From steps to home range formation: species-specific movement upscaling among sympatric ungulates

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Summary

1. Animals move to interact with the environment in order to find food resources and cover. Intrinsic characteristics affecting feeding and antipredatory strategies likely shape variation in movement patterns and home range formation between individuals, populations and species.
2. Browsing herbivores selectively forage on patchily distributed resources in areas with more canopy cover, whereas mixed feeders and grazers feed on more open grasslands and tend to aggregate as an antipredatory strategy. We therefore predicted that at small temporal scales, browsers will show greater net displacements (i.e. typical of searching patterns) than mixed feeders or grazers; but at larger temporal scales, we expect the opposite pattern, since gregarious species will need to use larger areas to feed the whole herd. We also predicted that the feeding/antipredatory strategy will determine the behavioural responses to other environmental factors.
3. To test this, we compared spatial movement patterns at multiple scales (from 20-min intervals to annual home ranges) of three sympatric, similar-sized, alpine ungulates which differ in their feeding/antipredatory strategy: roe deer (solitary browsers), mouflon (gregarious grazers) and chamois (intermediate feeders in smaller groups). We used location data from GPS-collared females of the three species in the French Alps.
4. As predicted, we found that multi-scale spatial patterns depended on the feeding/antipredatory strategy. Browsers foraged within smaller range areas, searching back and forth. Mixed feeders and, especially, grazers covered larger areas, presumably to satisfy herd needs. The feeding/antipredatory strategies also determined the interspecific variability in behavioural responses to factors such as maternal status, weather, habitat type or human disturbance, supporting our hypothesis.
5. Exploring interspecific variability, we showed how movement behaviour and home range formation vary substantially, even among species within the same guild. This mechanism might be important to maintain intra-guild multi-species associations and increase biodiversity, through contributing to niche segregation and, thus, coexistence.

Key-words: alpine ungulates, browser/grazer continuum, dietary and antipredatory strategy, GPS data, multi-scale movement patterns

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Introduction

Moving through space and time is one of the most direct mechanisms used by animals to interact with their environment (Jonsen, Myers & Flemming 2003; Pinaud &

Weimerskirch 2005). For non-sessile animals, movement behaviour will determine the probability of encountering food, congeners, competitors and predators, and thus, also the rate of energy acquisition, reproduction and survival (Revilla & Wiegand 2008; Morales *et al*. 2010). Individual movements depend not only on the external conditions, such as habitat composition and structure (Mysterud & Østbye 1999), climatic conditions (Gravel, Mazerolle & Villard 2012; Muldoon & Burke 2012) or topographic features (Dickson, Jenness & Beier 2005; Forester *et al*. 2007), but also on the intrinsic characteristics of animals (Forester *et al*. 2007; Ford & Fahrig 2008). That is, for example, their perception of the resources (i.e. foodscape; Searle, Hobbs & Gordon 2007) or of the risks in the landscape (Frair *et al*. 2005), their behavioural and locomotor capacity to reach food and escape predation (Kramer 2001; Lingle 2002; Wikenros *et al*. 2009) and their energetic requirements. Thus, animals are expected to differ in their response to similar environmental conditions due to their intrinsic characteristics, generating differences in movement patterns both among individuals (of different age, sex or reproductive status) and among species. This intra- and interspecific variation in movements will then translate into differences in daily, seasonal or annual range areas (Damuth 1981; Mysterud, Pérez-Barbería & Gordon 2001; Rivrud, Loe & Mysterud 2010). Mechanistic links between individual movements and home range formation have already been explored at the single-species level (e.g. Fryxell *et al*. 2008; Van Moorter *et al*. 2009; Rivrud, Loe & Mysterud 2010). In some cases, individual differences in movement patterns have been shown to lead to within-species segregation, such as sexual segregation in the case of ungulates (Ruckstuhl 1998; Ruckstuhl & Neuhaus 2002). However, to date few studies have explored the upscaling

process (i.e. from fine-scale movements to home range formation) at the interspecific level. Species-specific characteristics may lead to differences in home range formation (Douglass 1976; Mysterud, Pérez-Barbería & Gordon 2001; Le Mar & McArthur (2005); Owen-Smith, Fryxell & Merrill 2010; Buchmann *et al*. 2012), and potentially contribute to a better understanding of how space sharing occurs in multi-species communities.

Dietary diversification is one of the fundamental mechanisms defining differences among species within a community (Schoener 1974; Sinclair 1983; Demment & Van Soest 1985), especially among species of the same guild, such as large herbivores (e.g. Mysterud 2000; Prins *et al*. 2006), although a certain degree of diet overlap is common. Moreover, differing feeding strategies have been usually linked, through evolution, to specific risk-avoidance tactics (Lingle 2001; Fisher, Blomberg & Owens 2002; Caro *et al*. 2004), such as level of gregariousness and escape behaviour (Lima 1998; Caro *et al*. 2004; Cresswell & Quinn 2011; Hellström *et al*. 2011; Darmon *et al*. 2012). This link is mediated by the diet-driven use that each species makes of habitats differing in protective cover (Fig. 1a; Lingle 2001; Caro *et al*. 2004; Howery & Deliberto 2004). The interrelation of these two intrinsic species properties (i.e. gregariousness and feeding habits) has been well studied among ruminants. For example, Jarman (1974) highlighted the covariation between diet, body mass, habitat use and group sizes in African bovids. Browsers, mainly foraging on browse, forbs and fruits (Hofmann 1989; Mysterud 1998, 2000), use areas with more canopy cover, which in turn provide concealment possibilities and allow animals to reduce predation risk without needing to form groups (Jarman 1974; Hofmann 1989; Fritz & Loison 2006; Fig. 1a). On the other extreme, grazers have a diet based
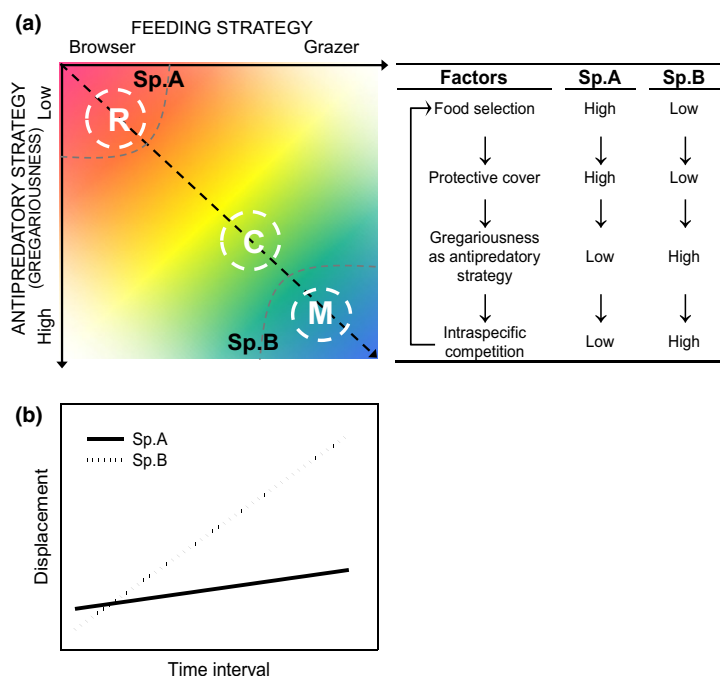

Fig. 1. (a) Conceptual scheme of the solitary browser/gregarious grazer continuum, and the factors differing between species placed at both ends of it. White circles correspond to the approximate location of the three study species (R: Roe deer, C: Chamois and M: Mouflon). (b) Hypothesis about the across-scale patterns of movement of species differing in their position on the continuum independently of body size (Sp. A: Browser and solitary and Sp. B: Grazer and gregarious).

on grasses (Hofmann 1989; Gordon 2003; Codron *et al.* 2007), which are mostly associated with wide-open areas where animals can be more easily detected by predators, forcing them to adopt a 'grouping' strategy to reduce predation risk (Hofmann & Stewart 1972; Watt, Nottingham & Young 1997; Lingle 2001; Caro *et al.* 2004; Fig. 1a).

Variation in position along the feeding/antipredatory strategy continuum (Fig. 1a) might lead to differences on movement patterns and home range formation among ungulates. Even under the same environmental conditions, the behaviour shown by each species type in order to optimize foraging and avoid predation will differ (Charnov 1976; Bergman *et al.* 2001; Searle, Thompson & Shipley 2005; Hengeveld *et al.* 2009). In this context, our aim was to investigate the effect of intrinsic feeding strategy and gregariousness level of species on movement behaviour at multiple spatial and temporal scales. To achieve this, we compared movement patterns at different scales of ecologically 'similar' species (i.e. mountain ungulates of similar sizes and, thus, *a priori* 'comparable' individual energetic requirements), coexisting within the same alpine area, but differing in their position on the feeding/antipredatory strategy continuum (Fig. 1a). We used a model system with three sympatric ungulate species: (i) a solitary browser (Roe deer, *Capreolus capreolus*), (ii) a gregarious grazer (mouflon, *Ovis gmelini musimon*) and (iii) a mixed feeder in small-sized groups (chamois, *Rupicapra rupicapra*) (*sensu* Hofmann 1989).

We hypothesized that roe deer as a selective forager, feeding mainly on patchily distributed resources (e.g. browse, forbs and fruits; Mysterud 1998; Searle & Shipley 2008), would show greater movement at smaller scales (i.e. typical of searching stages) than chamois (mixed feeder; Bertolino, Von Hardenberg & Ribetto 2000) or mouflon (mainly feeding on grasses; Marchand *et al.* 2013; Fig. 1a). However, we expected the trend to switch at large temporal scales as gregariousness becomes more important for grazers at those scales. We therefore predicted movement and range area to increase more for grazers than the other two species as we scaled up in time (Fig. 1b). That is, in aggregated species, such as grazers (Fryxell 1991; Owen-Smith 2008), the group movement dynamics and the need to satisfy the energetic requirements of the whole herd will push animals to cover larger areas than in the case of smaller groups of mixed feeders or of solitary browsers (Owen-Smith 2008; Searle & Shipley 2008; Darmon *et al.* 2012).

Additionally, since feeding habits and associated gregariousness of a species may condition their behavioural response to other factors, such as maternity, vegetation type, climatic conditions or human disturbance, we predicted that these factors would result in variation in movement patterns among browsers (roe deer), grazers (mouflon) and mixed feeders (chamois). More specifically, female ungulate browsers, which are solitary and linked to forested areas, rely more on hiding strategies to protect themselves and their offspring (Lent 1974; Fisher, Blomberg & Owens 2002), and thus, are expected to limit their

movements during risky periods, such as late gestation or early offspring life. As opposed to this, movement patterns of mixed feeders and grazers would be less affected by maternity, since they are associated with habitats that are more open and depend more on following the herd as protective technique (Richard-Hansen 1993; Langbein, Scheibe & Eichhorn 1998). We predicted species would also vary in their movement through different habitat types (i.e. forest vs. open areas), depending on whether they forage or only pass through the given habitat. Finally, we predicted grazers would be more exposed to the effects of climatic conditions and human disturbances than browsers and mixed feeders, with stronger movement responses. By examining the effects of species-specific traits (feeding regime and antipredatory strategies) on movement behaviour, our aim was to improve our knowledge of the mechanisms leading to interspecific differences in movement patterns and home range formation.

Materials and methods

STUDY AREA AND MOVEMENT DATA COLLECTION

The study was conducted in the game and wildlife national reserve of the Bauges in the French Alps (45°40′N, 6°13′E), an area of 5205 ha. It consists of a pre-alpine environment with elevations varying from 700 to 2200 m. Forests are dominated by beech *(Fagus sylvatica)* and fir *(Abies alba)*, and cover most of the area below 1500 m of elevation. The remaining 23% of the reserve consists of open grasslands and cliffs. Climate is characterized by cold winters and cool summers (0·3 °C and 16·5 °C of average, respectively). Mean annual precipitation is 1600 mm, which from November to March falls mainly as snow.

Females of three species of large herbivores coexisting in the reserve were captured through drive netting, falling nets baited with salt licks or cage traps baited with common ivy (*Hedera helix*) and bramble (*Rubus fructicosus*). They were then equipped with global positioning system (GPS) devices (i.e. Lotek GPS 3300S collars), which were later recovered through a remotely triggered drop-off mechanism. Location data were differentially corrected using post-processed correction with N4Win firmware (Lotek) based on a reference station in Strasbourg, France (48°35′N, 7°45′E). We obtained detailed information about locations of nine roe deer, 11 mouflon and 30 chamois between 2003 and 2008. Data time span of collars ranged from less than a month to 16 months, with year-round data for about 60% of the individuals. Despite variations in the frequencies at which fixes were collected, we were able to select fixes in four different time intervals, which were comparable across collars and species, that is, every 20, 40, 240 and 480 min.

STATISTICAL MODELS

In order to perform statistical tests, GPS data was used to generate seven variables characterizing animal movement patterns. That is, net displacements in metres (i.e. distance between consecutive fixes) at four time intervals (20, 40, 240 and 480 min) and range areas at daily, seasonal [i.e. winter (22 December to 20 March), spring (21 March to 20 June), summer (21 June to 22 September) or autumn (23 September to 21 December)], and annual scales. The range areas were calculated as the 95% minimum convex polygon (MCP; i.e. with 5% of the outliers being excluded from the computation) for locations falling within the same day, season or year, respectively. Since MCPs depend on sample size

(Hansteen, Andreassen & Ims 1997; Nilsen, Pedersen & Linnell 2008; Boyle *et al*. 2009), we used the same number of observations per range area scale for all individuals. For each individual, sample sizes were, thus, $n = 5$, $n = 20$ and $n = 100$ for the daily, seasonal and annual MCPs, respectively. We acknowledge that the low sample size at the daily scale might lead to an underestimation of real range area. However, to maximize the number of individuals and species included in the analyses, we had to limit sample sizes to adapt them to individuals with the lowest number of fixes available per scale (i.e. usually roe deer individuals). This was achieved by using a stratified random sampling to subsample individuals with a larger number of fixes available. Furthermore, the effect of the low sample sizes was partially compensated by the fact that fixes used in range area estimations were equally distributed throughout the entire sampling period (i.e. day, season or year) for all individuals. Some studies have shown that sampling regime might be even more important than sample size in affecting range area estimates (Börger *et al*. 2006). We used MCP instead of kernel estimators because the former performs better at low sample sizes, such as in the case of our daily ranges (Sharp 2009; Peters & Nibbelink 2011). Range area calculations were performed in the program R (version 2.11.1; R Development Core Team 2010) using package 'Adehabitat' (Calenge 2006).

Before the analyses, net displacements and MCPs were projected over a Digital Elevation Model of the area in order to calculate more realistic displacements between fixes and areas covered according to topography, given that animals move in 3-dimensional surfaces [i.e. varying in altitude according to mountains; mean slope = 35·69 (range = 1·10–72·28)], and not in a 2-dimensional planes. Turning angles were not used in this study since the bias caused by GPS errors (e.g. mean error of 24·4 m metres in our case) could lead to the overestimation of trajectory tortuosity in the species with shorter net displacements (Hurford 2009). Generalized linear mixed models (GLMMs) were used to relate variation in movement patterns at multiple temporal scales to species characteristics [see Fig. 1; i.e. solitary browsers (roe deer), gregarious grazers (mouflon) and intermediate species (chamois)]. All models were carried out using SAS PROC GLIMMIX (SAS Institute Inc., Cary, NC, USA), and their goodness-of-fit was assessed through the ratio of the obtained generalized chi-square to the degrees of freedom. Values near one imply that the model properly describes data variability (Fernandez *et al*. 2010).

Species-specific differences in movement and range areas

By combining all net displacements in one model and all MCPs in another, we investigated how net displacement and area covered varied as we scaled up in time (i.e. as the time interval of the measurements increases) for the different species. Net displacements and range area estimates were the response variables, respectively. These net displacements and range areas were summarized to the level of individual (i.e. mean value for each individual) prior to the analyses. As explanatory variables, we tested for the effect of *time* (interval of measure, i.e. 20, 40, 240 and 480 min, or daily, seasonal and annual ranges depending on the model), both linearly and curvilinearly, of *species* type [solitary browser (roe deer), mixed feeder in small groups (chamois) and gregarious grazer (mouflon)], and of the interaction of *time* and *species*. Note that the nonlinear effect of *time* tested in the first model was quadratic since net displacements at larger scales, such as the 480-min interval, are not the total cumulative net displacement, but rather the distance between two fixes separated 480 min in time. Thus, we wanted to model the possibility of net displacement at larger intervals being potentially shorter than at smaller scales, as it occurs in animals with diurnal patterns entailing coming back every day to the same areas. However, in the case of the range areas, the tested

time effect was logarithmic, to account for the fact that, as we scale up in time, area covered will reach an asymptote, but cannot decrease. In order to control for the non-independence of GPS data, in both models, we used three random factors: *collar*, to consider autocorrelation of data within individuals, *group*, to account for correlations among animals within a group, and *year*, to control for random inter-annual variability. Groups were defined within each year as individuals of the same species with range areas (i.e. calculated with all data available per individual) overlapping by at least two-thirds (66%). Individuals were never in more than one group. This factor is especially important in mixed feeders and grazers, whose higher level of gregariousness could have resulted in some marked individuals moving together at least for some time, thus, having non-independent movement patterns, or individuals moving within the same area, and thus, showing spatial correlation. These two models best fit using a log-normal distribution.

Species-dependent movement response to environment and maternal status

We performed seven additional GLMMs to investigate, at each specific time-scale, how the species characteristics [solitary browsers (roe deer), mixed feeders in small groups (chamois) and gregarious grazers (mouflon)] affect species-specific behavioural responses to certain reproductive and environmental conditions. Each model had as the dependent variable one of the seven movements measures (i.e. 20-, 40-, 240- and 480-min net displacements, and daily, seasonal and annual MCPs), which were best fitted by the log-normal distribution (Table 1). Prior to these analyses, net displacements were averaged by day within individuals. The non-independence of the GPS data was also accounted for in all models of this section by incorporating random factors (i.e. collar, group and year) according to the scale of each model (Table 1).

The reproductive and environmental conditions examined were the *maternal status*, *period of the year*, *vegetation*, weather conditions and human *disturbance*. The *maternal status* was categorized as breeding females (three roe deer, 20 chamois and seven mouflons) vs. non-breeding females (six roe deer, eight chamois and two mouflons), named as 'lactating' vs. 'non-lactating', respectively. The status of two chamois and two mouflon females was unknown, and therefore, their data were not included in these models. We used 'lactating', rather than 'breeding' or 'reproducing', to emphasize our focus on the period of the reproduction including parental care and late gestation, in which we expect substantial changes in movement behaviour. We chose to classify *period of the year* in only two levels (spring/summer (i.e. when calving takes place) vs. autumn/winter) despite the fact that we lose some detailed information on temporal variations, because we aimed at using a rather simple variable that was easily generalizable to all species and which allowed for straightforward three-way interactions.

Local *vegetation* was incorporated as the proportion of localizations per day that fell within forested habitat (as opposed to open grasslands). Data needed to calculate this proportion were obtained from raster maps of the National Office of Game and Wildlife of France and of Le Bauges Natural Regional Park. Climatic values were provided by meteorological stations near our study area through Météo-France. Weather conditions examined were *Snow depth* and relative temperatures (*rel_temp*). The latter variable was calculated as the difference between the temperature at a given day and the seasonal mean (i.e. the average of the calendar season to which that day belongs). This measure of temperature was meant to inform us about the behaviour of animals in days abnormally hot or cold for the given period and it was approximated in this way to eliminate its potential correlation with other variables such as *snow depth* or *period of the year*,

which would lead to problems of multi-collinearity. Human *disturbance* was categorized as weekends vs. weekdays, as an approximation of high vs. low levels of recreation, respectively.

More specifically, the GLMMs examining how net displacements of each species (i.e. at 20-, 40-, 240- and 480-min intervals) vary according to the context included simultaneously, as explanatory variables, the *species* type, *maternal status*, *period of the year*, local *vegetation*, linear and quadratic influence of *snow depth* and temperature (*rel_temp*), and human *disturbance*. In order to truly examine the species-specific response to these previous factors, we also included the two-way interactions between *species* and *vegetation, species* and *disturbance, species* and the linear and quadratic term of *rel_temp* and *snow depth,* and the three-way interaction among *species*, *maternal status* and *period of the year* (Table 1).

In the models examining variation in size of range areas depending on species-specific response to environmental and maternal conditions, we tested for the effect of the same variables as in the previous net displacement models. However, we had to do some modifications due to the scale differences (Table 1). *Vegetation* was adjusted for each scale as the proportion of the total number of localizations within a given daily, seasonal or annual range area that were found in forested habitat. At the scale of season, we also removed the effect of *disturbance* (weekend or weekday), and the impact of weather was evaluated through *mean_temp* (i.e. average temperature in each calendar season), *snow change* and their respective interactions with *species* type. *Snow change* was approximated by one factor with two categories: 'High change' to describe seasons including the first or last snows of the year as observed in the meteorological data of this area (i.e. usually spring and autumn) and 'Low change' for the other seasons (summer and winter). Snow conditions were characterized as such in order to decouple the potential correlation between temperature and snow. In addition, we aimed to emphasize in a simple way, which allowed for interactions, periods that may be perceived by animals as strong environmental changes (start or end of harsh conditions), and might potentially trigger vertical migrations in mountains as those described for mouflons (Djind-jieva 2009). Finally, at the annual level, and given the small sample size available (Table 1), we were only able to test the effect of *species*, *maternal status*, the interaction between them, *vegetation*, and weather, which again had to be adjusted and was included as mean annual temperature (*mean_temp*) and mean annual snow depth (*mean_snow depth*).

Results

SPECIES-SPECIFIC MOVEMENT PATTERNS AND RANGE AREAS AT DIFFERENT TEMPORAL SCALES

We found significant differences among ungulate species in movement patterns across scales, as shown by the significant interaction between *species* and *time* interval (Fig. 2). That is, as we scale up in *time,* net displacements increase more in chamois and, especially, in mouflons than in roe deer (Fig. 2, Left; $N = 196$; *species*, $F_{2,142} = 2\cdot10$, $P = 0\cdot1259$; *time,* $F_{1,142} = 495\cdot12$, $P < 0\cdot0001$; *time*^{2}, $F_{1,142} = 207\cdot13$, $P < 0\cdot0001$; *species*time*, $F_{2,142} = 39\cdot44$, $P < 0\cdot0001$), and the same applies to the size of the range area at multiple scales (Fig. 2, Right; $N = 124$; *species,* $F_{2,73} = 19\cdot69$, $P < 0\cdot0001$; *log(time),* $F_{1,73} = 2003\cdot01$, $P < 0\cdot0001$; *species*log(time)*, $F_{2,73} = 19\cdot79$, $P = 0\cdot0049$). That is, even though small-scale net displacements are similar for all three species, as we increase in temporal scale, the net displacements and area covered by mouflons become significantly larger than those travelled by chamois and roe deer (Fig. 2).

SPECIES-SPECIFIC RESPONSES TO ENVIRONMENTAL FACTORS AND REPRODUCTIVE STATUS

Intrinsic differences among the three ungulates resulted in species-specific movement responses to factors such as *maternal status*, *vegetation cover*, weather and human *disturbance* in a consistent way across scales. Net displacements and MCPs of mouflons and chamois did not differ substantially between *period of the year* or *maternal status* (Table 1; Figs 3a and 4a,b), while the spatial behaviour of roe deer females changed between periods of the year depending on whether they were breeding or not. Female roe deer having calves in a given year (i.e. lactating) showed much smaller net displacements and range areas than non-lactating ones, but only during the spring/summer period (Figs 3a and 4a, b). Species movement patterns also depended on vegetation (Table 1; Fig. 3b). At small temporal scales, net displacements of mouflon and chamois increase in forested areas contrary to roe deer (Fig. 3b). Similar trends are maintained at the daily MCPs (Fig. 4c), with roe deer range areas decreasing and mouflon ranges increasing as the proportion of forest localizations increased. However, at larger seasonal scales, the interaction between *species* and *vegetation* became non-significant (Table 1).

The three species also showed differences in their response to climatic conditions (Table 1; Figs 3c,d and 4d, e,f), although the effects were only significant at larger scales, as seen by the significant interaction between *species* and the linear or quadratic terms of *rel_temp* and *snow depth* at those scales (Table 1). Net displacements of mouflons and chamois seemed to be more affected by weather conditions than those of roe deer, with net displacements of the two former species significantly increasing with temperature and decreasing with snow depth (Fig. 3c,d). Daily MCPs also reflected differences in the behaviour of the species in response to climatic variables (Fig. 4d). Mouflons showed a strong quadratic response to temperature, not observed in chamois and roe deer, by reducing their range areas in especially cold or hot days. While snow depth had a slightly positive effect on roe deer daily MCPs, the other two species responded to snow depth with a more negative trend, especially the chamois (Fig. 4e). At seasonal and annual scales, temperatures (*mean_temp*) did not seem to affect range areas significantly (Table 1). Regarding the effect of *snow change*, seasonal MCPs of only chamois and mouflon increased significantly in seasons involving first or last snows of the year (i.e. spring and autumn) compared to the other two seasons (Table 1, Fig. 4f). Finally, species also responded differently to human disturbance (Table 1; Fig. 3e), although this interaction became significant only at small scales (i.e. 20- and 40-min intervals). Mouflon and chamois showed greater net displacements per interval at the weekends than during

Table 1. Determinants of ungulate spatial patterns at different scales, from 20-min intervals to annual home ranges. The size of the time intervals for the net displacement models is defined by the minutes between GPS fixes (i.e. 20′, 40′, 240′ and 480′). Non-significant factors are denoted by 'ns'

	Net displacement[†]							
	20′ (N = 5017)[§]		40′ (N = 4954)[§]		240′ (N = 2015)[§]		480′ (N = 2006)[§]	
	Estimate ± SE	*P*-value	Estimate ± SE	*P*-value	Estimate ± SE	*P*-value	Estimate ± SE	*P*-value
Intercept	4·09 ± 0·11		4·41 ± 0·14		5·51 ± 0·14		5·93 ± 0·22	
Species	ns			0·026		0·0002		<0·0001
Roe deer			−0·66 ± 0·23		−0·68 ± 0·25		−1·47 ± 0·30	
Chamois			−0·28 ± 0·15		−0·22 ± 0·16		−0·40 ± 0·24	
Mouflon			0		0		0	
Maternal status	ns		ns		ns		ns	
Lactating								
Non-lactating								
Period of the year	ns		ns		ns		ns	
Spring/summer								
Autumn/winter								
Vegetation	0·56 ± 0·071	<0·0001	0·51 ± 0·09	<0·0001	ns		ns	
Rel_temp	ns		ns		ns		0·011 ± 0·01	0·0338
Rel_temp²	ns		ns		ns		ns	
Snow depth	ns		ns		ns		ns	
Snow depth²	−0·0002 ± 0·0002	0·038	ns		ns		ns	
Disturbance		<0·0001		<0·0001	ns		ns	
Week day	−0·35 ± 0·05		−0·50 ± 0·062					
Weekend	0		0					
Species*maternal status*period of the year	Fig. 3	0·0030	Fig. 3	0·0168	Fig. 3	0·0002	Fig. 3	<0·0001
Species*vegetation	Fig. 3	0·0002	Fig. 3	0·0008	Fig. 3	0·003	ns	
Species*rel_temp	ns		ns		Fig. 3	0·013	ns	
Species*rel_temp²	ns		ns		ns		ns	
Species*snow depth	ns		ns		Fig. 3	0·013	Fig. 3	<0·0001
Species*snow depth²	ns		ns		ns		Fig. 3	0·0009
Species*disturbance	Fig. 3	0·011	Fig. 3	0·0002	ns		ns	

[†]Distribution = log-normal; link function = identity; random factors = collar+group+year.
[‡]Distribution = log-normal; link function = identity; random factors = group.
[§]Note that these represent total raw sample sizes, but in mixed models the effective sample sizes are much smaller lying somewhere between the total sample sizes and the number of clusters determined by the random factors (Snijders & Bosker 2012).

week days; however, roe deer did not show this significant variation with disturbance.

Discussion

Our findings about the interspecific variability in movement behaviour were consistent with: (i) the predicted role of feeding/antipredatory strategy in influencing variation in movement patterns across scales (Fig. 1), and (ii) in the behavioural responses to maternal and environmental conditions. As predicted, as we scale up in time, net displacement and area covered increased more strongly in the social species (mouflon and chamois) than in the solitary one (roe deer). The more solitary condition of browsers, like roe deer in our study area, allows them to optimally forage by concentrating their movements in smaller areas (i.e. going back and forth and selecting higher quality food items; Damuth 1981; Fryxell 1995; Owen-Smith 2008), due to the lower intraspecific competition. In contrast, mixed feeders (e.g. chamois) and especially grazers (e.g. mouflon), which, due to their association with open grasslands, group in larger herds as antipredatory strategy (Fryxell 1991; Owen-Smith 2008), are likely subject to higher local intraspecific competition and faster decline of local resources. Thus, they are forced to keep moving and use larger areas (i.e. greater home ranges) in order to meet the requirements of the whole herd (Charnov 1976; Damuth 1981; Fryxell 1995; Gower *et al.* 2008). These findings agree with Coppolillo (2000), who observed that in agro-pastoral systems, cattle in larger groups tended to walk

Table 1. (continued)

	Range areas							
	Day† (N = 1201)‡			Season† (N = 137)‡			Annual‡ (N = 30)‡	
	Estimate ± SE	P-value		Estimate ± SE	P-value		Estimate ± SE	P-value
Intercept	10·56 ± 0·53			15·91 ± 1·15			15·42 ± 1·87	
Species		<0·0001	Species		<0·0001	Species		0·030
Browser	−2·62 ± 0·74		Roe deer	−5·32 ± 1·46		Roe deer	−3·54 ± 0·68	
Mixed	−1·02 ± 0·59		Chamois	−2·83 ± 1·24		Chamois	−1·75 ± 0·45	
Grazer	0		Mouflon	0		Mouflon	0	
Maternal status	ns		Maternal status		0·0002	Maternal status	ns	
Lactating			Lactating	−0·45 ± 0·57		Lactating		
Non-lactating			Non-lactating	0		Non-lactating		
Period of the year	ns		Period of the year	ns				
Spring/summer			Spring/summer					
Autumn/winter			Autumn/winter					
Vegetation	ns		Vegetation	0·06 ± 0·88	0·0037	Vegetation	ns	
Rel_temp	ns		Mean_temp	ns		Mean_temp	ns	
Rel_temp^2	−0·018 ± 0·005	0·0002						
Snow depth	ns		Snow change	ns		Mean_snow depth	ns	
Snow depth^2	ns		High (spring and autumn)					
Disturbance	ns		Low (summer and winter)					
Week day								
Weekend								
Species*maternal status*period of the year	Fig. 4	<0·0001	Species*maternal status*Period of the year	Fig. 4	<0·0001	Species*maternal status	ns	
Species*vegetation	Fig. 4	0·0028	Species*vegetation	ns				
Species*rel_temp	Fig. 4	0·0093	Species*mean_temp	ns				
Species*rel_temp^2	Fig. 4	0·0198						
Species*snow depth	Fig. 4	0·0022	Species*snow change	Fig. 4	0·0137			
Species*snow depth^2	ns							
Species*disturbance	ns							

farther from home than smaller herds. Interestingly, although we expected that browsers would show greater net displacement at smaller temporal scales (Mysterud 1998; Searle & Shipley 2008), we did not observe significant differences among species at the lowest scale (i.e. 20-min net displacement). This result could be due to 20-min intervals not being sufficiently small to detect fine-scale browser movements or to high-quality resources being abundant in our study forest for roe deer. Non-foraging activities, such as mouflon local migrations, could also be partly obscuring the overall effect of foraging strategies on fine-scale movements.

Our results also support our hypothesis that dissimilarities in movement patterns among browsers, grazers and mixed feeders will be further emphasized by their differen-tial behavioural response to maternity and environmental factors (i.e. vegetation cover, weather and disturbance). The three-way interaction among species, period of the year, and maternal status was maintained across scales. Net displacements and range areas of lactating browser females were much smaller during the spring/summer period than outside it, while this difference was not observed in non-lactating females or in lactating females of the other two species. This could be the consequence of different antipredatory and maternal care tactics usually used by each species. Solitary ungulate browsers, such as roe deer, use hiding techniques in late gestation period and early off-spring life (Lent 1974; Fisher, Blomberg & Owens 2002), restricting foraging movements to areas around the place where offspring remains concealed (San Jose & Lovari
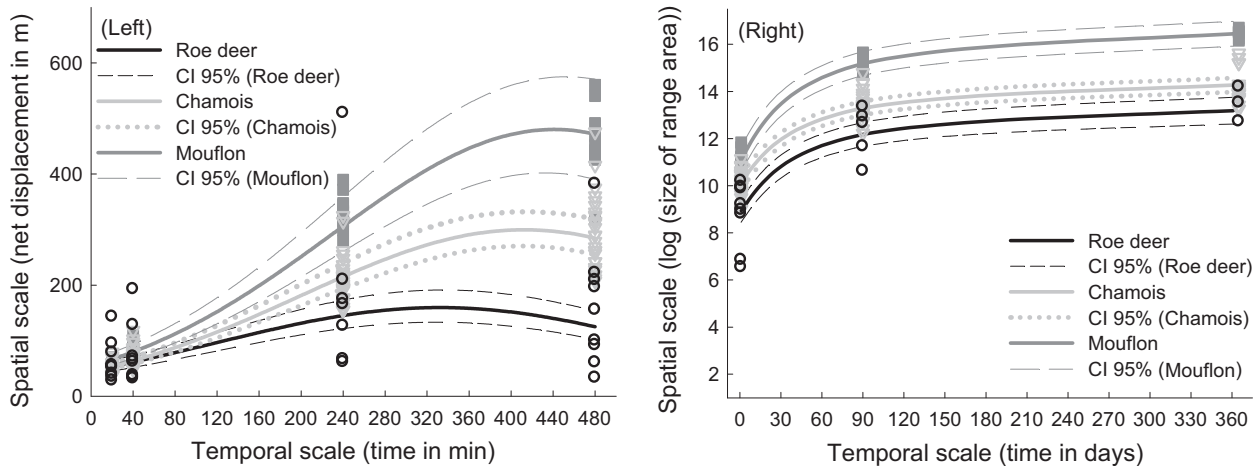
Fig. 2. Across-scale spatial trends of ungulates species varying their position in the browser/grazer continuum. (Left) Increase in net displacement with time for the three species. (Right) Changes in range areas (log) of the different species from daily to annual scale. Lines represent the outcome (mean and 95% CI) of the models, while symbols correspond to raw observations (i.e. mean values per individual and interval).

1998; Long *et al.* 2009). Thus, net displacements and range areas of breeding browser females during spring/summer period (i.e. including late gestation, offspring early life) become, on average, lower than in the autumn/winter period. Contrary to this, herbivores which feed in more open areas, and thus, are more gregarious, such as mouflons and chamois, tend to adopt a 'follower' strategy as protection, meaning that offspring remain with their mothers and mingle into the social groups (Richard-Hansen 1993; Langbein, Scheibe & Eichhorn 1998). Female spatial behaviour in grazers and mixed feeders is, thereby, less affected by the presence of the young or pregnancy and continues to depend on overall herd movements. It could be argued that the intra-annual variation in roe deer spatial behaviour is because this species is an income breeder, and thus, more sensitive to changes in food resources across seasons (Andersen *et al.* 2000; Toïgo *et al.* 2006). However, the fact that this response is not seen in non-lactating females of the same species suggests that observed intra-annual differences are more related to maternity.

As expected, vegetation cover also affected movements of the three species in different ways. Grazers and mixed feeders had lower net displacement in more open areas than in forested ones, as opposed to browsers that showed the opposite trend, with decreased net displacements and range areas in the forest. Mouflons and chamois, being grazers and mixed feeders, respectively, tend to forage more in open or semi-open grasslands (Hofmann 1989; Redjadj 2010; Darmon *et al.* 2012), and use forest patches mostly to move among foraging sites, whereas browsers like roe deer forage more selectively in wooded areas or forest edges (Hofmann 1989; Tixier 1996; Saïd *et al.* 2005), thus reducing their searching/foraging pace within those habitats. This effect on browsers could be also related to the relationship between increasing habitat quality and decreasing home range size, as already shown for several browsing species (Tufto, Andersen & Linnell 1996; Relyea,

Lawrence & Demarais 2000; Dussault *et al.* 2005; Saïd *et al.* 2005). Higher proportions of forest provide not only shelter and protection but also better forage for browsers, allowing them to reduce their range areas.

Our findings also confirm our predictions that browsers, grazers and mixed feeders differed in their response to weather conditions. Mixed feeders and grazers responded more strongly than browsers to changes in temperature. Increases in relative temperature led to greater net displacements in the former two species, as opposed to browsers, whose trends were slightly negative. In addition, mouflons substantially decreased their daily range area in days particularly cold or hot. This was not observed in the other two species and is consistent with the findings of Bourgoin *et al.* (2011), based on activity data. This pattern could be due to mixed feeders and grazers being more exposed to thermal stress since they forage more in open areas, while browsers may be partially sheltered by their use of habitats with canopy cover (Mysterud & Østbye 1999; Bourgoin *et al.* 2011). Additionally, in this particular case, the stronger spatial response of mouflons to temperature could also be partially explained by the fact that chamois and roe deer are native species, well adapted to extreme alpine environments (Randi, Pierpaoli & Danilkin 1998; Schaschl *et al.* 2003), while the mouflon is an introduced species (De Beaufort 1970; Cugnasse & Houssin 1993), originally inhabiting areas with milder temperatures (e.g. Corsica, Marcos-Carcavilla *et al.* 2009). The grazer and mixed feeder species also differed from the browser in their response to snow depth. While the association between snow depth and roe deer net displacements and daily range area tended to be slightly positive, chamois and mouflon showed a decrease in net displacements and daily range area as response to snow depth. These differences among species were also observed at larger scales, with seasons including snow arrival (autumn) and melting (spring) resulting in significantly larger seasonal range areas in grazer and mixed feeders but not in browsers.
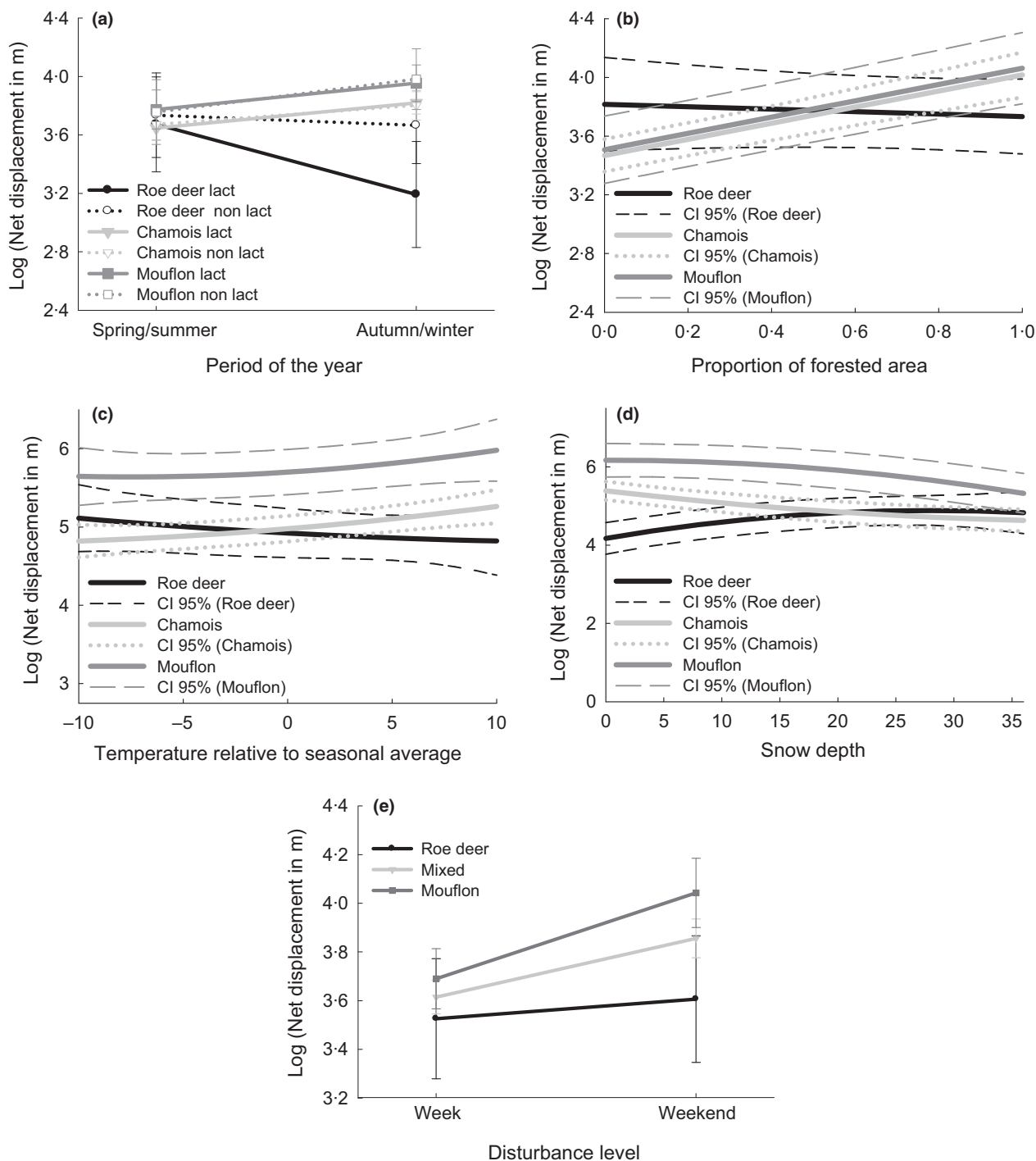
Fig. 3. Factors, other than species type, determining net displacement according to the results of the GLMMs (estimated averages and 95% CI in log scale for comparison purposes). (a) Influence on net displacement of the three-way interactions among species type, maternal status (lactating or not) and period of the year. (b) Movement of each type of species according to vegetation. (c) Interaction between species type and daily relative temperature, and (d) between species type and snow depth. (e) Effect of human disturbance on the movement of the different species. To avoid figure redundancy, and since the trends are maintained across scales, we only represented the 20-min-displacement case. This scale allows us to further focus on the effect of factors other than species, since at the 20-min interval level the differences among species are less marked (Fig. 2; Table 1). Since the interaction of species type with temperature and snow was not significant at the lowest scales, they had to be graphed using the 240-min scale.

The presence of snow causes higher heterogeneity in the distribution and availability of resources (Jenkins & Wright 1988; Heard 1992; Post & Stenseth 1999), forcing animals to increase net displacements and searching time in order to reach suitable forage. However, deep snow levels limit resource availability and accessibility to certain areas which may restrain animal large-scale displacements and daily range areas (Telfer & Kelsall 1984; Fancy & White 1987;
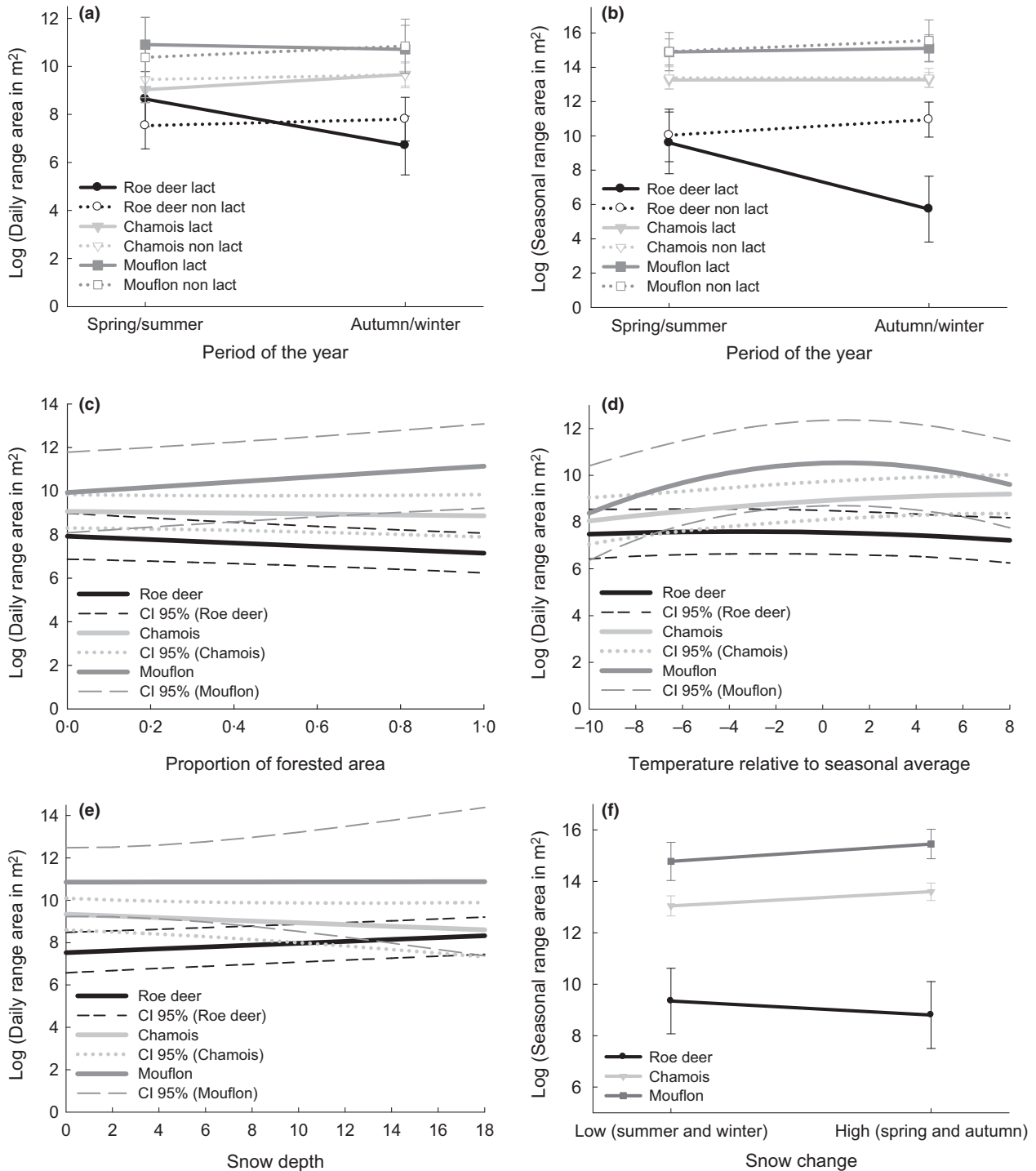
Fig. 4. Effects and interactions determining size of range areas in different alpine ungulates. Range area values represent GLMM estimated averages and 95% CI (expressed as logarithms, for comparison's sake). Daily (a) and seasonal (b) range areas of browsers, mixed feeders and grazers according to their maternal status and period of the year. (c) Effect of proportion of fixes located in forested areas on daily ranges. (d) Interaction between daily relative temperature and species type. Species-specific spatial response to snow conditions, that is, (e) daily range areas according to daily snow depth, and (f) seasonal range areas in seasons entailing low or high changes in snow cover. 'High changes' meaning snow arrival or snow melting periods (i.e. autumn and spring), and 'Low changes' representing the other two calendar seasons.

Luccarini *et al*. 2006). The latter effect is especially important for mouflons and chamois, since snow accumulation in open grasslands is usually higher than in forest (D'Eon 2004; Varhola *et al*. 2010). At the same time, deeper snow might motivate grazers and mixed feeders to perform local migrations to completely avoid certain areas during winter, which would explain the larger range areas observed in this species during the seasons including snow arrival and melting (i.e. autumn and spring; Bertolino, Von Hardenberg & Ribetto 2000; Bourgoin 2008).

Finally, in a similar way, we found that the grazer and mixed feeder species were more sensitive to disturbance by humans than the browser, probably because they tend to forage in open areas where the presence of humans can be more obvious. That is, mouflon and chamois showed greater net displacement on weekends than week days. This effect was not significant for roe deer, which may perceive less strongly the presence of humans within the forest or use 'hiding' instead of 'escaping' as a protective strategy (Lazarus & Symonds 1992; Mysterud 1996). Interestingly, the observed human-induced increases in net displacement were only significant at the smallest scales. These findings agree with previous studies relating more 'erratic' behaviours (i.e. less directional) to human disturbance (Brillinger *et al.* 2001; Bejder *et al.* 2006). This implies that, although the effect of human disturbance may go unnoticed at large temporal scales (i.e. home ranges), increases in tourism may have important consequences for energetic budgets of ungulates, especially those relying more on open habitats.

Other factors, such as individual body size, were not included in this study because we did not aim to examine the influence of individual traits but rather focus on differences among species. We did not include predation pressure as a potential driver of ungulate movement either because during the study period there were no natural predators of adult ungulates in the area. We are aware that this lack of predators might seem inconsistent with our purpose of studying the effect of diet-driven antipredatory gregariousness. However, the link between predation and social aggregation is the result of a process in evolutionary time, and it is unlikely that temporary absence of predators produces significant changes in that relationship (Farr 1975; Byers 1997; Caro *et al.* 2004). This is supported by studies such as that of Darmon *et al.* (2007), which showed that social structure of mouflons in our same study area is highly stable over time, or that of Byers (1997), about the maintenance of certain antipredatory adaptations even thousands of years after the disappearance of co-evolving predators. Moreover, our study area is subjected to substantial recreational disturbance, which has been suggested to be perceived by animals as a potential predation risk (Frid & Dill 2002; Beale & Monaghan 2004), and thus, could be acting as an additional force in maintaining antipredatory adaptations.

In conclusion, examining interspecific variability at different temporal scales, we revealed the role of the feeding/antipredatory strategy, both directly and through its interaction with other factors, in determining movement patterns and home range formation in three sympatric herbivore species and ecologically 'similar' alpine species. We recognize that a sample of three species in a single area is not sufficient to make strong generalizations about other species or circumstances. However, to our knowledge, this is the first time that detailed spatial data have been obtained simultaneously for multiple ungulate species sharing the same landscape and environmental conditions, and we believe that the clear patterns shown here are a good first step in that direction. Future studies should try to extend these hypotheses, either empirically, theoretically, or through meta-analyses, to other herbivore communities and systems with different food spatial distributions. Moreover, the implications of the patterns observed for the coexistence of species should be further investigated, since species-specific movement response and home range formation are likely to result in niche segregation among species, allowing sympatry of multiple species of the same guild. These types of studies will help us to further understand the mechanisms leading to species space use and coexistence, and to predict the responses of species and communities to future global change.

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Data accessibility

Data for this paper are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.qd73b (Tablado *et al.* 2015).

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