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RESEARCH ARTICLE

On this side of the fence: Functional responses to linear landscape features shape the home range of large herbivores

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Abstract

1. Understanding the consequences of global change for animal movement is a major issue for conservation and management. In particular, habitat fragmentation generates increased densities of linear landscape features that can impede movements.

2. While the influence of these features on animal movements has been intensively investigated, they may also play a key role at broader spatial scales (e.g. the home range scale) as resources, cover from predators/humans, corridors/barriers or landmarks. How space use respond to varying densities of linear features has been mostly overlooked in large herbivores, in contrast to studies done on predators. Focusing on large herbivores should provide additional insights to understand how animals solve the trade-off between energy acquisition and mortality risk.

3. Here, we investigated the role of anthropogenic (roads and tracks) and natural (ridges, valley bottoms and forest edges) linear features on home range features in five large herbivores. We analysed an extensive GPS monitoring database of 710 individuals across nine populations, ranging from mountain areas mostly divided by natural features to lowlands that were highly fragmented by anthropogenic features.

4. Nearly all of the linear features studied were found at the home range periphery, suggesting that large herbivores primarily use them as landmarks to delimit their home range. In contrast, for mountain species, ridges often occurred in the core range, probably related to their functional role in terms of resources and refuge. When the density of linear features was high, they no longer occurred predominantly at the home range periphery, but instead were found across much of the home range. We suggest that, in highly fragmented landscapes, large herbivores are constrained by the costs of memorising the spatial location of key features, and by the requirement for a minimum area to satisfy their vital needs.

5. These patterns were mostly consistent in both males and females and across species, suggesting that linear features have a preponderant influence on how large herbivores perceive and use the landscape.

KEYWORDS

behavioural barrier, cognitive map, habitat fragmentation, home range, landmark, landscape connectivity, movement ecology, ungulates

1 | INTRODUCTION

The effects of global change due to the rapid intensification of anthropogenic activities on natural habitats are increasingly evident (Parmesan, 2006; Travis, 2003). A major issue for wildlife conservation and management is to understand how these effects, such as habitat loss and fragmentation, will affect species distribution and population dynamics (Barnosky et al., 2012; Foley et al., 2005; Gaillard et al., 2010, 2013). In this context, a large body of literature has shown that animal movement is strongly influenced by landscape structure and its degree of fragmentation, notably in terms of connectivity among resource patches (Taylor et al., 2006). As movement is 'the glue' (sensu Van Moorter et al., 2016) connecting individual behavioural decisions to large spatio-temporal scale behaviours such as habitat use and selection, dispersal or migration, fragmentation also plays a major role in determining gene flow, disease spread, predator–prey relationships and source–sink dynamics (Hanski et al., 2000; James & Stuart-Smith, 2000; Pulliam, 1988; Wright, 1984). Hence, investigating the proximate behavioural processes individuals use to cope with different degrees of fragmentation may improve our understanding of the consequences of ongoing landscape modifications for animal movements and space use and, ultimately, population distribution and dynamics.

Landscape fragmentation can have a number of consequences, such as an increase in the number of habitat patches, a decrease in patch size or an increase in the density of edges and linear features in the landscape (Ellis, 2011; Fahrig, 2003; Jaeger, 2000; Taylor et al., 2006). The consequences for animals are manifold and complex (Fahrig, 2003) and can be either positive or negative, depending on the behavioural response to the physical landscape structure (Dickson & Beier, 2002; Poessel et al., 2014), as well as species-specific habitat preferences and sensitivity to habitat heterogeneity. Some species may also benefit from habitat fragmentation through greater local heterogeneity in resource patches with complementary functions (e.g. food resources and shelter in agricultural landscapes for roe deer; Hewison et al., 2001) or due to a higher density of corridors that are used for movement, especially in predators (e.g. seismic lines in black bears *Ursus americanus*, Tigner et al., 2014; roads or tracks for wolves *Canis lupus*, James & Stuart-Smith, 2000; Pigeon et al., 2020). In contrast, the dense network of linear landscape features in highly fragmented habitats may be detrimental when these features act as physical and/or behavioural barriers (e.g. caribou *Rangifer tarandus*, Leblond et al., 2013 or pronghorn *Antilocapra americana*, Seidler et al., 2015) or, for prey species, when

predators use them to increase kill rate (Dickie et al., 2017; McKenzie et al., 2012). Furthermore, even in the absence of natural predators, anthropogenic linear features can also be associated with increased risk of mortality due to collisions with vehicles (Saint-Andrieux et al., 2020).

To exploit information efficiently about feeding sites, risky areas or escape routes, individuals have to identify and memorise landmarks in the landscape, generating a cognitive map by which an individual will later navigate (Benhamou, 1997; Presotto et al., 2019; Spencer, 2012). In this context, linear landscape features play an important role in the sharing of space among individuals in territorial species (e.g. Hewison et al., 1998), and in the design of home ranges in species with area-restricted space use behaviour (Heap et al., 2012; Long et al., 2010; Marchand et al., 2015). However, across species, linear features may also serve different ecological functions (e.g. resources, cover from predators/humans and associated perceived risks, corridors/barriers, landmarks) depending on their habitat preferences and requirements, anti-predator behaviour and sensitivity to human disturbance. In addition, animals do not use or select resources and habitats proportionally to their availability, leading to the emergence of a functional response (e.g. Holbrook et al., 2019; Matthiopoulos et al., 2011) in connection with the concept initially proposed by Holling (1959) in the context of predator–prey dynamics. In an analogous way, the nature of an individual's response to a given linear feature may vary in relation to the degree of landscape fragmentation, generating another kind of functional response to variation in the density of linear features in their environment (Pigeon et al., 2020). For example, the cognitive processes involved in spatial memory may become costly or inefficient when the linear landscape features used by animals as landmarks are too dense to be memorised (Fagan et al., 2013). This kind of variation in behavioural response could represent a key component of phenotypic plasticity, which may help promote adaptation to major ongoing environmental changes (e.g. Chevin et al., 2010). As an example, the use of anthropogenic linear features by North-American large carnivores varied in relation to their density in the landscape (e.g. Dickie, 2015; Muhly et al., 2019; Pigeon et al., 2020), with fragmented landscapes often benefiting predators in their behavioural arms race with prey (e.g. Dickie et al., 2017; McKenzie et al., 2012). In contrast, although the avoidance of anthropogenic linear features by prey has often been reported (e.g. Beyer et al., 2016; Marchand, Freycon, et al., 2017), little is known about how large herbivores manage the multiple, and sometimes conflicting, ecological functions of other linear landscape features. Likewise, few studies have investigated the existence of

functional responses in large herbivores across a range of landscape fragmentation (but see DeMars & Boutin, 2018). Lastly, both in predators and prey, most of these studies have focused on anthropogenic linear features whereas fragmentation also alter the density of natural linear features in the landscape (e.g. ecotone).

We tried to fill this knowledge gap by investigating how varying densities of both anthropogenic and natural linear features influence home range establishment for five contrasted species of large herbivore (Table 1). We analysed an extensive GPS database (710 individuals) from nine populations living in contrasted landscapes, from mountain areas mostly divided by natural features, to lowlands that were highly fragmented by anthropogenic features (Figure 1). We focused on the home range spatial scale which is an emergent feature derived from the movement of an individual in response to the distribution of resources, cover from perceived risk of predation/disturbance and thermal shelter, corridors and barriers, and the presence of landmarks (e.g. Fagan et al., 2013; Van Moorter et al., 2009).

We first investigated the distribution of linear features in relation to the core and the periphery of the home range depending on their expected role for a given species (Table 2; Figure 2a). More specifically, based on previous knowledge of species-specific needs, we hypothesised that linear features that are either associated with a perceived risk, or that are not associated with any specific resource or risk, should preferentially occur at the home range periphery (H1a; Figure 2a; Table 2). In particular, this expectation concerned those linear features that have previously been identified as barriers and/or landmarks to large herbivore movements (roads, tracks, valley bottoms; Coulon et al., 2008; Dyer et al., 2002; Laurian et al., 2008; Table 2), and edges between forest and open habitats in mountain species that preferentially use grass-rich open habitats with high visibility (e.g. Marchand et al., 2015; Nesti et al., 2010). In contrast, we expected linear features that are associated with food or cover to be preferentially found within the home range core (H1b, Figure 2a; Table 2). This expectation concerned forest edges that provide high quality browsing habitats for roe deer (Saïd & Servanty, 2005), and ridges that offer both food and cover (for thermoregulation and against perceived risk of predation/disturbance; e.g. Bon & Campan, 1989; Nesti et al., 2010) for mountain species. Second, for linear features acting as landmarks or behavioural barriers, we expected the strength of selection in the periphery of the home range to decline as feature density in the local environment increased (i.e. a functional response; H2, Figure 2b). That is, due to the constraints of a minimum area for a viable home range and memory costs (Fagan et al., 2013), we assumed that when linear features were especially dense, an individual would be unable to avoid including them in its core range (Fagan et al., 2013).

2 | MATERIALS AND METHODS

2.1 | Study areas and species

We collected animal locations using GPS collars (*n* = 710 individuals) for five large herbivores: chamois *Rupicapra rupicapra*, Mediterranean

mouflon *Ovis gmelini musimon* × *Ovis* sp., Alpine ibex *Capra ibex*, roe deer *Capreolus capreolus* and red deer *Cervus elaphus* inhabiting seven study sites (Table 1; Figure 1). Roe deer were monitored on four sites, while a maximum of three species (roe deer, mouflon and chamois) were simultaneously studied on one site (Table 1). In total, we analysed nine species-site combinations, four involving both males and females, and five of which concerned only females (i.e. 13 sex-population datasets, see details in Table 1). The seven study sites differed in terms of landscape heterogeneity, habitat types and human activity, with pronounced variation in the density of linear features, ranging from 0 to 6197 m/km² (coefficient of variation (CV) of 0.76) for anthropogenic linear features and from 0 to 5,458 m/km² (CV of 0.90) for natural features (Figure 1; Table S1). Except in the Caroux-Espinouse massif where one wolf was regularly observed since 2013, all these areas were free of resident large carnivores during the study period (with occasional observations of wolves reported in Les Bauges and Bargy massifs). In contrast, hunting occurred in most areas except in the Caroux-Espinouse massif, with the studied populations targeted (except for Alpine ibex which is a protected species in France) from the beginning of June (Aurignac) or September (all the other study areas), to the end of February.

2.2 | GPS data and home range computation

Animals were captured with a variety of methods across study sites and mostly fitted with Lotek 3300S, 3300L and 4400M (revision 2; Lotek Engineering Inc.) or Vectronic (GPS Plus, Vectronic Aerospace) GPS collars (more details in Table 1 and references therein). All capture and marking procedures were done in accordance with local, national and European animal welfare laws, with specific accreditations depending on study areas/species, in agreement with the French environmental code (Art. R421-15 to 421-31 and R422-92 to 422-94-1): Ministerial Orders of February 11, 2014 delivered by the French Minister of Ecology, Sustainable Development and Energy, prefectural order 2009-014 delivered by the Préfecture de Paris, prefectural orders 2015062-0018, 2013274-0001 and DDT-2015-0513 delivered by the Préfecture de la Haute-Savoie, and prefectural order and agreement no. A31113001 delivered by the Préfecture de la Haute-Garonne and approved by the Departmental Authority of Population Protection. For our analyses, we only considered adults (i.e. individuals ≥2 years old, after the period of putative natal dispersal) and yearlings (e.g. roe deer in Aurignac; see Debeffe et al., 2012).

We collected GPS data with variable schedules (Table 1). Downgrading sampling frequency in the ibex-Bargy dataset from 1 location/hour (original) to 1 location/day (corresponding to the lowest frequency across datasets, Les Bauges, Table 1) and repeating the analysis detailed below provided qualitatively similar results. In the following, we restricted the analyses to animals with at least 70% of successful locations per month (from 20 locations per month for roe deer and chamois in Les Bauges to 250 locations for mouflon in Caroux-Espinouse). We plotted the relationship between number of

TABLE 1 Characteristics of each species, study site, monitoring period, sex, number of GPS-collared individuals and sampling design. Species were first ranked by habitat type (mountain vs. forest species) and body mass (from smaller to larger species) and then by topographic complexity of the study site (from lower to higher elevation ranges; Table 1). For foraging specialisation, we use '+' signs to indicate proximity to the 'obligate browser' or 'obligate grazer' ends of the gradient (i.e. nuancing the usual 'intermediate feeder' terminology, based on collective knowledge from the long-term programs; see also Péron et al., 2018)

Species	Habitat preferences	Feeding regime	Site	Elevation (m a.s.l.)	Habitat	Localisation (DD)	Monitoring period	Sex	n	Sampling frequency
Chamois (Rupicapra rupicapra)	Alpine meadows, cliffs, mountain forests[a]	Intermediate[f]	Les Bauges	700 to 2,217[h]	Meadows, cliffs, forest, valleys[h]	45.66°N, 6.21°E[h]	2003–2016	Males and females	15 and 117	1loc/day[h]
Mediterranean mouflon (Ovis gmelini musimon × Ovis sp.)	Mountain, highland[b]	Grazer ++[f]	Caroux-Espinouse	532 to 1,124[b]	Forest, moorlands, cliffs, gorges[b]	43.63°N, 2.96°E[b]	2010–2017	Males and females	47 and 72	1loc/2h[n]
			Les Bauges	700 to 2,217[h]	Meadows, cliffs, forest, valleys[h]	45.66°N, 6.21°E[h]	2004–2014	Females	20	1loc/day[h]
Alpine ibex (Capra ibex)	Alpine meadows, cliffs[c]	Grazer +[g]	Bargy	600 to 2,348[i]	Meadows, cliffs, valleys[i]	46.00°N, 6.46°E[i]	2013–2018	Males and females	14 and 60	1loc/h[o]
Roe deer (Capreolus capreolus)	Clearcut, edges, disturbed forest, agricultural landscape[d]	Browser ++[f]	Chize	47 to 101[l]	Forest[l]	46.08°N, −0.416°E[l]	2004–2009	Females	16	1loc/4h[k]
			Trois-Fontaines	130 to 230[k]	Forest[k]	48.70°N, 4.92°E[k]	2002–2009	Females	17	1loc/4h[k]
			Aurignac	250 to 400[l]	Forest, agricultural[l]	43.27°N, 0.88°E[l]	2002–2017	Males and females	103 and 137	1loc/4h and 1loc/6h[l]
			Les Bauges	700 to 2,217[h]	Meadows, cliffs, forest, valleys[h]	45.66°N, 6.21°E[h]	2005–2016	Females	16	1loc/day[p]
Red deer (Cervus elaphus)	Forest[e]	Intermediate +[f]	La Petite Pierre	200 to 400[m]	Forest, meadows[m]	48.83°N, 7.34°E[m]	2000–2018	Females	76	1loc/2h[m]

Notes: [a]Nesti et al. (2010); [b]Marchand et al. (2014); [c]Grignolio et al. (2003); [d]Tufto et al. (1996); [e]Clutton-Brock et al. (1987); [f]Redjadj et al. (2014); [g]Hofmann (1989); [h]Darmon et al. (2014); [i]Marchand, Freycon, et al. (2017); [j]Gaillard et al. (2013); [k]Gaudry et al. (2018); [l]Morellet et al. (2011); [m]Chassagneux et al. (2019); [n]Marchand et al. (2015); [o]Marchand, Garel, et al. (2017); [p]Tablado et al. (2016).
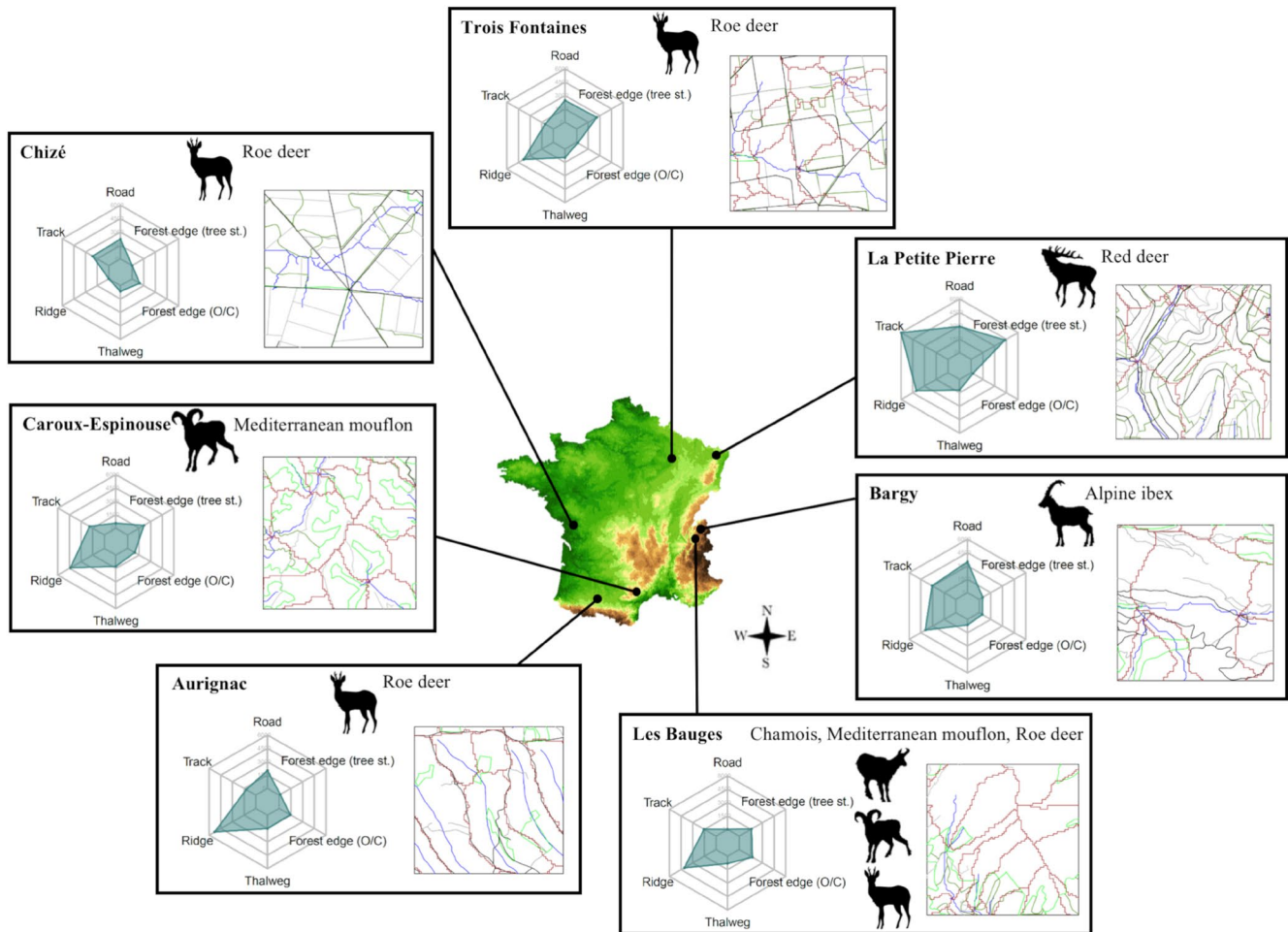
FIGURE 1 Map of the study sites. Each square corresponds to a 4 km^2 random block of each study site for visual comparison of the density of linear features among sites. In black: road, in grey: track, in brown: ridge, in blue: valley bottom, in green: forest edge between open and closed habitats, in dark green: forest edge between tree stands. On the topographical map of France, colours represent elevation, from green (0 m a.s.l.) to brown (4,810 m a.s.l.). Each spider chart has the same scale (from 0 to 6,000 m/km^2) to facilitate visual comparison of the density of linear landscape features among sites. For each site, the studied species are indicated. For the pictograms: ©C. Saint-Andrieux

locations and home range size for the site with the lowest location number (Les Bauges), which indicated that an asymptote for home range size was achieved at around 20 locations per month (see also Börger et al., 2006; Pellerin et al., 2008 on roe deer). We removed outliers (1.2% of the full dataset) based on unlikely movement characteristics (Bjørneraas et al., 2010).

We estimated the occurrence distribution for each animal using the fixed kernel method (Worton, 1989) with the LSCV method for the smoothing factor h (Seaman et al., 1998) implemented in the R package adehabitatHR (Calenge, 2006). We did not use autocorrelated kernel density estimates to compute home range size because the range distribution provided by this recent approach was less appropriate than the occurrence distribution provided by classical KDE (Fleming et al., 2015, but see Figures 19:20 in Supporting Information). Moreover, we checked that our results were robust regardless of the method used to compute home range size (see Table 1, Figures 19:20 and Table S4 in Supporting Information). We computed individual home ranges at the monthly scale to account

for individual heterogeneity in habitat selection within the year in relation to changes in food availability, physiological requirements and human disturbance (Bonnot et al., 2013; Marchand et al., 2014; Pettorelli et al., 2006; Richard et al., 2011; see Figures 1:9 in Supporting Information). This temporal scale allowed us to study a time window across which resource availability and disturbance were relatively stable, and during which individuals could be considered as stationary, with enough data to provide an unbiased estimate of home range size. Moreover, our approach allowed us to account for potential variation in the density of linear features in the local area related to monthly changes in animal behaviour (Holbrook et al., 2019).

2.3 | Linear landscape features

We included six linear landscape features extracted from the Institut Géographique National (https://geoservices.ign.fr/telechargement) in the analyses: four were considered natural (i.e. ridges, two types

TABLE 2 Expected functions (text) and position (colour) in the home range of anthropic and natural linear features for each species. In blue, the linear feature was expected to be selected at the home range periphery. In white, no selection was expected. In red, the linear feature was expected to be selected in the core home range. Species were first ranked by habitat type (mountain vs. forest species) and body mass (from smaller to larger species; Table S1 in Supporting Information) and then by topographic complexity of the study site (from lower to higher elevation ranges; Table 1). See text for details

	Anthropic		Natural			
	Road	Track	Ridge	Valley bottom	Forest edge (OC)	Forest edge (tree st.)
Mountain species						
Chamois	Barrier[a,b]	Landmark/Barrier[c,d]	Food/Refuge[e,f]	Landmark	Landmark[g]	
Mediterranean mouflon	Barrier[a,b]	Landmark/Barrier[c,d]	Food/Refuge[e,f]	Landmark[c]	Landmark[g]	
Alpine ibex	Barrier[a,b]	Landmark/Barrier[c,d]	Food/Refuge[e,f]	Landmark	Landmark[g]	
Forest species						
Roe deer	Barrier[a,b]	Landmark/Barrier[c,d]		Landmark[d]	Food[h]	Food[h]
Red deer	Barrier[a,b]	Landmark/Barrier[c,d]		Landmark		

Notes: [a]Dyer et al. (2002); [b]Laurian et al. (2008); [c]Marchand, Garel, et al. (2017); [d]Coulon et al. (2008); [e]Nesti et al. (2010); [f]Saunders (1955); [g]Marchand et al. (2015); [h]Saïd and Servanty (2005).

of forest edge and valley bottoms) and two were of anthropogenic origin (i.e. roads, tracks). Tracks included both hiking trails and pathways. None of these linear features were true physical barriers (e.g. fenced highways, large rivers) for any of the study species. Roads and tracks were extracted from the BD CARTO© dataset. We identified ridges and valley bottoms from the digital elevation model (resolution: 25 m; source: BD ALTI© dataset) using the r.param.scale tool in GRASS GIS 6.4.4 (Neteler et al., 2012). We extracted forest edges from the BD FORET© dataset. Then, we separated forest edges into two types: edges between open and closed habitats (noted 'O/C'), and edges between tree stands (i.e. different dominant tree species, noted 'tree st.'; Figure 1).

2.4 | Influence of linear landscape features and of their availability on the position of the home range core and periphery

We evaluated our predictions (Figure 2, Table 2) by estimating the relative densities of the various linear features within 19 segments of each individual's monthly home range, where each segment is defined by the 5% contours of the Kernel density distribution from [0%–5%] to [90%–95%]. For each linear feature, and for each segment, we computed a density ratio according to Equation (1) from Marchand, Garel, et al. (2017):

$$\text{Density ratio } i = \frac{\text{Linear feature density in the segment } i}{\text{Linear feature density in the 99\% home range}}. \quad (1)$$

First, if a linear feature is randomly distributed within the home range, the 95% confidence intervals (95% CI) of the density ratios averaged over all individual months should include 1. Alternatively, when the 95% CI for relative density was lower or higher than 1, this indicated that the linear feature was included less (i.e. avoided) or more (i.e. selected) often than expected in the focal home range segment i respectively. For this analysis, we considered that the periphery of the home range corresponded to the 90%–95% segment, while the core home range corresponded to the 0%–50% segment (White & Garrott, 2012; Figure 2). These UD values allowed us to investigate variation in the behaviour of large herbivores with respect to linear landscape features across the entire home range (Marchand, Freycon, et al., 2017; see Figures 10:18 in Supporting Information showing the relative density per 5% segment of the home range UD, for each study site and each linear landscape feature). Repeating the analyses considering the area just beyond the home range border rather than restricting our analyses to the home range periphery (90%–95% UD) did not qualitatively change the results (results not shown).

Second, we expected selection for a given linear feature in the periphery of the home range to decline as the density of that feature in the local environment increased (Figure 2b). We specifically evaluated this prediction for linear features presumed to act as landmarks or behavioural barriers (i.e. selected in the home range periphery), and for those that were distributed throughout the home range. This analysis was designed to evaluate whether the absence of selection at the home range periphery could be related to a particularly high density of a given feature in the landscape (Figure 2b). We tested our prediction using a multiplicative approach—a functional response in habitat selection sensu Holbrook et al. (2019)—focusing, for each sex and population, on the relationship between the density ratio of linear features in the periphery of the home range (90%–95% segment of the home range,
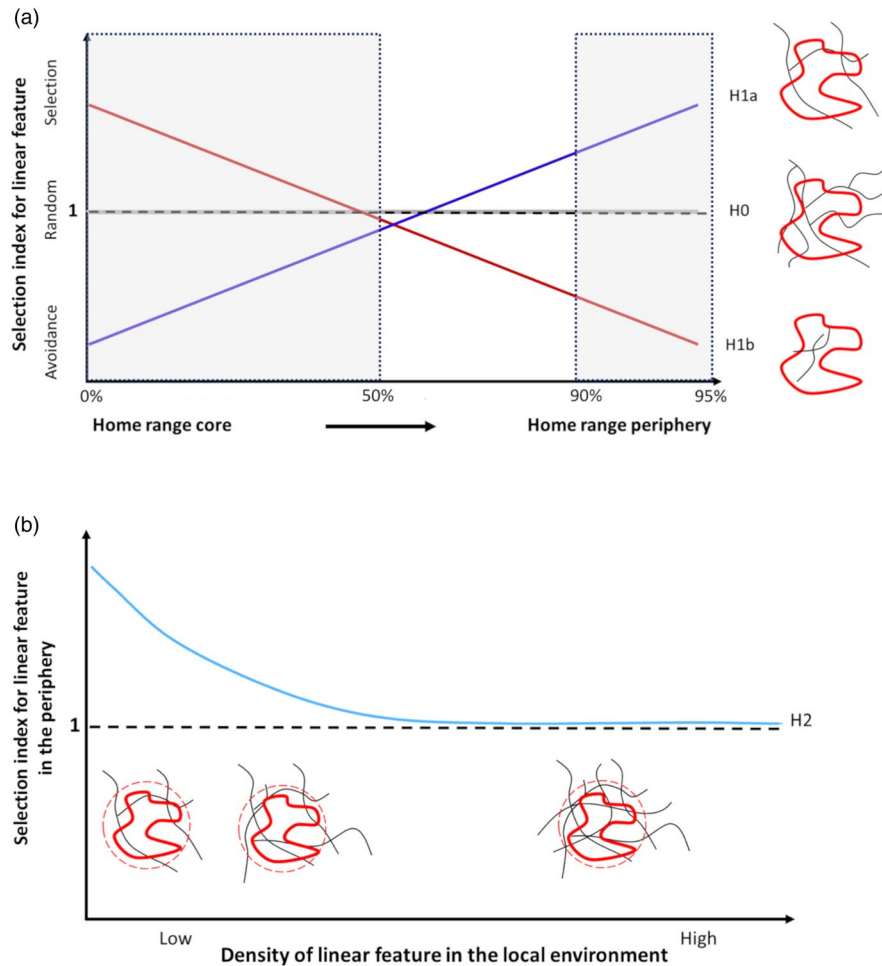
FIGURE 2 (a) Conceptualisation of how selection of linear landscape features should vary from the core to the periphery of the individual home range when these features are preferentially found at the home range periphery (H1a, blue regression line), within the home range core (H1b, red regression line) or randomly distributed across the home range (selection index of 1 along core/periphery continuum, constant grey line, H0). Home range is indicated on the right side by a red line while grey lines correspond to linear features. The grey boxes correspond to the UD percentage chosen to represent the core and the periphery of the home range. (b) Conceptualisation of how selection at the periphery of the home range for a given linear feature should vary with the density of this feature in the local area (dotted circle). We expected this selection to attenuate when the density of the linear feature increased in the local environment due to the costs of memory, but also because animals require a minimal area to live. Home range is indicated at the bottom by a red line while grey lines correspond to linear features

noted density ratio$_{95\%}$) and their density in the local area. We defined the local area for each individual as a circle centred on the home range centroid with a radius equal to the greatest width of the monthly home range at 95% (Figure 2b). The density of linear features in the local area defined by this circle was estimated for each individual and each month. This monthly approach allowed us to account for potential variation in the density of linear features in the local area related to monthly changes in animal behaviour (see also 'GPS data and home range computation' section; Holbrook et al., 2019).

We analysed the data by considering each sex and population separately. We fitted three models with the density ratio$_{95\%}$ as the response variable, and density in the local area as an explanatory variable. All the models included year, month (nested in year) and individual identity as random factors on both the intercept and the slope to account for repeated measurements of

the same individual and the same time period. We fitted the null model (i.e. no functional response, where the density ratio$_{95\%}$ is constant irrespective of the density of the linear feature in the local area), a linear model (the density ratio$_{95\%}$ varies proportionally with density of the focal linear feature in the local area) and a nonlinear model: Generalised additive mixed model (GAMM; the density ratio$_{95\%}$ varies nonlinearly with density of the focal linear feature in the local area). We used penalised regression spline type smoothers for GAMM and a Gaussian distribution. We compared these models using the Akaike information criterion with second-order adjustment (AICc) to correct for small sample bias (Burnham & Anderson, 1998) using the cAIC4 package which allows computation of the conditional AIC in mixed models estimated with both LME4 and GAMM4 packages. This metric is asymptotically equal to AIC as sample size increases (Anderson & Burnham, 2002). We ranked the three candidate models for each site, species and linear

feature combination using the difference in AICc (ΔAICc) between the focal model and the best one, as implemented in the R package aiccmodav (Mazerolle, 2020). Models with ΔAICc ≤ 2 were considered equivalent (Anderson & Burnham, 2002) and we selected the simplest model based on parsimony rules (Arnold, 2010). In preliminary analyses, we performed an analysis of deviance (ANODEV) to estimate how much of the among-population differences in density ratios of anthropogenic linear features in the periphery of the home range was explained by two measures of human pressure (namely the Human Footprint Index and the human population density; CIESIN, 2018; Tucker et al., 2018). For both LLF related to human activities (road and track), the two measures of human pressure only explained a low to moderate proportion of the among-population differences in density ratios (2.6%–12.4%) and was not detectably different from 0 (Table S5). Given this result and the low number of populations available here (nine populations, five species), we did not further investigate population-specific drivers that may explain the differences in how animal respond to or use linear landscape features. For all models, we ensured that the assumptions of normality and structure of residuals were fulfilled (Zuur et al., 2010). The R version 3.6.2 software was used for the analyses (R Core Team, 2019).

3 | RESULTS

3.1 | Influence of linear landscape features on the position of the home range core and periphery

For both sexes and across all species/populations, nearly all linear features were distributed non-randomly with respect to the individual home range, with almost identical results (90%) in males and females (Figure 3; Figures 10:18 in Supporting Information). As expected (H1a in Figure 2a; Table 2), in four species out of five, roads, tracks and valley bottoms consistently (>80%) occurred at relatively lower density in the home range core and, conversely, in relatively higher density at the home range periphery (Figure 3, see Figures 10:18 in Supporting Information for details). Female red deer were the only exception to this general pattern as most linear features were distributed evenly within their home range (but see sub-section 2 below). The numerator of the percentages above corresponds to the number of linear features across all population and sex combinations where we actually found the expected result (in the core or periphery of the home range). The denominator corresponds to the total number of linear features assessed across all population and sex combinations.
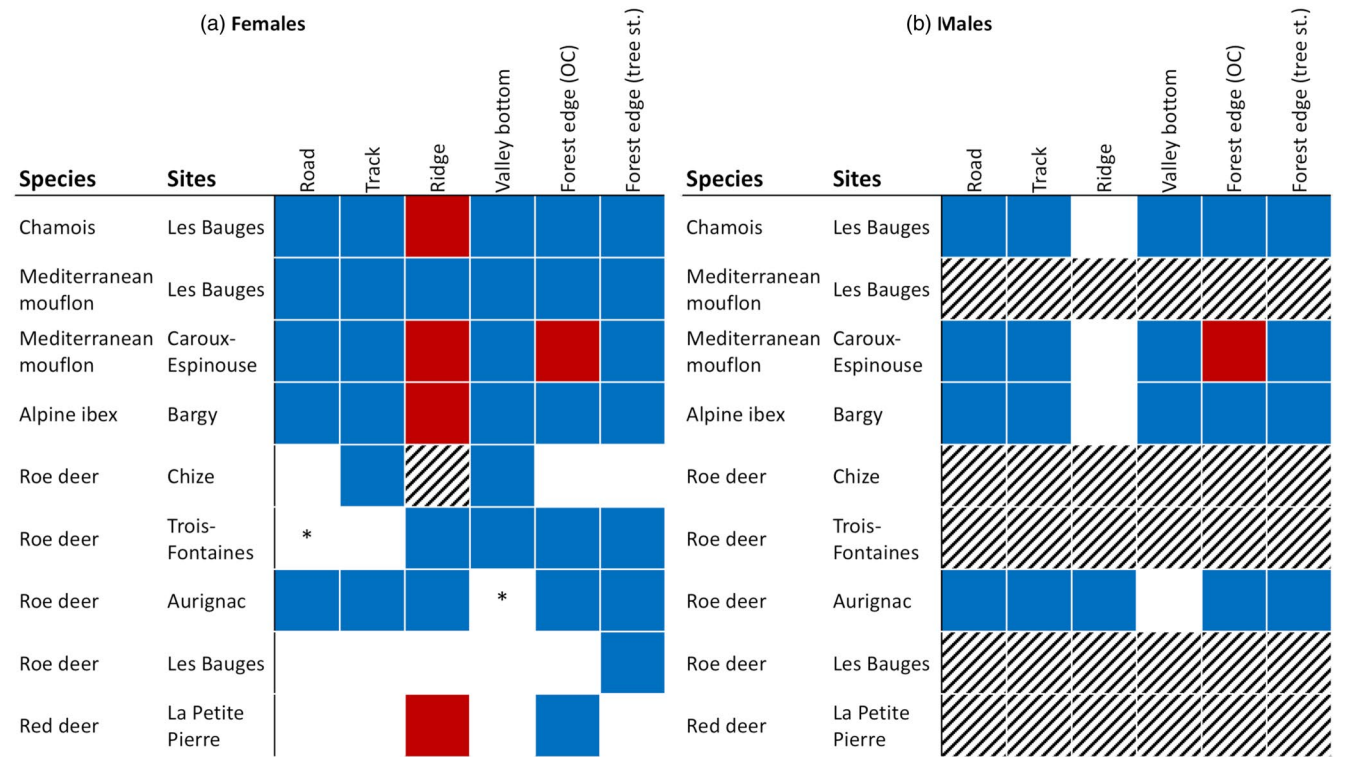

FIGURE 3 Relative position of linear features in the home range of each species and site for both sexes (a) for females and (b) for males. Hatched squares correspond to non-tested relationships, white squares correspond to an absence of selection, blue squares correspond to selection at the periphery of the home range (90%–95% segment; H1a) and red squares correspond to selection within the home range core (0%–50% segments; H1b; see Figure 2a and Figures 10:18 in Supporting Information). Squares with an asterisk indicate an equivocal pattern concerning selection of that linear feature in the home range core or periphery. Species are first ranked by habitat type (mountain vs. forest species) and body mass (from smaller to larger species; Table S1) and then by topographical complexity of the study site (from lower to higher elevation ranges; Table 1)

Contrary to our expectation (H1b in Figure 2a; Table 2), both types of edges (between open and closed habitats, and between tree stands) also tended to occur mostly at the periphery of the home range in roe deer (Figure 3). In contrast, forest edges occurred more frequently than expected in the core of the home range in mouflon of both sexes. Ridges also tended to be preferentially located within the core of the home range in females of chamois, mouflon and ibex or not selected at all for males of these species (Figure 3).

3.2 | Functional responses

When considering all combinations of sex, site and species, compared to linear models, constant or nonlinear models always better explained the relationship between the selection of linear landscape features at the home range periphery and the density of these linear features in the local landscape (Table 3; Table S3). We detected the expected functional response for many site/population/linear feature combinations. Accordingly, when a given linear feature was rare in the landscape, the difference in the density of that feature between the home range periphery and the local landscape was at its highest. In contrast, when a linear feature was widespread in the landscape, the density of that feature in the home range periphery did not differ from that in the local area. That is, selection for the feature decreased when the density of the feature in the local area increased up to some threshold density, ranging from 250 to 6,000 m of linear landscape feature per km^2 depending on sex and on the type of linear landscape feature considered (Figure 4). Above this threshold, the density ratio$_{95\%}$ of the linear feature in the home range periphery

was constant, even when the density of the feature in the local area increased (H2 in Figure 2b). As expected, the functional response for selection of a given linear feature at the home range periphery varied depending on the density of that feature in the local area for each sex-population combination. For example, in sites where the density of a linear feature in the local landscape was high, such as roads and tracks for red deer in La Petite Pierre (Figure 1; Table S2), the constant model was retained as the best model.

4 | DISCUSSION

Using a unique GPS dataset of 710 individuals encompassing five different species inhabiting contrasted environments subjected to low predation pressure by large predators, we provided a first comprehensive empirical evidence that large herbivores use linear landscape features to delimit their home range, despite the fact that they can potentially move across them (Beyer et al., 2016). We also found that the relative importance of these linear features for delimiting the home range decreased as their density in the local landscape increased. This functional response (sensu Holbrook et al., 2019) for selection of the linear feature relative to its density in the landscape was consistent in both sexes, and across all species, despite marked species-specific variation in the intensity of sexual segregation (e.g. Bonenfant et al., 2007) and in ecological requirements (e.g. Redjadj et al., 2014; reviewed in Table S1). We also suggest that both anthropogenic and natural linear features have a preponderant influence on how large herbivores perceive and use the landscape to establish their home range. These findings clearly broaden our

TABLE 3   Model selection evaluating the relationship between density ratio in the 95% section of the home range and the density of linear features in the local area, for each species, site and for both sexes. The selected models (lowest AICc, with a minimum ΔAICc of 2) are reported in the table. GAM models were selected when the density ratio$_{95\%}$ varied nonlinearly in relation to the density of the focal linear feature in the local area. Null models were selected when the density ratio$_{95\%}$ was constant irrespective of the density of the linear feature in the local area. Boxes with 'untested' correspond to linear features selected in the home range core (Figure 4). Species were first ranked by habitat type (mountain vs. forest species) and body mass (from smaller to larger species; Table S1 in Supporting Information) and then by topographic complexity of the study site (from lower to higher elevation ranges; Table 1)

| Sex	Species	Sites	Road	Track	Ridge	Valley bottom	Forest edge (OC)	Forest edge (tree st.)
F	Chamois	Les Bauges	GAMM	GAMM	*untested*	GAMM	GAMM	GAMM
	Mediterranean mouflon	Caroux-Espinouse	GAMM	GAMM	*untested*	GAMM	*untested*	Null
	Mediterranean mouflon	Les Bauges	Null	Null	Null	Null	GAMM	GAMM
	Alpine ibex	Bargy	GAMM	GAMM	*untested*	GAMM	GAMM	GAMM
	Roe deer	Chize	Null	GAMM	*untested*	GAMM	GAMM	GAMM
	Roe deer	Trois-Fontaines	Null	GAMM	Null	GAMM	Null	Null
	Roe deer	Aurignac	GAMM	GAMM	GAMM	GAMM	GAMM	GAMM
	Roe deer	Les Bauges	Null	Null	Null	GAMM	GAMM	Null
	Red deer	La Petite Pierre	Null	Null	*untested*	GAMM	GAMM	GAMM
M	Chamois	Les Bauges	Null	GAMM	*untested*	Null	GAMM	GAMM
	Mediterranean mouflon	Caroux-Espinouse	GAMM	GAMM	Null	GAMM	*untested*	Null
	Alpine ibex	Bargy	Null	Null	Null	GAMM	GAMM	GAMM
	Roe deer	Aurignac	Null	Null	GAMM	Null	GAMM	GAMM
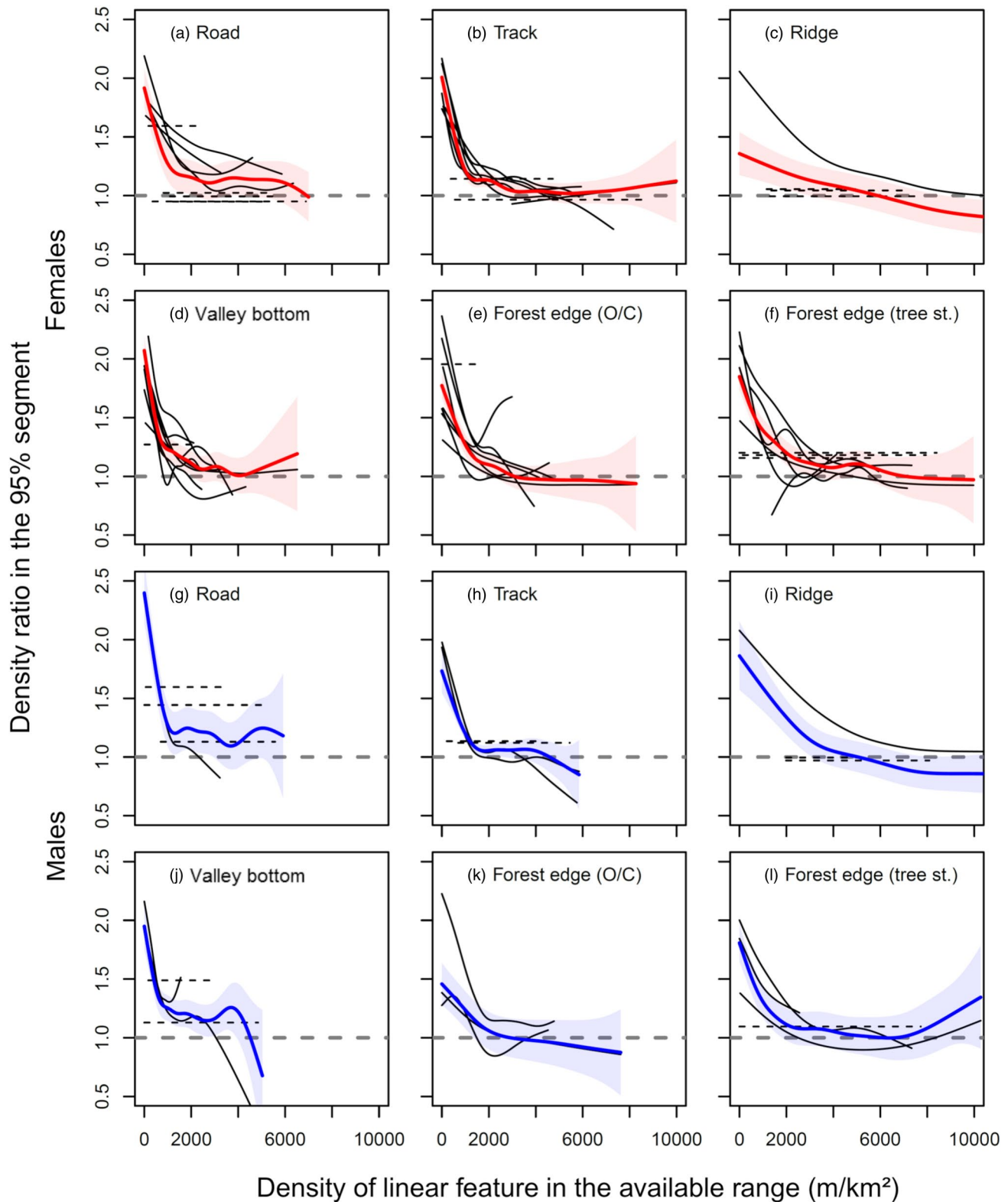
FIGURE 4 Functional responses in the selection of each linear feature in the home range periphery (density ratio in the 90-95% segment) relative to the density of each linear feature in the local area, from (a) to (f) for females and from (g) to (l) for males (see Figure 2b). The grey curves correspond to relationships between density ratios in the 90-95% segment and in the local area only for populations for which the null or gam models were selected (Table 5). The dotted lines indicate that the null model was selected, while solid lines indicate that the gam model was selected. The curve in bold represents a global model where all populations–species for a given sex and linear feature were pooled to include the entire continuum of local densities: red curves for females, blue curves for males, with year, month (nested in year), individual identity and population as random factors

knowledge about the impact of linear landscape features on animal space use since previous studies mainly focused on predators (e.g. Muhly et al., 2019; Pigeon et al., 2020), or to prey in the narrower context of habitat selection (e.g. Bonnot et al., 2013). Previous studies have also mostly been focused on anthropogenic linear features (e.g. Beyer et al., 2013; Dabros et al., 2018) while we extended here the analyses to natural anthropogenic linear features (e.g. ecotone, ridges). Our findings thus fill an important knowledge gap by providing clear evidence that functional response of large herbivores to linear features of all types consistently shape their home range position in the landscape independently of sex, habitat type or species lifestyle.

As expected, linear landscape features that may represent lethal risk (e.g. roads due to vehicle collisions, hunting activities; Padié et al., 2015; Saint-Andrieux et al., 2020), or could be perceived as risky (e.g. tracks, due to human presence for recreational activities and associated disturbances; Tablado & Jenni, 2017), were preferentially positioned at the periphery of the home range when at low density. These results contributed to highlight the overwhelming influence of human infrastructure on the behaviour of large herbivores (Ciuti et al., 2012; Moreau et al., 2012) and questioned on the wide-ranging consequences for ecosystems. In addition, the recovery of large carnivores in Europe (Chapron et al., 2014) may also potentially reshape the prey-anthropogenic features relationships. Indeed, functional responses to anthropogenic features have also been found in large carnivores which are increasing their use of these features as they become more common on the landscape (Dickie et al., 2017; McKenzie et al., 2012; Pigeon et al., 2020). In this context, prey species might suffer higher rates of mortality due to predation in areas of higher anthropogenic features (Dabros et al., 2018; Latham et al., 2011; Leblond et al., 2013) and might adapt, accordingly, the way of including such features in their home range when their density increases.

Differences in the response of individuals and populations to anthropogenic linear features may also arise from how intensively and regularly the feature is used by humans. For example, roads were over-represented in the periphery of the home range of roe deer only in the population with the highest road traffic (i.e. in Aurignac), but not in the three other populations where traffic was limited (i.e. in the enclosed populations of Chizé and Trois-Fontaines and the mountain population of Les Bauges). Unfortunately, we had no empirical measure of the intensity of use of each linear feature by humans and we were thus not able to investigate the influence of spatial variation in relative disturbance/mortality risk. Likewise, the limited number of populations and species studied here was not high enough to evaluate further the impact of variation in the intensity of human activities for explaining differences among populations or species (see e.g. Tucker et al., 2018).

Linear features that were associated with neither risk nor resources (e.g. valley bottoms; Table 2) were also preferentially found at the periphery of the home range. Hence, natural linear features and, to some extent, anthropogenic features, appear to provide spatial cues for large herbivores on which they can base their cognitive map of the limits of their home range (Benhamou, 1997). Conversely,

there was only partial support for the hypothesis that linear landscape features linked to resource availability occurred preferentially in the core of the home range. For instance, forest edges were preferentially found at the periphery of the home range in three of the four roe deer populations (Figure 3), despite the fact that this linear feature likely provides high quality food resources (Saïd & Servanty, 2005; see Table 1). This result might suggest that the role of linear landscape features as barriers to movement and/or as landmarks for delimiting the home range prevails over all other ecological functions. In line with our expectations, ridges were the only linear feature that occurred preferentially at the core of the home range in females of all mountain-dwelling species (i.e. chamois, ibex and mouflon). This can be explained by the fact that mountain ridges have complementary functions for mountain ungulates by including a high diversity of slopes and aspects that offer food resources and cover (Hamel & Côté, 2007; Marchand et al., 2014). While this result highlights the need to elucidate the multiple functions played by linear features when studying the ecological consequences of habitat fragmentation on home range extent (Gaudry et al., 2018), the contrasted responses to forest edges in the two populations of Mediterranean mouflon illustrate that the function of a given linear feature could also be context dependent. Indeed, in the low elevation range of the Caroux-Espinouse population (Table 1; Figure 3), forest edges offer both refuge and thermal shelter on one side (i.e. in the forested area) and food on the other (i.e. in open grass-rich areas; see Marchand et al., 2015) and are, therefore, preferentially found in the core home range. In contrast, the marked altitudinal gradient in Les Bauges population constrains individuals to choose between lowland forests and open highlands to limit movement costs, so that habitat edges were consequently mostly found in home range periphery for this population.

The strength of selection for a given linear landscape feature at the home range periphery depended on the density of that feature in the local landscape, indicating a functional response at the home range scale (sensu Holbrook et al., 2019). Linear features were avoided, and occurred disproportionately at the home range periphery, only when their density in the local landscape was low. When their local density was high, linear features occurred across the entire home range (Figure 4). This situation is exemplified by the red deer population, for which we found virtually no selection of linear landscape features, either in the home range core or at the periphery. This is likely because individuals in this population are unable to use linear features as efficient landmarks due to the combined effect of their very high density and the very large home ranges reported here (Table 1 in Supporting Informations). Similarly, DeMars and Boutin (2018) did not observe variation in the response of caribou to linear features, probably because these features were so densely distributed across the landscapes. These results highlight the importance of using a comparative approach (Holbrook et al., 2019) to show that the inclusion of a given linear feature in the core or in the periphery of the home range varies a lot in relation to the relative density of this feature (Figure 4). Our findings suggest that animals are unable to modify their behavioural response to linear landscape features above a certain density threshold of these features (Beyer et al., 2013), but also that small changes

in the density of linear infrastructures can have large effects on how individuals use their home range.

Our results also raise questions about the potential responses of animals to an ever-increasing density of linear features due to ongoing habitat fragmentation (Tucker et al., 2018). When the available habitat was interspersed with a high density of roads, Jerina (2012) observed smaller home range sizes in Slovenian red deer. However, animals need to include enough resources within their home range (food, cover/refuge, conspecifics/partners; Macdonald, 1983) to survive and reproduce (Burt, 1943). Given these constraints, when linear landscape features are particularly dense, an animal likely has no option to locate their home range in a way that restricts most linear features to the periphery of the range, while fulfilling its basic needs. In addition, linear landscape features may be less useful as landmarks to delineate a home range in this situation, especially as memory processes may become costly or inefficient when cues are overly complex (Fagan et al., 2013).

For all these reasons, and as supported by the consistent functional responses that we highlighted in our study (Figure 4), large herbivores could be constrained to include linear landscape features in the core of their home range, rather than only at the periphery, when linear features exceed a given density. However, functional responses may occur at multiple spatial scales: a functional response within an individual's home range might occur if the range includes a highly variable density of linear features. However, functional responses may also occur across individuals that live in habitats with a wide range of linear feature densities.

While previous studies have revealed that landscapes with high densities of anthropogenic features provide benefits to predators (Dickie et al., 2017; Muhly et al., 2019; Pigeon et al., 2020), our findings suggest that it may be different for large herbivores. The evidence found here of different functional responses to anthropogenic linear features between prey and predators contributes to fill the knowledge gap in how predators and prey use space in relation to landscape structure (DeMars & Boutin, 2018). The next step will be to link these functional responses to individual fitness. One possible approach would be to relate selection coefficients to changes in individual performance, as proposed by Matthiopoulos et al. (2016, 2019) at the population level.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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