

# Partial migration in roe deer: migratory and resident tactics are end points of a behavioural gradient determined by ecological factors

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Ungulate populations exhibiting partial migration present a unique opportunity to explore the causes of the general phenomenon of migration. The European roe deer *Capreolus capreolus* is particularly suited for such studies due to a wide distribution range and a high level of ecological plasticity. In this study we undertook a comparative analysis of roe deer GPS location data from a representative set of European ecosystems available within the EURODEER collaborative project. We aimed at evaluating the ecological factors affecting migration tactic (i.e. occurrence) and pattern (i.e. timing, residence time, number of migratory trips). Migration occurrence varied between and within populations and depended on winter severity and topographic variability. Spring migrations were highly synchronous, while the timing of autumn migrations varied widely between regions, individuals and sexes. Overall, roe deer were faithful to their summer ranges, especially males. In the absence of extreme and predictable winter conditions, roe deer seemed to migrate opportunistically, in response to a tradeoff between the costs of residence in spatially separated ranges and the costs of migratory movements. Animals performed numerous trips between winter and summer ranges which depended on factors influencing the costs of movement such as between-range distance, slope and habitat openness. Our results support the idea that migration encompasses a behavioural continuum, with one-trip migration and residence as its end points, while commuting and multi-trip migration with short residence times in seasonal ranges are intermediate tactics. We believe that a full understanding of the variation in tactics of temporal separation in habitat use will provide important insights on migration and the factors that influence its prevalence.

The ecology of movement has been recently recognised as a unifying paradigm in ecological research, where the identification of a movement phase or a movement mode helps clarify the interactions between individuals, and the surrounding ecosystem (Nathan et al. 2008). In turn, recent research has investigated how individual movement behaviour affects (and determines) population distribution (Turchin 1998, Mueller and Fagan 2008, Morales et al. 2010). Migrations are among the most studied movement patterns (Dingle and Drake 2007). The observation and analytical modelling of the individual-based, behavioural process of migration has been spurred on by the recent advances in tracking technologies (Alerstam 2006, Jonsen et al. 2006, Cagnacci et al. 2010, Hebblewhite and Haydon 2010). Migrations also have obvious

consequences on population structure and dynamics (Taylor and Taylor 1977, Cheke and Tratalos 2007).

However, unifying definitions of migration have not been set, despite the numerous studies (Drake and Gatehouse 1995, Dingle 1996, Berthold et al. 2003, Holland et al. 2006). Dingle and Drake (2007) summarise and define a variety of migration patterns which have been described in the literature. Of these, partial migration, i.e. when one fraction of the population is migratory, while the other remains resident, either in the breeding or non-breeding area (see also Lundberg 1988), has attracted much attention among researchers (Chapman et al. 2011). Contrasting measures of performance from migrant and non-migrant individuals offers the opportunity to empirically evaluate the adaptive

significance of migration (Lundberg 1988, Nicholson et al. 1997). In fact, in long-lived vertebrates, migration can be seen as a tactic to enhance lifetime reproductive success, which in turn is a combination of survivorship (access to food, escape from predators, avoidance of risky environmental conditions) and birth rate (Fryxell and Sinclair 1988). As such, migration is presumably driven by changes in habitat suitability in time (e.g. seasons) and space, and can be seen as movements that allow animals to exploit temporary resources (Dingle and Drake 2007). When seasonal habitat suitability is highly variable through time, but not extreme, and some form of density dependence exists, then partial migration may evolve (Lundberg 1988, Taylor and Norris 2007). Very high variability of habitat suitability in time and space should favour migration as a 'direct, proximate' response to the deterioration of local conditions (Dingle and Drake 2007), whereas stable periodicity of habitat suitability should lead to seasonal cue-driven migration (Sabine et al. 2002). Habitat instability can therefore lead to animals migrating only in certain years or late in the season, for a short period or with several migratory trips for given individuals (Nelson 1995, Nicholson et al. 1997, Sabine et al. 2002, Fieberg et al. 2008). This behaviour is known as 'facultative migration' (Dingle and Drake 2007; 'conditional migration' has also been used to describe the same phenomenon).

When resources satisfying different needs are variable 'in space', e.g. very patchy, but relatively constant over time, we expect home ranges to comprise spatially separated resource patches, and animals to 'commute' between them, sensu Dingle and Drake (2007). This behaviour is a de facto example of third order habitat selection, i.e. within the home range (sensu Johnson 1980).

When resources are variable 'in space and time' (i.e. spatially separated patches constitute a suitable resource discontinuously, e.g. seasonally), commuting behaviour may become discontinuous, or opportunistic. Moreover, if travelling to these separated patches implies a trade-off in terms of survival (e.g. for energetic travelling costs, or exposure to predators; Nicholson et al. 1997), commuting may turn into prolonged, uninterrupted phases of residence in these patches, that if they extend over a season, can be considered as 'seasonal' migration (shift in use of habitat, Dingle 1996). Under this view, the distinction between third order habitat selection, commuting behaviour and seasonal migration (including partial and facultative migration) are rather unclear. Ball et al. (2001) underlined that migration is better viewed as a continuous phenomenon, where 'resident' and 'migrant' are the end points of a behavioural gradient. Dingle and Drake (2007) encouraged investigations of migratory adaptations beyond the 'extremes', such as, for example, facultative migration, since this could reveal tradeoffs between migration and alternative adaptive strategies.

The European roe deer *Capreolus capreolus* is a small, solitary cervid species, with a high degree of behavioural plasticity (Jepsen and Topping 2004), and a rather peculiar combination of life history traits among large herbivores of temperate areas. Indeed, this species has a relatively short generation time (Gaillard et al. 2008), is situated close to the income breeder end of the energy allocation tactic continuum (Andersen et al. 2000), shows a limited degree of sexual size dimorphism and presents two clear physiologically and behaviourally

distinct phases of the annual cycle, with birth, territoriality and rutting concentrated between May and August throughout its range (Hewison et al. 1998, Sempéré et al. 1998). Seasonal migrations, including partial migrations, have been observed in northern environments (Wahlström and Liberg 1995, Danilkin and Hewison 1996, Mysterud 1999) and in the Alps (Ramanzin et al. 2007), where some individuals also behaved as facultative migrators. Overall, a range of tactics in seasonal space use have been described in these studies. However, surprisingly for one of the most widely and intensively studied large mammal species in the world, little formal analysis has been devoted to this important aspect of its behaviour. In particular, insights can be obtained by contrasting space use strategies in populations living under very different climatic and ecological conditions. The roe deer is particularly suited for such studies due to its wide distribution range in the temperate region (Andersen et al. 1998) and since detailed GPS data are available from a number of contrasting study sites across this range due to the existence of a data set repository which has recently been set up at the European scale (EURODEER; Fondazione E. Mach Trento, Italy: < www.eurodeer.org >).

In this study, we analysed year-round GPS location data of roe deer from five contrasting study areas representing different climatic conditions, from the harsh winters of Scandinavia to the mild sub-Mediterranean climate of southern France. First, we quantified the degree of separation of seasonal ranges 'in space and time'. Then, we investigated what criteria could be used to discriminate between migrators and commuters, and therefore describe the migratory continuum. Finally, we analysed the impact of climatic (snow) and topographic (slope) factors, as well as sex, on the onset and patterns of migration, starting from the following set of expected results.

In cervids, seasonal migration is often triggered by snow cover, or snow depth, or snow quality (e.g. mule deer *Odocoileus hemionus*: Nicholson et al. 1997; white-tailed deer *Odocoileus virginianus*: Sabine et al. 2002, Brinkman et al. 2005, Fieberg et al. 2008; moose *Alces alces*: Ball et al. 2001; roe deer: Mysterud 1999), since it influences both the availability of food and the cost of locomotion. However, a large variability has been observed in the responses of different species and populations in terms of migration pattern (e.g. timing, duration, number of trips between ranges). We expected to observe migration in roe deer in areas with persistent snow cover, with partial and/or opportunistic migrations prevailing in less predictable climates. Moreover, we expected a direct relationship between the locomotion costs of migration and the probability of a single-trip migration, particularly given the small size of this cervid (allometric effect on costs of movement: White and Seymour 2005).

In several species of cervids, including roe deer, different patterns of migration have been observed between the sexes, but this is highly variable (e.g. only female mule deer showed partial migration, while males were obligatory migrators: Nicholson et al. 1997; a higher proportion of migrators and longer migration distances were observed in female roe deer than in males: Mysterud 1999, but this was not observed by Ramanzin et al. 2007; no sex effect recorded in white tailed deer: Van Deelen et al. 1998). The low sexual

size dimorphism in roe deer leads to the expectation of similar costs and benefits of migration in both sexes.

Overall, we expected the marked ecological plasticity of roe deer to be mirrored by similarly marked variation in migratory behaviour, both in terms of occurrence (migration tactic) and space use (migration pattern).

## Methods

### Study areas and datasets

This study was based on a database maintained by the collaborative EURODEER project (<www.eurodeer.org>, accessed on 15 April 2011), i.e. a data sharing project that stores and manages roe deer data sets from across this species distribution range, involving 18 research groups from nine European countries. In particular, this repository includes more than 1 000 000 GPS locations from 354 marked individuals in 13 study sites from seven countries. For this study, we selected macro-regions that represent the range of conditions under which most roe deer occur in Europe, and where a suitable sample was available (we excluded data from reintroduction projects or with a small sample of individuals). Study areas, sample sizes and GPS collar models are shown in Table 1: Bavarian Forest, data from Bavarian Forest National Park (site 1: average coordinates: 49°00'57"N, 13°39'99"E; central European sub-mountainous forest; 650–1450 m a.s.l.); southern France, Coteaux de Gascogne, data from French National Inst. for Agricultural Research (INRA) (site 2: average coordinates: 43°32'21"N, 00°82'47"E; hilly agricultural landscape with fragmented oak woodland; altitude <400 m a.s.l.); Italian eastern Alps, Trentino province, data from Fondazione Edmund Mach (site 3: average coordinates: 46°03'27"N, 11°02'11"E; Alpine mountain range from 400 to 1600 m a.s.l.); southern Scandinavia, two sites, data from Swedish Univ. of Agricultural Sciences (SLU), Norwegian Inst. for Nature Research (NINA), and Univ. of Oslo (UoO) (site 4: NINA-UoO, average coordinates: 60°73'15"N, 08°60'09"E; hilly area dominated by boreal forest in valleys and tundra at higher elevations, extending above the treeline; 200–1000 m a.s.l.; site 5: SLU, average coordinates: 58°10'96"N, 12°40'78"E; mainly flat boreal forest (70%) with some arable land and pastures (20%); 70–200 m a.s.l.). GPS data collection spanned from 2002 to 2011 and concerned 88 individuals (Table 1), with a total number of 88 760 locations. For each animal, we retained only one sampling year to avoid individual autocorrelation

(average sampling duration:  $324.68 \pm 5.32$  days). Daily frequency of localisation was not more than 6 (i.e. one fix every four hours), and this was the case for 21% of locations in the data set used; otherwise, inter-fix interval was six h for 32% of the data (i.e. four fixes day<sup>-1</sup>), and eight h for 32% of the data (i.e. three fixes day<sup>-1</sup>); all other fixes were at a longer interval (from 12 to 24 h), mainly due to missing fixes. Due to this slight imbalance in sampling design of animal trajectories, only those summary parameters which can be considered independent from data density (within the above limits) were calculated.

GPS data were organised in a PostgreSQL 8.4.1 + PostGIS 1.5.2 (<www.postgresql.org/; http://postgis.refractor.net/>) spatial data base, as described in Cagnacci and Urbano (2008) and Urbano et al. (2010). GPS data were related to climatic and geographic variables from remote sensing sources, with a raster based automated procedure (Table 2). Snow cover was derived from the MODIS MOD10A2 eight-day composite maximum snow extent data at level V005 (data downloaded from NASA WIST, <https://wist.echo.nasa.gov>). If snow cover was found for at least one day in the interval of eight considered, the cell was indicated as 'snow'. Using this eight-day compositing technique, the impact of clouds is minimized (Riggs et al. 2003). The data were processed in GRASS GIS (Neteler 2005) and snow presence/absence data extracted for the EURODEER GPS fixes.

### Data analysis

#### *Migrant and resident individuals*

We defined migration as a clear shift of an individual between non-overlapping ranges or habitats at a seasonal temporal scale (Dingle 1996), regardless of the actual Euclidian distance between those ranges. Pragmatically, we defined 'migration' as the process involving the shift of individuals between non-overlapping ranges ('spatial separation') and, ultimately, some stabilisation in each range ('temporal separation'). We analysed the GPS locations of individuals to ascertain the occurrence of seasonal partial migration within our roe deer populations using an adaptive data-mining procedure. Our sample units were individuals or, for patterns of migration, individual trajectories in a given season. With a conservative approach, we considered individuals as migrants when 1) they were not fawns (not to confound migration with natal dispersal), 2) a movement between non-overlapping ranges was observed (i.e. spatial separation: individuals used non-overlapping ranges), 3) each range was continuously and solely used for a period of time (i.e. 'temporal separation' in space use), and 4) return

Table 1. Sample size, proportion of migratory individuals and migratory trajectory parameters in each study area.

Study site	GPS collar brand and model	Period of reference	Migrant individuals (m-f)	Resident individuals (m-f)	Mean no. transitions in migratory traj.	Mean Euclidean distance (m) of migratory traj.
Bavarian Forest	Vectronic Aersospace Gmbh, GPS Plus 1	2006–2009	7 (4-3)	8 (5-3)	$5.36 \pm 1.64$	$2754.27 \pm 670.78$
Southwest France	Lotek 3300, revision 2	2002–2008	3 (1-2)	21 (11-10)	$9.5 \pm 8.5$	$2752.75 \pm 954.91$
Italian Alps	Vectronic Aersospace Gmbh, GPS Plus 1	2005–2008	11 (4-7)	10 (3-7)	$2.04 \pm 0.33$	$2776.26 \pm 213.86$
Norway	Vectronic Aersospace Gmbh, GPS Pro-light	2008–2011	7 (3-4)	8 (3-5)	$1.83 \pm 0.67$	$13876.25 \pm 2004.58$
Southern Sweden	Vectronic Aersospace Gmbh, GPS Plus 1	2007–2010	0	13 (7-5)	–	–

Table 2. Climatic and geographic variables associated with the EURODEER GPS locations and used in the analyses.

Variable	Source	Resolution	Website
Landuse (forest cover)	EEA-Corine Landcover (CLC) 2000 (Forest: CLC 311, 312, 313, 323, 324; no forest: all others, except urban areas and inland water)	vector, raster 100 m	< <a href="http://www.eea.europa.eu/data-and-maps/data/corine-land-cover-2000-2006">www.eea.europa.eu/data-and-maps/data/corine-land-cover-2000-2006</a> >
Altitude (m a.s.l.)/ Slope (0-45°)	<60°N: CGIAR-DEM/SRTM <sup>1</sup> >60°N: NASA –ASTER relative DEM <sup>2</sup>	90 m 30 m	< <a href="http://srtm.csi.cgiar.org">http://srtm.csi.cgiar.org</a> > < <a href="http://asterweb.jpl.nasa.gov/content/03_data/01_Data_Products/release_DEM_relative.htm">http://asterweb.jpl.nasa.gov/content/03_data/01_Data_Products/release_DEM_relative.htm</a> >
Snow cover (presence/8day)	NASA-MODIS snow <sup>3</sup>	500 m	< <a href="http://modis-snow-ice.gsfc.nasa.gov/MOD10A2.html">http://modis-snow-ice.gsfc.nasa.gov/MOD10A2.html</a> >

<sup>1</sup>Jarvis et al. 2008

<sup>2</sup>Hirano et al. 2003

<sup>3</sup>Hall et al. 2002

movements between ranges were observed. We considered individuals as residents in all other cases.

**Spatial separation: non-overlapping ranges definition (clustering)**

We applied a supervised clustering procedure (SAS 9.2, PROC CLUSTER) to identify non-overlapping ranges of individuals: we plotted the spatial distribution of fixes in GIS software, and we counted the number of non-overlapping clusters (1 to 2). We used the method by Ward (1963) to minimize the within-cluster sum-of-squares and each fix was assigned to a given cluster  $i$  ( $i = 1, 2$ ). We then refined the definition of each cluster to remove outlying fixes by distinguishing between locations within the cluster and excursions outside of the cluster itself using the following procedure. We considered the average distance of each fix from the nearest 10 fixes ( $d_{near}$ ) and the average distance among all fixes in a cluster  $i$  ( $d_{all}$ ) and its standard deviation  $s_{all}$ . If  $d_{near} \leq d_{all} + s_{all}$ , we considered the fix as part of the cluster  $i$  (assigned a cluster code of  $i$ ), otherwise, the value 0 was assigned. A fix with code 0 therefore represented a spatial outlier.

When more than one cluster was used by an animal, we defined each cluster  $i$  as a ‘summer’ or ‘winter’ cluster. We computed the average date of fixes for each cluster  $i$  (Fisher 1993) and compared it to the 15 July (assumed to be the peak of the summer period): the summer clusters were those temporally closer to the 15 July, whereas winter clusters were all others. Migration movements were therefore studied as transitions between summer and winter clusters.

**Migration movements (‘shifts’) and season definition**

We determined migration movements by considering the temporal sequence of fixes, and their cluster code. We distinguished three types of fix sequence: a) movements within the same cluster, i.e. sequences of fixes with the same cluster code (e.g. movement within cluster 1: 1→1→1; or movement within cluster 2: 2→2→2); b) excursions outside the perimeter of a given cluster, i.e. sequences of fixes with a single cluster code alternating with spatial outliers (e.g. movement from cluster 1 to outliers, and back: 1→0→0→1); c) shifts between ranges, i.e. sequences of fixes with different cluster codes (e.g. movement between cluster 1 and 2: 1→2; or, movement between cluster 1 and 2, with two fixes between clusters: 1→0→0→2); shifts are obviously directional and can be from winter to summer clusters, or vice versa. We therefore defined two seasons of transition: ‘spring’, starting on 15 February and recording transitions between

winter and summer clusters, and ‘autumn’, starting on 15 September and recording transitions between summer and winter clusters. The starting date for spring is somewhat early to ensure that the earliest spring migrations in the most southern areas are not missed, given the very different climatic conditions across Europe at this time of year.

**Temporal separation: residence time, selection of migratory individuals and definition of migration trajectories**

For individuals with separated spatial ranges, we calculated the maximum residence time, i.e. the longest period of time when an animal occupied continuously (and solely) a given (winter or summer) range (i.e. residence time in days: sequences of type a) and b), scaling them as proportions of one year (Fig. 1). We graphically distinguished different groups of animals, and, in particular, we compared the position of females

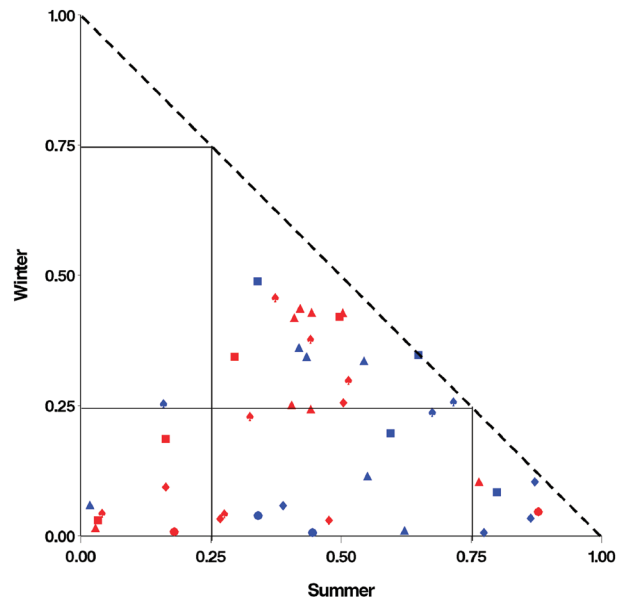


Figure 1. Maximum residence time (i.e. the maximum continuous period of residence) of migrant roe deer individuals in winter (y-axis) and summer (x-axis) ranges, expressed as a proportion of the whole year. The dashed line represents the limit of possible values (maximum residence time in winter and summer ranges combined sums to one year). Blue symbols: males; red symbols: females. Squares: Bavarian Forest; diamonds: southwest France; triangles: Italian Alps; spades: Norway; circles: southern Sweden.

and males on the graph by using a bivariate test computed by SAS 9.2. PROC GLM, MANOVA statement (SAS Inc. 2010); a useful discussion on the use of the Hotelling test can be found in Batschelet (1981). We then considered the frequency distribution of residence times, i.e. 'all' periods of 'at least' two days spent continuously (and solely) by animals within a given range, and compared them across sites (Fig. 2). We used the average individual residence time as a threshold value to ascertain 1) actual temporal separation in range use (and therefore to discriminate between migrant and resident individuals) and 2) stabilisation of migratory trajectories:

1) among individuals presenting a spatial separation between ranges, only those with a maximum residence time in 'each' range of 'at least' the population average residence time were retained as migrants. Importantly, all others were designated as resident individuals. For this reason, the approach we used to ascertain the occurrence of seasonal partial migration was an 'adaptive' data-mining procedure based on clustering (i.e. spatial separation of ranges combined with an evaluation of actual temporal separation in range use);

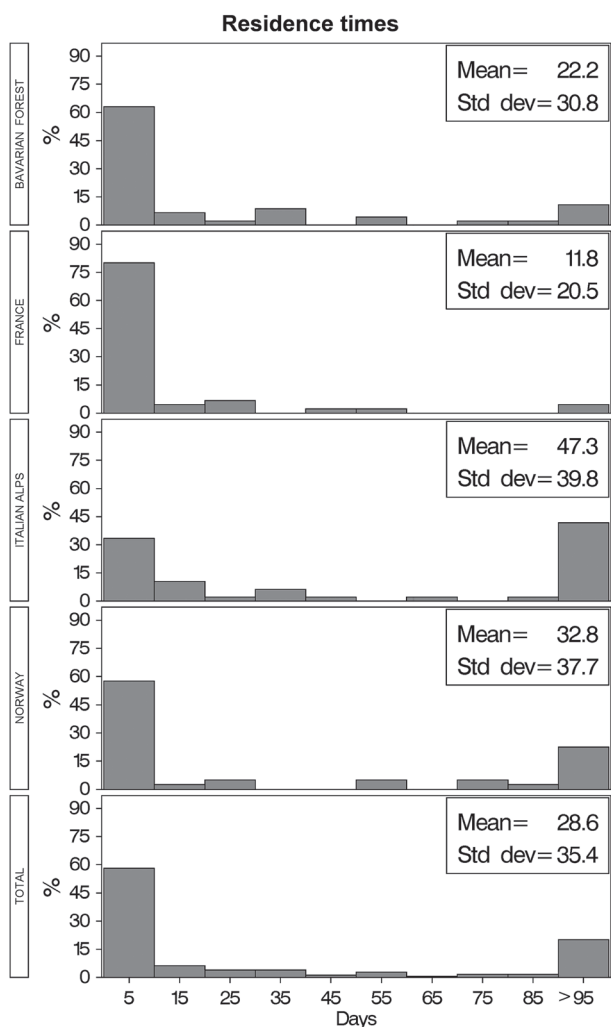


Figure 2. Frequency distribution of the duration of residence (i.e. continuous periods of residence) of all migrant individuals, both in winter and summer ranges, for each study area (except Sweden, where no migrations were recorded), as well as averaged across areas. Residence periods of 1 day or less were not included.

2) in each season of transition, we assessed individual migratory trajectories as sequences of fixes including migratory movements between seasonal ranges (sequences of type c). Since not all individuals presented 'one-hop' migrations, i.e. with only one migratory shift between ranges, but moved several times back and forth between ranges before stabilising, we defined the migratory trajectory as follows: in each season of transition, the sequence of fixes starting with the first shift between seasonal ranges, and finishing with the last seasonal shift before stabilising for a period of time 'equal to or greater than' the population average residence time as obtained from Fig. 2. The duration of these trajectories could therefore potentially vary from a few hours or days ('one-hop' migrations between ranges, e.g., movement between range 1 and 2, with one fix between clusters: 1→0→2→2→2), to weeks or months ('multi-hop' migrations, e.g. movement between cluster 1 and 2, followed by return to cluster 1, followed by return to cluster 2, to then stabilise in cluster 2: 1→0→2→1→2→2→2).

### Timing of migration

For each migrant individual (defined as above), we calculated the average timing of migration from winter to summer range, and vice versa, as the average of all range shifts in that direction (sequence of type c). Timing of migration was then averaged by site (Fig. 4), sex (Fig. 3b), and over the whole dataset (Fig. 3a). Timing of migration across different sampling years was necessarily represented as a circular variable, where a year is represented on the trigonometric circle with a phase of 365 and the 1 January at 0 radian. Using this approach, a date is an angle  $\alpha$ . The average date of a set of dates (as, for example, the average timing of migration) is therefore the average of a set of angles  $\alpha_1, \alpha_2, \dots$ , defined as a vector of angle  $\theta$  (the average angle) and length  $\rho$  with a value between 0 and 1.  $\rho$  is inversely proportional to the standard deviation of angles and expresses the synchrony among dates: if all dates (and angles) are the same (i.e.  $\alpha_1 = \alpha_2 = \dots$ ) then  $\rho = 1$ ; conversely, if dates (and angles) are distributed at random, then  $\rho = 0$ .

Differences in timing of migrations were compared across study areas and sexes using the Watson-William test (Batschelet 1981), using 5000 bootstrap simulations (Fisher 1993).

### Factors affecting migration, and the pattern of migration

Migration trajectories (i.e. sequences of fixes between the first seasonal range shift and the last before stabilisation in the seasonal range, as defined above) were compared with similar sequences of fixes in resident individuals (i.e. animals with only one cluster and hence no migratory movements). Trajectories of non-migrants were defined as the sequence of fixes comprised between the average initial date of migration and the average final date of migration for that population.

In study areas where no migrations were observed, we used the average dates calculated on the total data set.

For trajectories of both migrants and residents, we summarised climatic and geographic variables associated with each fix as those in Table 2 (presence of snow cover; presence of forest cover; average slope) and calculated the Euclidean distance between the first and last fixes of the trajectory. The binomial variable 'presence of snow' indicates presence of snow cover at the time of any one fix of the trajectory. The binomial variable 'presence of forest' was determined as follows: for all trajectories in a given population, we calculated

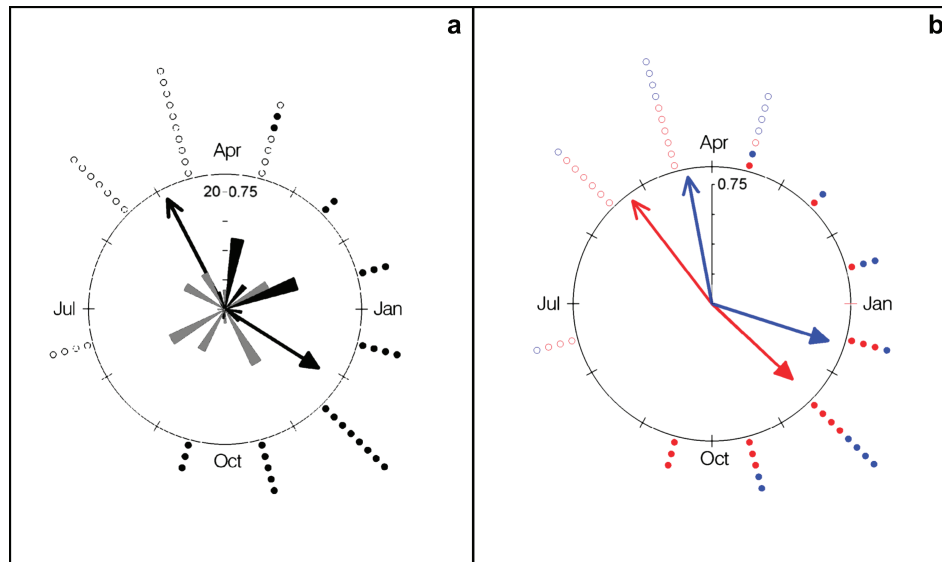


Figure 3. Timing of migrations in roe deer pooled across sample areas in Europe (panel a, grey and black), and pooled across sample areas in Europe, but classified by sex (panel b, red and blue). Goniometric circles represent the year (months to be read anti-clock wise, from January to December). Panel a: dots indicate the individual average time of migration from winter to summer ranges (open dots) and from summer to winter ranges (filled dots). Arrows point to the average migration date across the population, in spring-summer (open headed arrow) and in autumn-winter (closed headed arrow). The length of the arrow ( $\rho$ , from 0 to 1) is inversely proportional to the standard deviation of migration dates among individuals, therefore indicating the degree of migration synchrony among individuals (high  $\rho$ , long arrow = high degree of synchrony). Triangles within the goniometric circle represent the circular histogram of the frequency distribution of excursion movements (i.e. those movements that did not result in the animal reaching a second range) originating from summer ranges (grey bars) and from winter ranges (black bars). Values are expressed as a percentage of all excursions throughout the year. Panel b: symbols as in panel a except: blue dots and arrows: males; red dots and arrows: females.

the proportion of fixes with forest cover, as well as the overall median. All values greater than the median were assigned a value of 1; all values lower than the median were assigned a value of 0.

We analysed factors affecting partial migration in roe deer populations by modelling the effect of sex, season, snow cover, presence of forest and slope on the occurrence of migration (i.e. on trajectories of both migrant and resident individuals). In particular, we fitted a generalized linear mixed model (GLMM) with binomial error distribution to a full model that included the additive factors listed above, including the interaction snow  $\times$  slope  $\times$  season, as fixed factors, and study area as a random factor (Table 3). For migration trajectories only, we analysed factors affecting the pattern of migration by modelling the effect of sex, season, snow cover, presence of forest, slope and Euclidean distance on the occurrence of a single trip ('one-hop') migration. In particular, we fitted a generalized linear mixed model (GLMM) with binomial error distribution to a full model that included the additive factors listed above, including the interaction snow  $\times$  slope, as fixed factors and study area as a random factor. By co-plotting the response variables and the groups of predictor variables we observed that the interaction between snow, slope and season was especially informative. Individual identity was not included as a random factor since only one year's monitoring per individual was retained in order to analyse a balanced dataset. All linear analyses were run in R (ver. 2.9.1: R Development Core Team 2009, lme4 R package: Bates and Maechler 2009).

Response variables were modelled for dependence on predictor variables using the model selection procedure based on the Akaike information criterion (AIC) (Burnham and

Anderson 2002). We calculated AIC values corrected for small sample size ( $AIC_c$ ) for all possible models derived from the a priori full model and ranked the models according to  $AIC_c$  values. From the differences in  $AIC_c$  values ( $\Delta AIC_c$ ), we calculated  $AIC_c$  weights ( $\omega$ ) and relative evidence ratios. When  $\Delta AIC_c < 4$  (relative likelihood  $< 0.135$ ), we evaluated parameter estimates by model averaging, also computing predictor weights (Burnham and Anderson 2002). To improve reliability, given the large number of models included within this cut-off, we also reassessed AIC in 999 bootstrap simulations per model, searching for the most robust model evaluations. The list of averaged models and corresponding parameters, including the proportion of bootstrap simulations in which they obtained the lowest AIC, are reported in Appendix 1.  $R^2$  of the average mixed models was calculated as the average sum of the rate between the variance of each model and the total variance.

## Results

### Spatial and temporal separation of ranges: definition of migratory individuals

Out of the 87 individuals from five study areas considered in the analysis, we identified 42 individuals with non-overlapping seasonal ranges. For each individual, we calculated the maximum residence time in its winter and summer range and plotted these as proportions of the whole year (Fig. 1). Note that Fig. 1 should not to be read as an X–Y chart of independent versus dependent variables, but rather as a bivariate distribution plot (i.e. seasonal maximum residence times), where

Table 3. Parameter estimates using model averaging to describe the seasonal migration of *C. capreolus* in Europe. Estimates were obtained from generalized linear mixed models with a binomial distribution of errors. Model selection was based on the Akaike information criterion corrected for small sample sizes (AIC<sub>c</sub>). The full a priori model is given, with parameters estimated by model averaging, based on a cut-off of relative likelihood of model *i* versus the 'best' model of about 0.15 ( $\Delta\text{AIC}_c \approx 4$ , evidence ratios  $\approx 7$ ). Models describe (a) the occurrence of migration, (b) the occurrence of direct (i.e. one-hop) migration trajectories between seasonal ranges (migrant individuals only).

Full model	N <sup>f</sup>	N. averaged models	R <sup>2</sup>	Coefficients	Estimate mean $\pm$ SE	Confidence intervals	Predictor weight
Migration $\sim$ snow <sup>a</sup> $\times$ slope <sup>b</sup> $\times$ season <sup>c</sup> + forest <sup>d</sup> + sex + (1 studies)	154	17	0.31	intercept	$-3.07 \pm 1.15$	$-5.37; -0.77$	–
				snow $\times$ slope $\times$ season	–	–	0.00
				snow $\times$ slope	$6.83 \pm 2.21$	2.40; 11.26	0.60
				snow $\times$ season (wint)	$-1.22 \pm 0.15$	$-1.51; -0.92$	0.17
				slope $\times$ season (wint)	$-0.67 \pm 0.12$	0.42; 0.91	0.03
				snow	$-0.87 \pm 1.17$	$-3.20; 1.46$	0.80
				slope	$5.14 \pm 2.36$	0.41; 9.87	0.95
				season (wint)	$-0.07 \pm 0.29$	$-0.65; 0.50$	0.42
				forest	$1.36 \pm 0.55$	0.25; 2.47	0.93
Direct trajectory $\sim$ snow <sup>a</sup> $\times$ slope <sup>b</sup> + season <sup>c</sup> + forest <sup>d</sup> + sex + distance <sup>e</sup> + (1 studies)	50	13	0.33	intercept	$-9.9 \pm 3.63$	$-17.16; -2.65$	–
				snow $\times$ slope	–	–	0.00
				snow	$0.23 \pm 0.10$	0.03; 0.43	0.13
				slope	$4.52 \pm 1.5$	1.52; 7.52	0.49
				season (wint)	$-0.13 \pm 0.07$	$-0.27; 0.02$	0.10
				forest	$-1.49 \pm 0.60$	$-2.69; -0.28$	0.75
				sex (male)	$-0.96 \pm 0.26$	$-1.49; -0.43$	0.32
				distance	$1.30 \pm 0.46$	0.37; 2.22	1.00

<sup>a</sup>presence of snow cover along the migratory trajectory

<sup>b</sup>mean slope along the migratory trajectory, arcsine transformed

<sup>c</sup>seasons of transitions, starting on 15 February (spring-summer) and 15 September (autumn-winter)

<sup>d</sup>presence of forest cover along the migratory trajectory; all values above the median of all trajectories were set to 1; 0 otherwise

<sup>e</sup>Euclidean distance between first and last point of the migratory trajectory, log transformed

<sup>f</sup>sample size

both X and Y are dependent variables. This representation is useful for clarifying the pattern of contrasting use of non-overlapping ranges by different individuals:

The dashed line in the graph represents the limit of possible values, since the maximum residence time in winter and summer ranges combined cannot exceed one year. In this case (i.e. sum = 1), the animal would stay continuously in one range, then move very fast (< 1 day) to the second one and immediately 'stabilise' there. This was actually the case for one individual in the Bavarian Forest.

All points below the dashed line do not sum to 1.0, meaning that the continuous periods of residence in one range were interrupted by several shifts to the other range (or by a migratory shift lasting several days).

Moreover, we identified the following 'patterns' of use of non-overlapping ranges:

#### Pattern 1

All individuals within the central triangle of the graph had a long maximum residence time in both winter and summer ranges (i.e. between one and three quarters of the year: values = 0.25–0.75). They all showed a similar use of non-overlapping ranges: they were stable in one range for a long continuous period, then shifted a few times between ranges, before finally stabilising again in the second range. These animals could therefore be considered as performing a 'classical' migration, showing a clear spatial 'and' temporal separation in range use.

#### Pattern 2

All individuals below the central triangle stayed continuously in the winter range for less than a quarter of the year. Mov-

ing from values of 1.0 to 0.0 along the horizontal axis, these individuals spent a decreasing length of time as residents in the summer range.

In particular, individuals within the small triangle at the extreme right of the graph, were resident in the summer range for most of the year, before moving to the winter area for a short residence period. These animals appear to have a main range and a secondary one, used as a 'winter refuge'.

#### Pattern 3

When the imbalance between summer and winter range use becomes extreme, it is always the summer range that is predominantly used, with only very short (e.g. two days) interruptions in a secondary range. In the graph, these individuals are represented by the points which virtually lie on the horizontal axis. These animals appear to have non-overlapping ranges that are 'selected' differently.

#### Pattern 4

Finally, individuals within the extreme left square area of the graph have similar length, but very short, continuous residence times in both non-overlapping ranges. These animals appear to use spatially separated ranges in a similar way, without any clear temporal separation and therefore appear to be 'commuting' between ranges.

Pattern 3 and pattern 4 look like 'dead ends' on the migratory continuum, where only one of the two conditions for migration is respected: i.e. 'spatial, but not temporal', separation in range use.

We might expect pattern 2 and pattern 3 to be mirrored on the vertical axis, i.e. individuals that mostly use the winter range, with summer refuges used for only short periods. However, interestingly this behaviour was never observed.

The distribution of females and males on the graph of seasonal residence times differed significantly. Females showed similar residence times in both winter and summer ranges (average winter residence time = 0.22, SD = 0.17; average summer residence time = 0.37, SD = 0.21), while most males (except three individuals) had longer continuous periods of residence in summer ranges than in winter ones (average winter residence time = 0.18, SD = 0.15; average summer residence time = 0.54, SD = 0.23). Residence time in summer and winter ranges differed between sexes (statistical comparison of the difference between bivariate averages: Largest Roy's root = 0.18,  $p = 0.04$ ).

We then plotted the frequency distribution of 'all' periods of residence (>1 day) in each range, for each study area and for all populations combined (Fig. 2). The French population exhibited the shortest mean residence time (mean = 11.8, SD = 20.5), while roe deer in Italian Alps had the longest residence time (mean = 47.3, SD = 39.8). The average residence time in the entire population was about 30 days (mean = 28.6, SD = 35.4). As outlined above, this value was chosen as a threshold to discriminate between migrant and non-migrant individuals. Therefore, migrant individuals were defined as those having a clear spatial separation between seasonal ranges 'and' a maximum residence time in 'each' range of 'at least' 28 days. The outcome of this evaluation is shown in Table 1. Populations of all study areas included migratory and stationary individuals, although in differing proportions, except for southern Sweden, where no migration was recorded. When migrating, individuals in the Italian Alps and Norway mostly moved in a direct way between clusters, with one-hop migratory trajectories, while migrating roe deer in France and the Bavarian Forest generally moved several times between seasonal ranges before settling (multi-hop or multi-trip migrations). The mean Euclidean distance between ranges was similar in all areas (about 3 km, Table 1), except for Norway, where roe deer migrated much longer distances (about 14 km  $\pm$  2 on average).

### Timing of migration

The average timing of migration among individuals (i.e. averaged over all migratory trips) is shown in Fig. 3a by black dots (summer to winter ranges) and open dots (winter to summer ranges). On average, spring migration occurred on 1 May, while the shift between summer and winter ranges occurred on 1 December. When average migration dates were calculated for each site separately (Fig. 4), spring transitions were found to be rather synchronous (range: 15 April – 15 May;  $F = 1.86$ ,  $p = 0.19$ ). In contrast, transitions from summer to winter ranges spanned a wider period (range: 1 November – 15 February;  $F = 4.18$ ,  $p = 0.05$ ), including some very late shifts that occurred in February and March in the Bavarian Forest and France, although autumn migrations were earlier and more synchronised in Norway and the Italian Alps. The degree of synchrony of migration is represented by the length of the migration vector  $\rho$ ; indeed, in Fig. 3a,  $\rho$  was greater in spring than in autumn, while in Fig. 4  $\rho$  was greatest in Norway.

Figure 3b contrasts timing of migration between the sexes; on average, spring migration tended to occur earlier in males than in females ( $F = 2.52$ ,  $p = 0.13$ ), while in autumn, males migrated significantly later ( $F = 4.18$ ,  $p = 0.05$ ; Fig. 3b). As a result, males spent longer time than females in their summer ranges (total average residence time in summer range: males =  $259.92 \pm 19.49$  days; females =  $188.49 \pm 14.95$ ;  $F = 8.45$ ,  $p < 0.01$ ), which is consistent with what we observed in Fig. 1.

### Factors affecting migration, and pattern of migration

The occurrence of migration in our roe deer study populations was not explained by a single best model, since several models showed very similar  $AIC_c$  values ( $n = 17$  within the cutoff of  $\Delta AIC_c = 4$ ; Appendix 1). Fixed effects most frequently included in the best models were slope (predictor weight = 0.95), forest (predictor weight = 0.93), snow (predictor weight = 0.80) and the interaction between snow and slope (predictor weight = 0.60). These fixed effects consistently made up the model with the lowest  $AIC_c$  in the majority of bootstrap simulations (Appendix 1).

Therefore, the occurrence of migration in roe deer seemed to be a function of variable topography (slope), in combination with climatic factors (snow cover) and habitat (forest cover). The coefficients of the fixed effects estimated by model averaging (Table 3) indicated a strong positive effect of the presence of snow cover in interaction with slope ( $6.83 \pm 2.21$ ), of slope itself ( $5.14 \pm 2.36$ ) and, to a lesser extent, forest cover ( $1.36 \pm 0.55$ ) on the occurrence of migration in our roe deer study populations, while snow cover itself had an inconsistent effect ( $-0.87 \pm 1.17$ ). These variables combined in the averaged model explained 31% of the variance.

Similarly, the occurrence of one-hop migratory trajectories in migrating roe deer was not explained by a single best model, and we therefore used model averaging for coefficient estimates (Appendix 1, Table 3). The fixed effects most frequently included in the best models were the Euclidean distance between the first and last points of the migratory trajectory, forest cover and the slope along the trajectory (predictor weights = 1.00, 0.75, 0.49, respectively), that also in this case made up the model with the lowest  $AIC_c$  in the majority of bootstrap simulations, with the addition of sex (predictor weight = 0.32). The occurrence of one-hop migration in roe deer was strongly positively affected by slope ( $4.52 \pm 1.5$ ) and the distance between clusters ( $1.30 \pm 0.46$ ), and negatively affected by the occurrence of forest along the migratory trajectory ( $-1.49 \pm 0.60$ ). Males seemed to have a lower probability of performing one-hop migrations than females ( $-0.96 \pm 0.26$ ).

### Discussion

This paper analyses in detail, using an individual-based approach, the behavioural continuum in roe deer migrations. The presence of a wide variability in migratory behaviour was expected from previous research, both on roe deer (Wahlström and Liberg 1995, Mysterud 1999, Ramanzin et al. 2007) and on other species with a similar ecology, such as the white-tailed deer (Sabine et al. 2002, Brinkman et al. 2005, Fieberg et al. 2008). The possibility of analysing

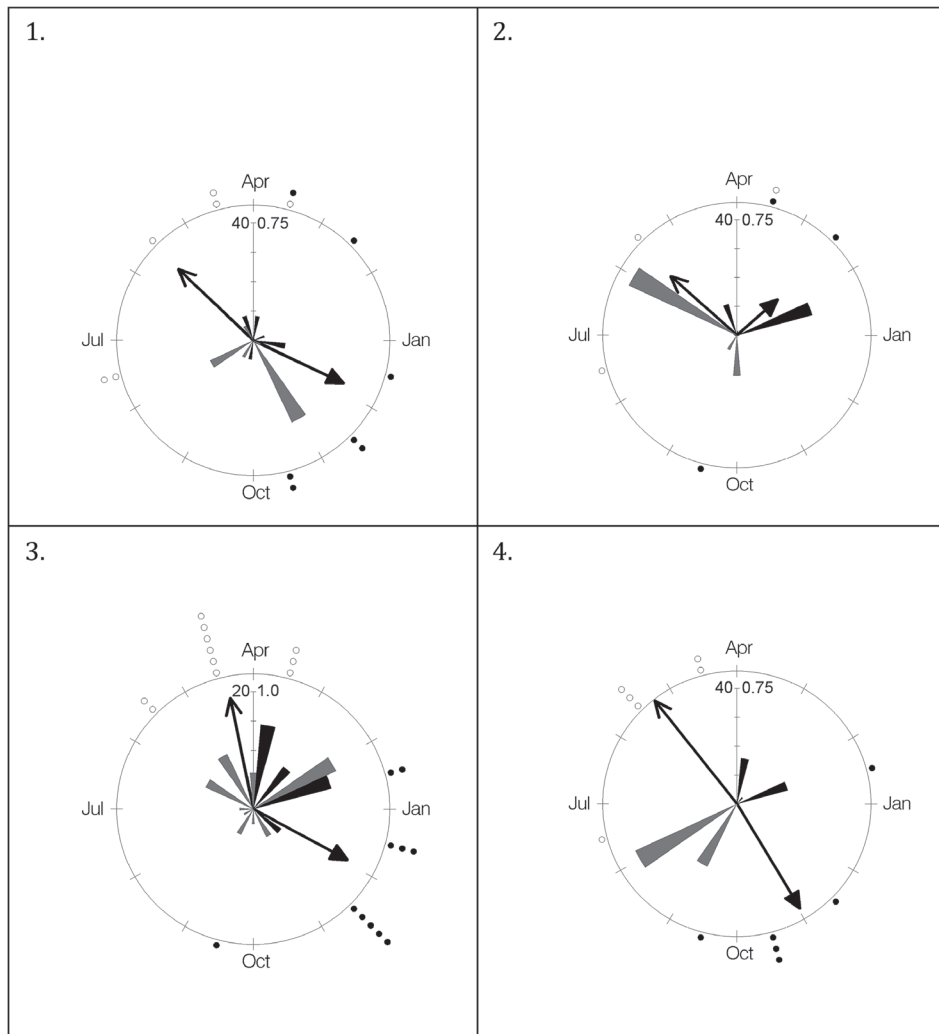


Figure 4. Timing of migrations in roe deer in the four study areas where migration was observed: the Bavarian Forest (1), southwest France (2), the Italian Alps (3) and Norway (4). Symbols as in Figure 3a.

a large scale data set that covers a considerable part of the roe deer's distribution range, available here through the collaborative EURODEER project, allowed us to identify some unexpected features in the pattern of roe deer space use and migratory behaviour in general. First, the occurrence of migration was not affected by the simple presence of snow as a 'sole factor', but mainly by the interaction between topographic variation (expressed as average slope) and snow cover. Contrary to expectations (Wahlström and Liberg 1995, Mysterud 1999), migrations were indeed not observed in areas with considerable snow cover, but which are topographically flat (southern Sweden), while some degree of migratory behaviour was observed in areas with virtually no snow cover, but which are rather hilly (southern France).

Second, when migration was observed, roe deer individuals concentrated their range use within a wintering area for at least part of the winter, before migrating to a separate summer range, with a high degree of synchrony of this movement among study areas. Indeed, summer ranges were used for an equal duration or, in most cases, for longer than winter ranges across all study sites.

Third, autumn migration was highly asynchronous across study sites, and included a few very late departures from the

summer range (i.e. 'autumn' migration in February–March in some study areas; Ramanzin et al. 2007, Fieberg et al. 2008); as a consequence, residence in the winter range was often fragmented in time (i.e. interrupted by several 'return' trips to the summer range) or limited to a very short period. Several of these patterns have been observed in deer in areas with mild or unpredictable winter conditions, and are common in facultative migrators (Nelson 1995, Sabine et al. 2002, Brinkman et al. 2005).

Fourth, the occurrence of migration did not differ between sexes, however, we observed a clear difference between the sexes in terms of the attachment to their summer range: males migrated later than females in autumn and resided longer in the summer range than females. This is not always the case in other deer species (e.g. mule deer, Nicholson et al. 1997).

The European roe deer takes full advantage of the evident seasonality in the European temperate region, concentrating its reproductive physiology and behaviour in the summer months (Sempéré et al. 1998, Liberg et al. 1998); this, together with the observation that it is an income breeder (Andersen et al. 2000), strongly suggests the importance of the summer range for maximising reproductive success in this species, with a positive effect of habitat quality and/

or range size in both sexes (McLoughlin et al. 2007, Vanpé et al. 2010). Mysterud et al. (2011) suggested that minimal residence time of migratory red deer in winter habitats is supported by the avoidance of competition, although they did not consider a higher quality of summer range as a necessary condition for migration to occur (Mysterud 1999). In turn, deterministic models on partial migration (Taylor and Norris 2007) predicted that density dependence during the season in which migrating and non migrating individuals use separate sites is necessary for the onset of partial migration, together with a better quality of migratory breeding sites than resident breeding sites. From this viewpoint, the synchronous spring migrations in roe deer should be movements towards more favourable sites for reproduction, while the asynchronous autumn migrations, together with minimal winter range residence times, likely indicate avoidance of situations hampering survival, either directly (i.e. snow cover limiting locomotion and food accessibility), or indirectly (e.g. search for early-growth forage in late 'autumn' migration in February–March).

The strong effect of topographic variation in interaction with snow cover in determining the occurrence of migration supports the latter interpretation. Snow depth is known to negatively affect the cost of locomotion in small and medium deer species (Mysterud 1999, Sabine et al. 2002, Ramanzin et al. 2007). In this study, we could not access a consistent measure of snow depth over a large scale, so we used a robust remote sensed index of snow cover instead (Hall et al. 2002). On a more general level, migratory movements can only be cost-effective if resources are heterogeneous on a scale that is accessible to moving individuals. Mysterud et al. (2011), studying partial migrations in red deer, showed that topography is important for modulating migrations, in accordance with the forage maturation hypothesis (Hebblewhite et al. 2008). In the case of roe deer, the importance of slope may also suggest that some form of forage maturation process might be involved. Roe deer are considered a concentrate selector (van Soest 1994), with a strong seasonal specialisation of diet (Duncan et al. 1998). However, Cornelis et al. (1999) reviewed feeding habits throughout Europe and showed that, in spring, roe deer may double their exploitation of the graminoids and herbs typical of open pastures compared to the annual average. The similar timing of spring migration in males and females is consistent with this hypothesis, since digestive capabilities are similar in both sexes. Indeed, under density dependence, migration towards summer ranges with high food quality/availability would be adaptive in both sexes: availability of resources during the birth period in females would enhance fawn survival in this income breeder, while high habitat quality would allow males to attain better physical condition prior to the rut (Vanpé et al. 2010). Furthermore, if a high proportion of bucks remained on their winter ranges, this would result in small territory size per individual, whereas migration may allow migrators to obtain larger territories and hence achieve higher breeding success (Vanpé et al. 2009; competition avoidance hypothesis: Mysterud et al. 2011). However, this hypothesis needs to be tested. For this, the ranges of migrants and non-migrants could be compared for plant productivity in summer using a large scale index, such as NDVI (Pettorelli et al. 2005, Hebblewhite et al. 2008). Then, some index of performance, such as male territory size, could be

compared: it would also be interesting to evaluate whether migrant bucks obtain larger territories than residents.

In autumn, we observed a quite different situation than in spring, with low inter-individual synchronicity and females migrating sooner than males. The large inter-individual variation in the timing of autumn migrations suggests that these events are opportunistically triggered by climatic factors, which span a large diversity of conditions across the roe deer's distribution range. In Scandinavia, the autumn migration is much earlier and more synchronised than in Germany and, to some extent, the Italian Alps. Sabine et al. (2002) suggested that, in regions with severe winter climatic conditions, autumn migration is driven by seasonal cues to avoid deep snow that would almost certainly hamper survival; in regions with moderately severe and variable, or unpredictable, winter climate, autumn migration is more likely a response to proximate stimuli (e.g. snowfalls, lack of food), since the costs of late departure would not be so high as in severe environments. This is consistent with our observations of a generally strong attachment to the summer range that was stronger in males than in females. As a matter of fact, no animal exhibited a maximal residence time that was longer in winter than in summer. One can wonder if this (a) originates in a sampling bias in our, albeit large, data set or (b) represents an intrinsic feature of roe deer biology. The peculiar feature of roe deer territoriality in summer which occurs across all European populations studied to date suggests there should be a strong tendency (especially for males) to maximise site fidelity to the summer range, a prediction which matches the results of our analysis.

The degree of winter severity has been shown to affect the dichotomy of obligate and facultative migration which parallels that of early and late migrants (Nelson 1995, Nicholson et al. 1997, Ramanzin et al. 2007, Fieberg et al. 2008). In this study, we could not distinguish between facultative versus obligatory migrators over consecutive years, since we limited our analysis to one year's monitoring per individual. Moreover, Fieberg et al. (2008) showed that assessment of facultative migration is observation-time dependent. However, facultative migration has been associated with a range of behaviours that we observed in this study, including late migration and opportunistic migration, i.e. with several trips between ranges and short winter range residence time (Ball et al. 2001, Sabine et al. 2002). Indeed, a main insight of our comparative analysis of roe deer spatial behaviour is the observation that in some locations (where the climate is harsher), animals performed one-hop trips during migration, whereas deer in areas with milder or variable winter climate performed numerous trips between winter and summer ranges before taking a final decision to stabilize their range. Contrary to predictions, the probability of performing one-hop (single trip) migrations did not depend on snow occurrence, but on factors influencing the cost of movement, such as between-range distance and slope. Interestingly, the presence of open habitats favoured one-hop migration, probably due to the higher level of disturbance and perception of risk in such landscapes. Overall, migration trajectories included a higher proportion of forest than trajectories within ranges, again indicating the cost of migration in terms of exposure to risk in habitats outside the usual range (i.e. along the migratory trajectory).

It seems likely that frequent shifts between ranges are exploratory movements, necessary for evaluating the suitability of the new range and the appropriate timing for settling. We presume that such a strategy would be favoured when the costs of range shifts are low, while when such costs are large a one-hop trip should be more effective.

The pattern of migration in southern France appears to be rather different from the other study areas, with a less clear separation between spring and autumn migrations, short residence times in alternative ranges and multi-hop trajectories. This higher variability strongly suggests that, in this environment, roe deer behave as commuters (Dingle and Drake 2007), moving between separate ranges throughout the year, with very limited continuous residence time. This tactic of seasonal space use may 'collapse' into third order habitat selection of multi-patch home ranges in the most extreme cases.

The results of our large scale analysis overall suggest that, in roe deer, migratory behaviour is quite opportunistic, and partial migration appears to be the rule rather than the exception in this species. Similar conclusions were derived from a long-term study on white-tailed deer (Fieberg et al. 2008). The high ecological plasticity and wide distribution range of these deer species may allow us to empirically investigate the fundamental nature of migration as a tactic of space use, where the costs of residence in spatially separated ranges are traded-off against the costs of migratory movement. As such, 'migratory' behaviour is the end point of a behavioural gradient that includes 'residence' at the other extreme, with 'commuting' and 'facultative' or opportunistic (multi-trip) migration as intermediate tactics. Interestingly, facultative migration between two separate ranges challenges the distinction between second and third order habitat selection (Johnson 1980), or at least requires the extension of this definition to cover an extended period of the life-time of individuals (i.e. at least across seasons). Despite some papers suggesting that migratory behaviour is a continuum (Ball et al. 2001, Dingle and Drake 2007), the presence of intermediate space use tactics, between the extremes of migration and residence, was rarely specifically studied. This paper is one of the rare examples of such research. In particular, the application of circular statistics is especially useful (Batschelet 1981, Fisher 1993) to describe inter-individual variability in the timing of migration events. Indeed, we showed that the existence of range separation is a necessary, but not sufficient, condition for the onset of migration. This is, for instance, the case in southern Sweden, where a certain degree of spatial range separation was evident, but this could not be considered as migration because both ranges were used all the same (i.e. animals never stabilised in either range for a prolonged period). In this study, we fixed the limit between 'commuting' behaviour and 'migration' to the mean residence time in each separate seasonal range, averaged across all populations. This is a simple and repeatable empirical criterion that robustly discriminated between types of range use.

In our large scale analysis, several ecological factors affected both migratory tactics and pattern. Many more could be evaluated, including population density (Mysterud et al. in 2011), age of individuals and survival (Nicholson et al. 1997), productivity (Hebblewhite et al. 2008), predation risk (Hebblewhite and Merrill 2009), human disturbance

and habitat fragmentation, or genetic and physiological profiles (Dingle and Drake 2007, Bolger et al. 2008). We believe that a full understanding of the behavioural gradient in space use leading to different kinds and degrees of migration, and the factors affecting it (Dingle and Drake 2007), should be one of the main fields of research of spatial ecology.

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## Appendix 1

Statistical analysis of variables describing the seasonal migration of *C. capreolus* in Europe. Generalised linear mixed models with a binomial distribution of errors were used to examine the effects of sex, season, presence of snow cover and forest cover, mean slope and Euclidean distance between the start and end points of the migratory trajectory. We modelled (a) the occurrence of migration, (b) the occurrence of direct (i.e. one-hope) migratory trajectories between seasonal ranges. Model selection was based on the Akaike information criterion corrected for small sample sizes ( $AIC_c$ ), beginning from an a priori model including the variables listed above, as well as the interaction between snow cover, season and mean slope.  $\Delta AIC_c$  = difference in  $AIC_c$  between the best model and the tested model;  $\omega_i$  = Akaike weight; evidence ratios = ratio of the Akaike weights between the best model and the tested model. Multimodel inference was based on a cut-off of  $\Delta AIC_c = 4$ , relative likelihood = 0.135.

Appendix Table 1.

Full model	Fixed effects	$AIC_c$	$\Delta AIC_c$	$\omega_i$	E. ratios	Boostrap ( $\pi_i$ ) <sup>a</sup>	R <sup>2</sup>
migration ~	snow × slope + snow + slope + forest	163.68	0.00	0.14	1.00	0.17	0.29
snow × slope ×	snow × slope + snow + slope + season + forest	165.08	1.40	0.07	2.01	0.046	0.25
season +	snow + slope + forest	165.31	1.63	0.06	2.26	0.041	0.36
forest + sex + (1 studies)	slope + forest	165.37	1.69	0.06	2.33	0.054	0.46
	snow × slope + snow × season + snow + slope + season + forest	165.51	1.83	0.06	2.49	0.104	0.22
	snow × slope + snow + slope + forest + sex	165.68	2.00	0.05	2.72	0.04	0.25
	forest	166.46	2.78	0.03	4.02		0.62
	snow + slope + season + forest	166.48	2.80	0.03	4.06	0.03	0.30
	snow × slope + snow + slope	166.91	3.23	0.03	5.03	0.044	0.36
	slope + season + forest	167.01	3.33	0.03	5.29	0.015	0.36
	snow × season + snow + slope + season + forest	167.08	3.40	0.03	5.47	0.039	0.25
	snow × slope + snow + slope + season + forest + sex	167.21	3.53	0.02	5.83		0.22
	snow × slope + slope × season + snow + slope + season + forest	167.31	3.63	0.02	6.13	0.017	0.22
	snow × slope + snow × season + snow + slope + season + forest + sex	167.47	3.79	0.02	6.65	0.032	0.19
	snow + slope + forest + sex	167.48	3.80	0.02	6.69		0.30
	slope + forest + sex	167.51	3.83	0.02	6.79		0.36
	snow × slope + snow × season + snow + slope + season	167.58	3.90	0.02	7.02	0.036	0.25
direct trajectory ~	slope + forest + distance	59.94	0.00	0.16	1.00	0.18	0.29
snow × slope +	forest + distance	60.84	0.90	0.10	1.56	0.063	0.39
season + forest + sex +	forest + sex + distance	61.53	1.59	0.07	2.21	0.047	0.30
distance + (1 studies)	sex + distance	61.77	1.83	0.06	2.49	0.06	0.40
	distance	62.03	2.09	0.06	2.84	0.03	0.56
	slope + forest + sex + distance	62.03	2.09	0.06	2.84	0.036	0.24
	slope + season + forest + distance	62.46	2.52	0.05	3.53	0.032	0.24
	snow + slope + forest + distance	62.52	2.58	0.04	3.63	0.032	0.24
	slope + distance	62.77	2.83	0.04	4.11		0.41
	snow + forest + distance	63.09	3.15	0.03	4.83	0.032	0.31
	season + forest + distance	63.31	3.37	0.03	5.39	0.021	0.31
	slope + sex + distance	63.44	3.50	0.03	5.75	0.036	0.31
	snow + forest + sex + distance	63.82	3.88	0.02	6.96	0.18	0.25

<sup>a</sup>percentage of total Bootstrap simulations (999 per model) that indicated a particular model as the best one (i.e. that converged to the minimum AIC value for that particular model).