>51</b>	<b>0.00</b>	<b>1.000</b>	<b>0.20</b>	<b>0.48</b>
		Month + Age + % Grasslands	18	157.95	0.000	0.18	0.46
		Month + % Grasslands	15	241.21	0.000	0.08	0.34
		% Grasslands	4	1421.48	0.000	0.0	0.21
		Null model	3	1423.74	0.000	0.00	0.20
HRS	Roe deer	<b>Month + Age + % Woodlands</b>	<b>17</b>	<b>0.00</b>	<b>0.606</b>	<b>0.35</b>	<b>0.64</b>
		Month + Age + % Woodlands + Month*Age	39	0.79	0.393	0.36	0.66
		Month + % Woodlands	15	14.99	0.001	0.33	0.63
		% Woodlands	4	163.05	0.000	0.23	0.53
		Null model	3	251.27	0.000	0.00	0.53
	Mouflon	<b>Month + % Grasslands</b>	<b>15</b>	<b>0.00</b>	<b>0.635</b>	<b>0.45</b>	<b>0.74</b>
		Month + Age + % Grasslands	18	1.08	0.365	0.47	0.73
		Month + Age + % Grasslands + Month*Age	51	22.86	0.000	0.49	0.75
		% Grasslands	4	403.95	0.000	0.24	0.64
		Null model	3	480.44	0.000	0.00	0.16

Models were ranked according to AIC selection criteria using the difference in AIC values ( $\Delta\text{AIC}$ ), the number of estimated parameters (K) and the AIC weight of each model. The three best ranked models are presented followed by the habitat type model and the null model. The best supported model is in bold.  $R^2\text{m}$  and  $R^2\text{c}$  are marginal and conditional  $R^2$ , respectively (see Nakagawa & Schielzeth, 2013).



**Figure 2.** Predicted daily distance travelled of (a) roe deer males and (b) mouflon males, and monthly home range size in (c) roe deer males and (d) mouflon males over the year (1 = January) for different age classes. We used a logarithmic scale on the y axis. Points and bars represent the predicted estimates and associated standard errors derived from the selected model.

**Table 3**

Candidate linear mixed models to investigate variation in log-transformed daily distance travelled (DDT) and monthly home range size (HRS) in roe deer and mouflon females, with individual identity as a random effect on the intercept

Response variable	Species	Models	K	$\Delta$ AIC	AIC weight	$R^2_m$	$R^2_c$
DDT	Roe deer	<b>Month + % Woodlands</b>	<b>15</b>	<b>0.00</b>	<b>0.846</b>	<b>0.24</b>	<b>0.42</b>
		Month + Age + % Woodlands	17	3.59	0.141	0.24	0.43
		Month + Age + % Woodlands + Month*Age	39	8.35	0.013	0.26	0.45
		% Woodlands	4	247.90	0.000	0.11	0.28
		Null model	3	322.33	0.000	0.00	0.25
	Mouflon	<b>Month + Age + Month*Age</b>	<b>50</b>	<b>0.00</b>	<b>0.654</b>	<b>0.13</b>	<b>0.26</b>
		Month + Age + % Grasslands + Month*Age	51	1.27	0.346	0.13	0.26
		Month + Age + % Grasslands	18	85.32	0.000	0.11	0.26
		Month + % Grasslands	15	154.36	0.000	0.09	0.25
		% Grasslands	4	967.70	0.000	0.00	0.16
HRS	Roe deer	<b>Month + Age + % Woodlands + Month*Age</b>	<b>39</b>	<b>0.00</b>	<b>0.99</b>	<b>0.41</b>	<b>0.62</b>
		Month + Age + % Woodlands	17	5.34	0.01	0.39	0.61
		Month + % Woodlands	15	11.06	0.00	0.38	0.61
		% Woodlands	4	814.87	0.00	0.04	0.25
		Null model	3	839.96	0.000	0.00	0.27
	Mouflon	<b>Month + Age + % Grasslands</b>	<b>18</b>	<b>0.00</b>	<b>0.947</b>	<b>0.18</b>	<b>0.64</b>
		Month + % Grasslands	15	5.78	0.053	0.16	0.64
		Month + Age + % Grasslands + Month*Age	51	23.82	0.000	0.23	0.68
		Null model	3	77.02	0.000	0.00	0.40
		% Grasslands	4	78.69	0.000	0.00	0.42

Models were ranked according to AIC selection criteria using the difference in AIC values ( $\Delta$ AIC), the number of estimated parameters (K) and the AIC weight of each model. The three best ranked models are presented followed by the habitat type model and the null model. The best supported model is in bold.  $R^2_m$  and  $R^2_c$  are marginal and conditional  $R^2$ , respectively (see Nakagawa & Schielzeth, 2013). For DDT in mouflon females, we included the best ranked model without age (Month+Grasslands) to facilitate comparison of  $R^2_m$  and  $R^2_c$  values with the best selected model.

females (March:  $0.97 \pm 0.05$  km/day) and 14.0% higher than that of >8-year-old females (March:  $1.00 \pm 0.7$  km/day); these differences disappeared the following month, in April, when most birth events occur (Fig. 3b). Concerning prediction H4b, the monthly HRS of old females was consistently 14.2–20.3% smaller than that of younger females throughout the year (Fig. 3d), making it difficult to conclude whether the presence of a lamb generated age-related differences in space use during the birth period.

#### Age-specific Space Use Outside Reproductive Periods

In roe deer, outside of the territorial and rut periods for males and the parturition period for females, there was some age-related variation in monthly HRS only. Monthly HRS of adults of both sexes was generally lower than that of younger individuals. Specifically, monthly HRS of adult males was, on average, 14.7% and 18.4% lower than those of juveniles and yearlings, respectively. No clear pattern of age-related differences in space use were observed in roe deer females. These results do not support our predictions H5a and H7a that older individuals should have lower movement rates than younger individuals, but do support our prediction H5b (but not H7b) that they should have smaller home ranges linked to increased experience and/or lower locomotor capacity.

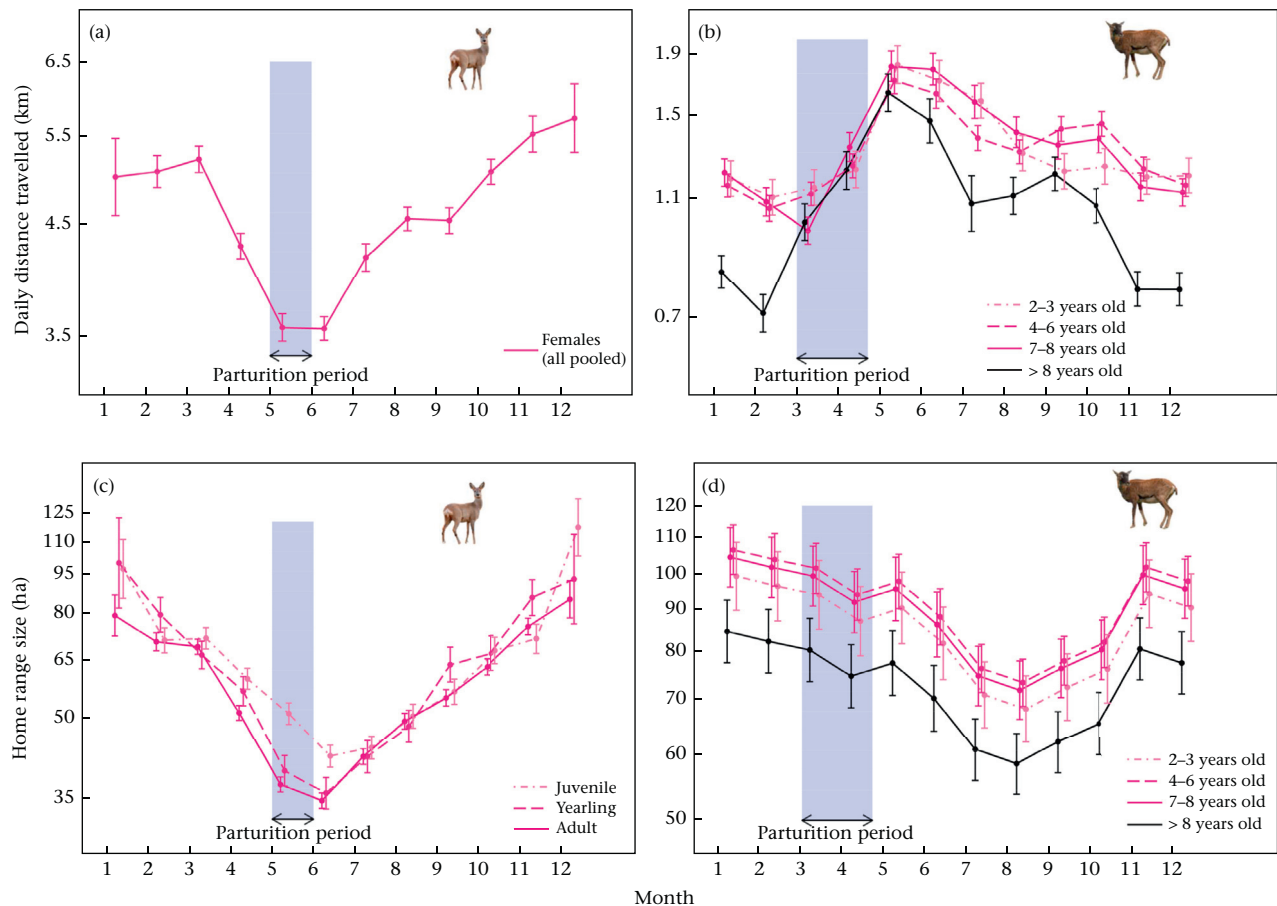
In mouflon, the DDT of the oldest males were systematically smaller than those of younger males (except for 7–8-year-old males in July and August), as the oldest individuals (>8 years old) travelled between  $0.59 \pm 0.05$  km/day (January) and

$1.16 \pm 0.10$  km/day (July) per day, which was 13.6–32.0%, 12.8–48.8% and 32.1–58.2% lower than the DDT of 7–8, 4–6 and 2–3-year-old males, respectively (Fig. 2b). The oldest mouflon females (>8 years old) also had a lower DDT, mainly from June to February, compared to the other female age classes, i.e. between  $0.71 \pm 0.1$  km/day (February) and  $1.4 \pm 0.12$  km/day (June) per day, that is, 10.3–34.5%, 9.7–36.4% and 0.1–35.6% lower than 7–8, 4–6 and 2–3-year-old females, respectively (Fig. 3b). Second, monthly HRS was also markedly lower in the oldest females (>8 years old) across the entire year (Fig. 3d; 14.2–20.3% smaller than all other age classes), while no such age-related effect was observed for males. This supports our predictions H6a, H8a,b that old mouflon, particularly females, have lower movement rates and smaller ranges than younger individuals (see Table 4).

Overall, when included in the selected model, the percentage of variance attributed to age-related variation in space use (obtained by comparing the conditional  $R^2$  of the best model and the marginal  $R^2$  of the same model with no age-related effect) ranged between 2 and 12%, representing between 0.001 and 14% of the total variance explained by the selected models (Tables 2, 3). The variance explained by the random effect of individual identity ranged between 11% and 46% of the total explained variance.

#### DISCUSSION

Investigating the age-specific impact of reproduction (rutting for males, parturition and care for females) on movements and



**Figure 3.** Predicted daily distance travelled for (a) roe deer females and (b) mouflon females, and monthly home range size in (c) roe deer females and (d) mouflon females over the year (1 = January) for different age classes. We used a logarithmic scale on the y axis. Points and bars represent the predicted estimates and associated standard errors derived from the selected model.



**Table 4**  
Summary of predictions and results

Sex	Species	Breeding period Age-related differences linked to reproductive constraints, i.e. rutting (and territoriality in roe deer) in males, parturition in females		Outside breeding period Age-related differences linked to increased experience and lower locomotor capacity in older individuals	
		DDT	HRS	DDT	HRS
Males	Roe deer	H1a: Adults > younger males due to adult patrolling behaviours Supported	H1b: Adults < younger males due to adult territorial behaviours Partially supported	H5a: not supported	H5b: supported
Males	Mouflon	H2a: younger subordinates > older dominant males Supported	H2b: younger subordinates > older dominant males Not supported	H6a: supported	H6b: not supported
Females	Roe deer	H3a: Older females < younger females due to the hider tactic of fawns. Not supported	H3b: Older females < younger females due to the hider tactic of fawns. Supported	H7a: not supported	H7b: not supported
Females	Mouflon	H4a: No age-related differences expected as lambs adopt a follower tactic Partially supported	H4b: No age-related differences expected as lambs adopt a follower tactic Not supported	H8a: supported	H8b: supported

home ranges in two contrasting ungulate species allowed us to infer (1) that male spatial behaviour varied with age, reflecting the contrasting mating tactics of the two species, and (2) that females of all ages modified their movement patterns and/or home range size during parturition, but, particularly, the extent of these modifications differed markedly between reproductive and nonreproductive females in roe deer. In addition, we clearly demonstrated that (3) throughout the year, the oldest individuals tended to move the least and/or occupy the smallest ranges, particularly in mouflon. Age-specific alternative male mating tactics have previously been reported (Dominey, 1984; Hogg, 1984), while certain authors have suggested that individuals may modify their ranging behaviour as a result of experience and ageing (Daugherty & Sheldon, 1982; Wunderle, 1991). However, empirical studies of the extent of age-specific spatial behaviour, particularly in relation to reproduction, have until recently been limited to a few situations where direct observation of known-aged individuals was possible (e.g. Corlatti et al., 2012; Foley et al., 2015; Taylor et al., 2020). Our findings, based on a large GPS data set of aged individuals, therefore, illustrate the range of variation in space use tactics, both within and between populations of large herbivores, and provides strong evidence that age is a major determinant of spatial behaviour.

In large herbivores, the time and energy males invest in reproduction depend strongly on their age, and the mating tactics that they adopt to access reproductive females during the breeding period (Corlatti et al., 2012; Foley et al., 2015; Hogg, 1984; Liberg, Johansson, Andersen, & Linnell, 1998; Willis & Neuhaus, 2009). However, these findings were mostly based on observational studies of male–male and male–female interactions and territoriality. From a comprehensive investigation of movement behaviour throughout the year, we found age-specific patterns of mobility in two species of large herbivores for which direct observations are seldom feasible. Furthermore, the pattern of age dependence in movement behaviour differed markedly between species, strongly suggesting that life histories may have an important influence on spatial behaviour. For example, we found that adult roe deer males, which are territorial from March to August (Vanpé et al., 2009), had high levels of mobility, but smaller home ranges, than younger males. This is probably due to the patrolling behaviour required to successfully delimit a territory and to exclude other males (Liberg et al., 1998). In contrast, most 1- and 2-year-old males are unable to defend a territory (Vanpé et al., 2009). Despite this, mobility of males of both younger age classes also increased during the rut, although to a lesser extent than for older males,

possibly related to attempted courting of receptive females (Melis, Hoem, Linnell, & Andersen, 2005). Indeed, subadults may attempt to mate with a female within an adult male's territory ('satellite' tactic), or through use of buffer zones between adult territories, allowing them to perform short raids towards unattended females ('peripheral' tactic, Liberg et al., 1998). Alternatively, young males may be more mobile due to harassment by territorial adults (Wahlström, 1994).

Age-specific movements during the rutting period were less pronounced in male mouflon than in roe deer. In contrast to roe deer, young male mouflon travelled relatively more during the peak of the rutting period compared to older animals. Subordinate/young males (4–6 years old) generally reproduce by courting females (i.e. breaching the defence of a dominant male to chase after the female, Bon et al., 1992; Hogg, 1984), whereas dominant old males (i.e. 7–8 and >8 years old) generally tend receptive females (i.e. directly or indirectly impeding attempts by other males to mate). However, the higher mobility of young males did not translate to relatively larger home ranges during the rutting period. Instead, the range of males of all ages increased markedly at that time (Fig. 2d), probably linked to excursions outside their usual home range (Bon et al., 1992; Portanier et al., 2017). Courting is probably a behaviour that occurs at a very local scale, that is, the rutting area, and is thus not detectable at the home range scale. Further work to better understand the link between spatial behaviour and mating tactics should investigate fine-scale movements and habitat selection of males versus females and their interactions (Bourgoin et al., 2018; Marchand et al., 2015).

Because habitat use of female large herbivores is constrained by the presence of dependent young (Bongi et al., 2008; Ciuti et al., 2006, 2009), we expected marked stage-specific variation in mobility and home range size during the critical perinatal period depending on maternal care tactics. While no age-related differences were expected in mouflon, a gregarious species, with young that are able to follow their mother within 24 h after birth (Langbein, Scheibe, & Eichhorn, 1998), we particularly expected a postnatal reduction in mobility and space use in roe deer which express a hider tactic for the first 2–3 months of life. During the birth period, all mouflon females travelled longer distances, indicating that the presence of a lamb did not impede their mobility. In contrast, roe deer females of all ages, including those that did not reproduce, decreased their daily mobility and home range size during late spring. However, reproductive females had smaller monthly home ranges than nonreproductive females (i.e. juveniles) during the last month of pregnancy, and during parturition and



lactation, but maintained a similar level of mobility, compared to nonreproductive females. Owing to the hidden tactic of their offspring, lactating roe deer females must frequently commute between their hidden fawn(s) and the richest foraging patches to offset the energetic costs of lactation, which are particularly high in this income breeder. This may explain why the mobility of reproductive roe deer females was not markedly lower than that of nonreproductive does, while their monthly home range size was lower during the parturition period (see Bongi et al., 2008, for similar results). Previous studies reported that movements and space use of females in both species were strongly influenced by food availability and quality during this period of resource flush (Morellet et al., 2013; Marchand et al., 2015; see Appendix). Further research is hence needed to disentangle the relative influence of offspring presence and behaviour from resource distribution and quality on female mobility during the parturition period.

Outside the reproduction periods, we expected age-related differences in space use related to increased experience with age and/or senescence in locomotor performance in the oldest individuals (Catry et al., 2006; Froy et al., 2018; MacNulty et al., 2009; Montgomery et al., 2013). We found strong support for our predictions in both sexes and both species, but at different spatial scales (Table 4). In roe deer, adults tended to use smaller monthly home ranges than younger individuals all year round, and this pattern was more pronounced in males than in females (see also Saïd et al., 2009). This was also observed in mouflon females, but, interestingly, not in mouflon males. In contrast, no clear age-related differences in distance travelled were detected in roe deer, whereas in mouflon this was much lower in older animals of both sexes for most of the year. Older individuals may have a more accurate cognitive map of the distribution of resources and risks within their environment, and so may be more efficient at locating and navigating between resource patches, resulting in lower distances travelled and smaller range sizes (Froy et al., 2018; Morellet et al., 2013). Indeed, memory and familiarity have been revealed as key components involved in mobility and home range emergence in both theoretical and empirical studies (Gehr et al., 2020; Marchand et al., 2017; Piper, 2011; Wolf, Frair, Merrill, & Turchin, 2009). In addition, decreasing locomotor performance with age could also lead to lower daily mobility and range size (Froy et al., 2018). As animals get older, a complex process of physiological and physical deterioration (i.e. functional senescence, Nussey, Froy, Lemaitre, Gaillard, & Austad, 2013; Soulsbury & Halsey, 2018) has been observed in laboratory research (Kirkwood, 2005; Niccoli & Partridge, 2012; López-Otín, Blasco, Partridge, Serrano, & Kroemer, 2013), altering locomotor performance, space use and foraging behaviour in later life (Catry et al., 2006; Froy et al., 2018; MacNulty et al., 2009), and underpinning demographic senescence in survival and reproduction (Jones et al., 2014; Nussey et al., 2013). Our results indicate that this may occur in one of our study species as we found that, outside the reproduction periods, the mobility of both sexes and the monthly home range size of females were lowest among the oldest mouflon. We were unable to quantify age-related senescence in the mobility of roe deer due to the absence of an adequate sample of old known-aged individuals. Indeed, lack of accurate information about an animal's age in most studies probably explains why the relative contribution of experience and locomotor performance to age-dependent patterns of movement and space use remains poorly understood. Further research should aim to clarify this issue by taking advantage of the long-term monitoring of individual space use provided by technological improvements in biologists (Froy et al., 2018). Experiments whereby individuals of known age are translocated to novel environments would also allow us to tease apart the role of experience and physiological ageing on mobility and range use.

Finally, while we have demonstrated marked age-related variation in space use in two large herbivores, many other intrinsic and extrinsic factors that are difficult to control for in the wild may drive individual movement decisions. For example, large herbivores must adjust their behaviour in response to the spatiotemporal dynamics of both resource availability (green-up in spring, senescence in autumn, Morellet et al., 2013) and risk (hunters and natural predators, Benhaïem et al., 2008; Bonnot et al., 2013). By analysing relative variation in space use among age classes over the same monitoring period and landscape, we assumed that individuals of each age class had, on average, experienced roughly the same environmental conditions so that the resulting patterns are a fair representation of age-dependent space use at the population level. However, our modelling approach also revealed that a large proportion of intraindividual variation in space use was not related to age and remained unexplained. Consistent between-individual differences in movement behaviours have been increasingly reported (Bonnot et al., 2015; Gervais et al., 2020; see Hertel, Niemelä, Dingemanse, & Mueller, 2020 for a review), with consequences for life histories (Bonnot et al., 2018). To better evaluate the consequences of global change for the mobility of wild populations, further research should aim to disentangle the intrinsic drivers of interindividual variability in space use, such as personality (Dingemanse, Kazem, Reale, & Wright, 2010; Jolles, King, & Killen, 2019; Réale, Gallant, Leblanc, & Festa-Bianchet, 2000), from extrinsic factors such as adverse environmental conditions (Marchand et al., 2015) and habitat fragmentation (Marchand et al., 2017).

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## Appendix

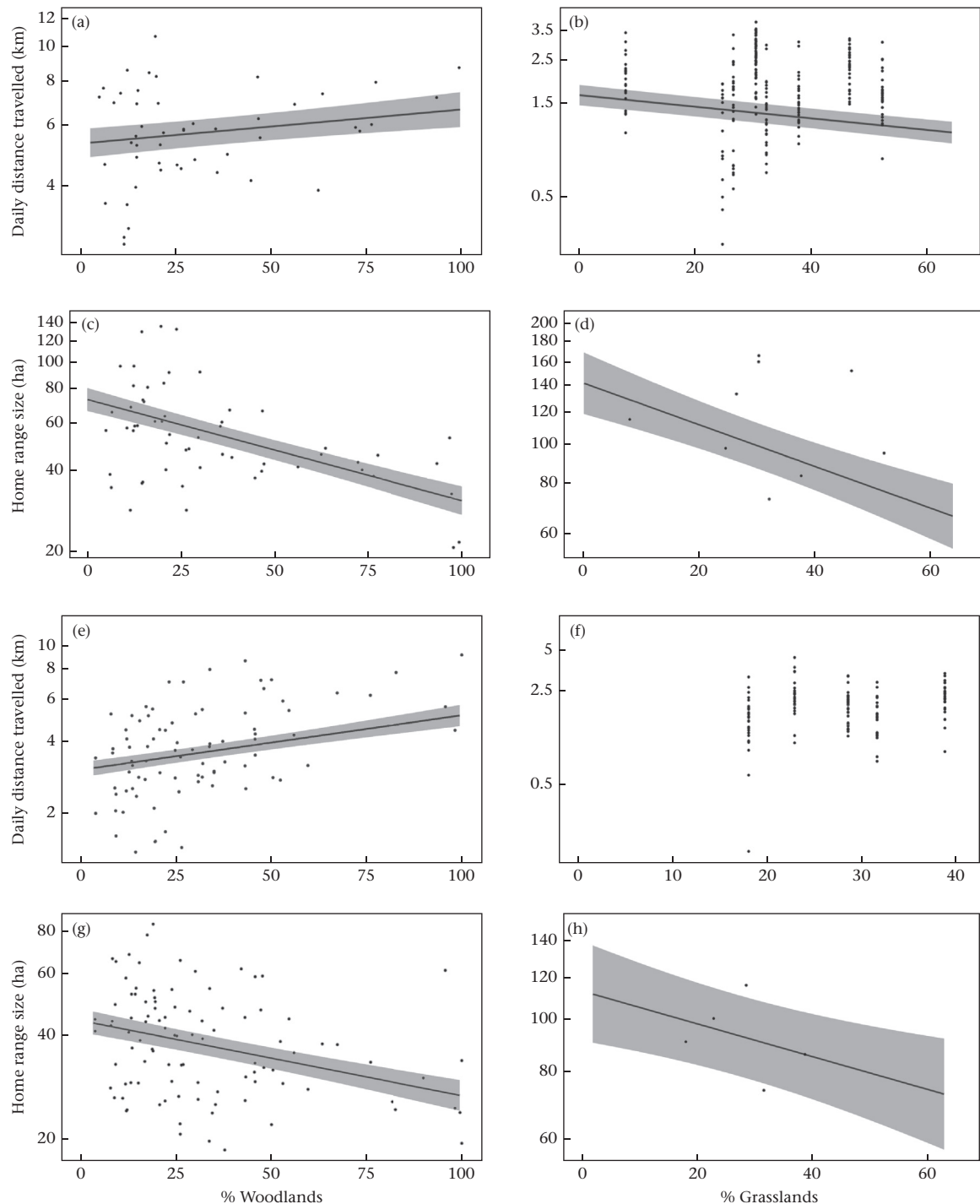
As habitat composition of the home range has the potential to markedly influence individual movements and space use (Mysterud et al., 1998; see Gaudry et al., 2018 for a recent example), we considered the percentage of woodlands and of grass areas in individual ranges to index habitat composition/landscape configuration for roe deer and mouflon, respectively. Indeed, these habitat types have been revealed as major drivers of habitat selection in the studied populations of roe deer and mouflon (Garel et al., 2007; Marchand et al., 2014; Morellet et al., 2011). Indeed, the habitat productivity hypothesis (Harestad & Bunnell, 1979) suggests that individuals should adjust their home range size to resource availability in order to minimize the area used for sustaining their energy requirements, while limiting energy expenditure during foraging movements (see e.g. Naidoo et al., 2012; Tufto, Andersen, & Linnell, 1996; Van Beest, Rivrud, Loe, Milner, & Mysterud, 2011 for empirical support of this hypothesis in large herbivores). For the Aurignac study site, the land cover map was based on aerial photographs (BD Ortho from the Institut Géographique National, <http://professionnels.ign.fr/bdortho-50cm>) for which homogeneous habitat polygons (in ArcView GIS 3.3, Esri, Redlands, CA, U.S.A.) were manually digitized and assigned to a habitat type that was determined annually by field observations during summer. For the Caroux-Espinouse study area, we derived habitat types from the processing (k-means unsupervised classification) of a SPOT satellite image taken in July 2005 and field validation in a 25 × 25 m grid (Tronchet, 2008) and classified habitat types following Marchand et al. (2015).

Habitat type was selected in the best supported model describing variation in DDT and in monthly HRS for both sexes and for both species (Tables 2, 3), except for DDT in mouflon females (see Table 3, Fig. A1f). In roe deer males DDT increased by 0.64 km/day (from 5.63 ± 0.25 to 6.28 ± 0.32 km/day, an 11.3% increase; Fig. A1a) between the first quartile (27.6%) and the



third quartile (75.6%) of the percentage of woodlands in the monthly HRS for adult males in May, while in mouflon males, DDT decreased by 0.29 km/day (i.e. a 19.6% decrease, from  $1.48 \pm 0.11$  to  $1.19 \pm 0.12$  km/day; Fig. A1b) from the first quartile (16.3%) to the third quartile (48.3%) of the percentage of grass areas in the monthly HRS for males 7–8 years old in May. The monthly HRS of roe deer males decreased by 20.45 ha (from

$58.63 \pm 2.48$  ha to  $38.18 \pm 1.87$  ha, i.e. a 34.9% decrease; Fig. A1c) between the first quartile (25%) and the third quartile (75%) of the percentage of woodland, while in mouflon males, the monthly HRS decreased by 36.98 ha (from  $117.45 \pm 8.39$  to  $80.46 \pm 6.01$  ha, i.e. a 31.5% decrease; Fig. A1d) between the first quartile (16.3%) and the third quartile (48.3%) of the percentage of grass areas in the monthly HRS.



**Figure A1.** Data points and predicted daily distance travelled (DDT) in (a) roe deer males and (b) mouflon males, and monthly home range size (HRS) in (c) roe deer males and (d) mouflon males in relation to habitat composition of the home range (i.e. % of woodlands or grasslands in the monthly HRS in May in adult roe deer males, and in 7–8-year-old mouflon males). Data points and predicted DDT for (e) roe deer females and (f) mouflon females (data points only), and monthly HRS for (g) roe deer females and (h) mouflon females in relation to habitat composition of the home range (i.e. % of woodlands in the monthly HRS in May in adult roe deer females, and in 7–8-year-old mouflon females). We used a logarithmic scale on the y axis and the line represents the estimated slope derived from the selected model and its 95% confidence interval.



The DDT of roe deer females increased by 1.00 km/day (from  $3.51 \pm 0.11$  to  $4.50 \pm 0.18$  km/day, i.e. a 28.4% increase; Fig. A1e) between the first quartile (25.4%) and the third quartile (75.4%) of the percentage of woodlands in the monthly HRS in May. The monthly HRS of roe deer adult females decreased by 8.17 ha (from  $38.38 \pm 1.30$  to  $30.21 \pm 1.26$  ha, i.e. a 21.3% decrease; Fig. A1g) between the minimum first quartile (27.4%) and the third quartile (75.4%) of

the percentage of woodlands in the monthly HRS, while in mouflon females, the monthly HRS decreased by 18.83 ha (from  $99.34 \pm 9.02$  to  $80.51 \pm 8.10$  ha, i.e. a 19.0% decrease; Fig. A1h) between the first (17.9%) and the third quartile (47.9%) of the percentage of grass areas in the monthly HRS.