

SPECIAL FEATURE: STUCK IN MOTION? RECONNECTING QUESTIONS AND TOOLS IN MOVEMENT ECOLOGY

How many routes lead to migration? Comparison of methods to assess and characterize migratory movements

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Summary

1. Decreasing rate of migration in several species as a consequence of climate change and anthropic pressure, together with increasing evidence of space-use strategies intermediate between residency and complete migration, are very strong motivations to evaluate migration occurrence and features in animal populations.
2. The main goal of this paper was to perform a relative comparison between methods for identifying and characterizing migration at the individual and population level on the basis of animal location data.
3. We classified 104 yearly individual trajectories from five populations of three deer species as migratory or non-migratory, by means of three methods: seasonal home range overlap, spatio-temporal separation of seasonal clusters and the Net Squared Displacement (NSD) method. For migratory cases, we also measured timing and distance of migration and residence time on the summer range. Finally, we compared the classification in migration cases across methods and populations.
4. All methods consistently identified migration at the population level, that is, they coherently distinguished between complete or almost complete migratory populations and partially migratory populations. However, in the latter case, methods coherently classified only about 50% of the single cases, that is they classified differently at the individual-animal level. We therefore infer that the comparison of methods may help point to 'less-stereotyped' cases in the residency-to-migration continuum. For cases consistently classified by all methods, no significant differences were found in migration distance, or residence time on summer ranges. Timing of migration estimated by NSD was earlier than by the other two methods, both for spring and autumn migrations.
5. We suggest three steps to identify improper inferences from migration data and to enhance understanding of intermediate space-use strategies. We recommend (i) classifying migration

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behaviours using more than one method, (ii) performing sensitivity analysis on method parameters to identify the extent of the differences and (iii) investigating inconsistently classified cases as these may often be ecologically interesting (i.e. less-stereotyped migratory behaviours).

Key-words: adehabitat, home range overlap, movement patterns, Net Squared Displacement, red deer, reindeer, residence behaviour, roe deer, spatial clusters

Introduction

Migration is a widespread phenomenon in the animal kingdom, known since ancient times. Complete migration (all individuals in a population migrating with a clear separation of ranges) is being viewed as the exception, rather than the rule (Dingle & Drake 2007). In particular, partial migration, or migration of a portion of the population, is 'the' migration strategy across diverse taxa (Chapman *et al.* 2011). Partial migration is common when habitat suitability is highly variable through time, and some form of density dependence exists (Taylor & Norris 2007). Partial migration is often associated with facultative migration, that is, individuals may vary their strategy across years (Fieberg, Kuehn & DelGiudice 2008). Moreover, under unpredictable, but not extreme conditions, 'less-stereotyped' or 'mixed' migratory behaviours are observed, such as short and/or multiple trips between ranges (Cagnacci *et al.* 2011), or commuting (Dingle & Drake 2007). Therefore, the distinction between migratory and non-migratory behaviour becomes less defined, so that some authors now preferred the concept of a 'migratory continuum' (Ball, Nordengren & Wallin 2001; Dingle & Drake 2007; Cagnacci *et al.* 2011).

As a consequence of climate change and anthropic pressure that in turn affects heterogeneity and temporal predictability of the environment, we can expect a decreasing rate of migration or changes in migration patterns (Wilcove & Wikelski 2008). For example, if partial migration is a true conditional strategy, we may expect an increased variability of space-use tactics within and between populations of the same species (Middleton *et al.* 2013). Either way, quantifying migration occurrence and migration parameters, such as timing or distance of migration, is fundamental to (i) understanding animals' plasticity in this movement tactic (Dingle & Drake 2007), (ii) conserving migratory species (Bolger *et al.* 2008) and (iii) monitoring cascading effects on community structure and function resulting from changes in migratory behaviours (Bauer & Hoyer 2014).

To quantify migration, the first step must be to formulate a clear definition of the phenomenon. In an incomplete review of the vast literature on migration, we could list a diversity of definitions (reviewed in Table 1). Typically, the particular definition arose from different themes of research that looked at different components of this complex phenomenon. Then, we tried to fit the definitions from disparate themes into well-established theoretical frameworks of migration (Drake, Gatehouse & Farrow

1995: holistic model of a migration system) and movement (Mueller & Fagan 2008: link between movement mechanisms, animal distribution and landscape structure; Nathan *et al.* 2008: the movement ecology paradigm), which we schematized in Fig. 1. Nathan *et al.* (2008) focus on how the structure of movement paths is determined by interactions between the internal state of individuals and the external environmental conditions, conditional on their navigation and movement capacities. Mueller & Fagan (2008) take a more comprehensive approach and add the population consequences (sedentary, migratory, nomadic) resulting from the individual decisions. Drake, Gatehouse & Farrow (1995) and Dingle & Drake (2007) adopt similar categories and refer to these as 'migration syndromes' (population trajectories or pathways) and evoke the ultimate evolutionary causes.

In attempting to characterize migration, we had some specific requirements. In particular, we needed quantities easily measurable (i) in standardized ways and (ii) at the individual level (given we wanted to investigate individual variability of migration). Animal trajectories satisfied these two requirements because they are expressed as sequence of locations that are measurable with a standardized technology by fitting devices on individual animals [e.g. global positioning system (GPS) telemetry, Cagnacci *et al.* 2010]. The advantage of 'measuring' movements at the level of the individual is also that the outcome can be easily scaled up to the population level (Dingle & Drake 2007). We therefore adopted the definitions related to movement patterns of migration (Table 1), and assessed what methods would allow us to quantify migration consistently with those definitions.

The main goal of this paper was therefore to compare three methods to quantify animal movement to identify migration types using data sets of GPS telemetry locations of real deer species. We chose three methods: overlap between seasonal home ranges (overlap), spatio-temporal separation of seasonal clusters (cluster) and Net Squared Displacement (NSD) from a point of origin.

Early work defines migration as 'allopatric seasonal home ranges' (Craighead, Atwell & O'Gara 1972; definition 14, Table 1). Overlap of seasonal ranges is the way to quantify migration according to such definitions. Although intuitive, we did not find in the literature a standardized methodology. We applied the Battarchaya's index (Fieberg & Kochanny 2005) on seasonal utilization distributions (UD; Worton 1989) to quantify seasonal overlap of home ranges. One problem could be the defini-

Table 1. Research questions related to migration, corresponding definitions and matching conceptual components of existing theoretical frameworks on movement

Research themes related to migration	Definitions of migration from cited literature	Observation scale	Conceptual framework 1 (Drake, Gatehouse & Farrow 1995)	Conceptual framework 2 (Mueller & Fagan 2008)	Conceptual framework 3 (Nathan <i>et al.</i> 2008)
Individual mechanisms of migration (physiological and genetic determinants)	[1] Behavioural and physiological switch in response to internal and environmental cues (Liedvogel, Akesson & Bensch 2011) [2] Genetically determined behaviour (Lundberg 1988).	Individuals	Migration syndrome + Genetic complex	Undefined behavioural rules	Internal state + Navigation + and Motion capacities
Functional nature of migration (ecological, evolutionary)	[3] A tactic to enhance lifetime reproductive success (survivorship*birth rate) (Fryxell & Sinclair 1988). [4] Movements leading to redistribution within a spatially extended population (Dingle & Drake 2007). [5] Movements with direct trophic effects and indirect transport effect on communities and meta-communities (Hollo <i>et al.</i> 2011).	[3] Individuals [4] Populations [5] Community	Population trajectory + Overarching natural selection	Population pattern	na
External context of migration	[6] Regular, long-distance pattern of movements in systems with regular, seasonal fluctuations in environmental conditions (Sinclair 1983) [7] Seasonal to-and-from movement of populations between regions where conditions are alternatively favourable or unfavourable (Roshier & Reid 2003; Dingle & Drake 2007). [8] Migration emerges in landscapes that vary at increasingly longer temporal and broader spatial scale, so that animals will be required to travel increasingly larger (spatiotemporal) distances between resource patches, provided there is sufficient repetition to the seasonal changes (Mueller & Fagan 2008).	Populations	Migration arena	Landscape structure	External factors
Movement pattern of migration (locomotion)	[9] Persistent and straightened out movement effected by the animal's own locomotory exertions or by its active embarkation upon a vehicle (i.e. currents). It depends on some temporary inhibition of station keeping responses but promotes their eventual disinhibition and recurrence (Kennedy 1985).	Individuals	Migratory behaviour	Movement mechanisms	Movement path (trajectory-sequence of movement steps)

(continued)

Table 1. (continued)

Research themes related to migration	Definitions of migration from cited literature	Observation scale	Conceptual framework 1 (Drake, Gatehouse & Farrow 1995)	Conceptual framework 2 (Mueller & Fagan 2008)	Conceptual framework 3 (Nathan <i>et al.</i> 2008)
Movement pattern of migration (spatial outcome)	[10] A type of locomotory activity that is persistent, undistracted and straightened out (Drake, Gatehouse & Farrow 1995)	Individuals	Migratory behaviour	Movement mechanisms/patterns	Movement path (Movement phase)
	[11] Journeys involving either individuals moving in relatively small stages, exploiting habitat more or less continuously during the journey; or, travelling directly between a relatively small number of widely separated, more or less discrete, sites (Robinson <i>et al.</i> 2009; Bischof <i>et al.</i> 2012).				
	[12] Movements of longer duration and greater displacement than those seen in more trivial daily patterns of movement (Holdo <i>et al.</i> 2011).				
	[13] Migration is a systematic increase followed by a systematic decrease in the average distance between an animal's present position and a given release point during a given time (Bunnefeld <i>et al.</i> 2011).				
	[14] Allopatric seasonal home ranges (Craighead, Atwell & O'Gara 1972).				
	[15] Predictable return journey of individuals (Fryxell & Sinclair 1988).				
	[16] Separation in the use of ranges in space and time (Cagnacci <i>et al.</i> 2011).				
	[17] Displacement with return to a point of origin (Bunnefeld <i>et al.</i> 2011).				

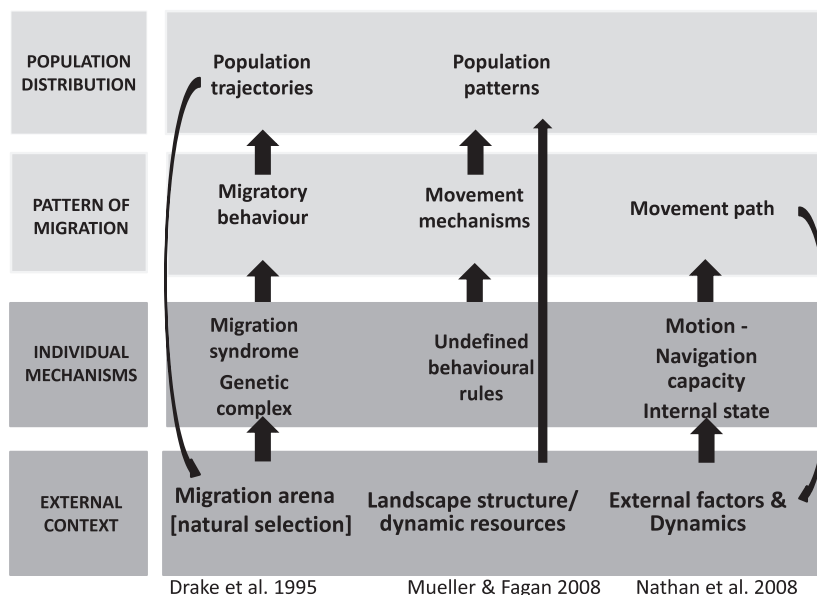


Fig. 1. Harmonization of three theoretical frameworks on movement and migration in a unified conceptual scheme related to migration. Four main themes of research emerge: the individual mechanisms prompting migration, the role of the external context for migration to emerge, the form, or pattern of migratory movements, and how they result in a population-level phenomenon. Definitions of migration from an incomplete literature review were grouped in the same categories in Table 1. Lighter grey refers to spatial-explicit phenomena.

tion of 'seasons', which can vary across species or latitude or environments. In a multi-population study on roe deer, Cagnacci *et al.* (2011) showed that the migration phases differed across the distribution range of the species. To address this issue, we defined seasons with multiple combinations of shifting time windows. Overlap is a spatially explicit, descriptive method based on probabilistic estimates of home range use.

The alternation of 'stationary' and 'mobile' phases is another common way to describe migration (Kennedy 1985; definition 9, Table 1; see also definitions 11 and 16, Table 1). The spatio-temporal separation of seasonal clusters in Cagnacci *et al.* (2011) takes this definition upfront by computing spatial clusters based on topological rules (Ward 1963) and 'linking' them through the migratory trajectory. Cluster is a spatially explicit, descriptive method based on geometrical estimates of clusters of animal locations.

Finally, several definitions of migration are based on characteristics of the migratory trajectory, and particularly the distance travelled during this movement phase ('locomotory activity that is persistent, undistracted and straightened out', Drake, Gatehouse & Farrow 1995, covering a distance 'which is greater than in other daily patterns of movement', Holdo *et al.* 2011; see definitions 10, 12, 13, 17, Table 1). NSD is a convenient metric to measure the distance travelled relative to a point of origin. Bunnefeld *et al.* (2011; further developed in Börger & Fryxell 2012) fitted a set of competing nonlinear models to individual NSD trajectories, each corresponding to a specific movement behaviour (home range, dispersal, migration, and nomadic). Migration was defined by a double sigmoid function, indicating a displacement with return to the point of origin.

For our analysis, we used each method to assess whether the yearly trajectory of each individual animal corresponded to a 'migratory movement'. If so, we mea-

sured metrics to characterize migration, specifically residence time in summer range, distance and timing of migration. Because we applied the methods on real animal trajectories, we did not have a 'true value' against which to evaluate accuracy. Rather, we performed a relative comparison of results across methods to assess their consistency at the population and individual level. We argued that the probability to obtain a consistent classification is related to the variability of seasonal space-use behaviour in the residency-to-migration continuum, hence to migratory plasticity of populations, and individuals.

Materials and methods

SAMPLE POPULATIONS AND DATA SETS

Data sets from five populations of three deer species were used to compare methods for characterizing migration: roe (*Capreolus capreolus* L. 1758) and red deer (*Cervus elaphus* L. 1758) in Germany and Norway, and wild mountain reindeer (*Rangifer tarandus* L. 1758) in Norway (Table S1, Supporting information). The species of choice share some common characteristics (terrestrial species; herbivores; partly overlapping distribution range) so that we could compare movement data with standard location sampling and seasonality. Moreover, the migratory behaviour of these or neighbouring populations has been described previously using some but not all of the three methods. For example, reindeer have been described as obligatory migrants in some parts of Norway (NSD: Panzacchi, Van Moorter & Strand 2013), whereas roe deer and red deer populations in Norway and Germany were considered partially migratory (overlap: Mysterud 1999; cluster: Cagnacci *et al.* 2011; NSD with additional criteria: Mysterud *et al.* 2012). We therefore considered these populations as suitable for reassessing migratory behaviour to evaluate their consistency among methods.

All individual animals were fitted with GPS collars for at least 1 year. We therefore obtained a time series of GPS locations with a fix interval between 1 and 4 h (Table S1). We assessed the

occurrence and characteristics of migration in yearly individual trajectories, which were our sampling units. For standardization, we assigned locations to a year starting on 15 February, or the date of the first capture if it fell between 15 of February and 15 April. We extended each yearly data set to 14 February of the following year, or to the end of monitoring, if monitoring occurred after 1 December. In all other cases, we did not use an animal's trajectory because it was considered incomplete (thus, we only used complete yearly data sets).

OVERLAP OF SEASONAL HOME RANGES

As there is no standardized methodology to determine seasonal time intervals to compute home range overlap, we formalized a new, flexible approach to delimit seasons by shifting time windows (resolution of 1 month) to obtain all possible combinations of two- or three-seasonal ranges (winter–summer–winter). The full procedure is described in Appendix S1. We computed the overlap between successive ranges using Bhattacharyya's affinity index (BA) applied on kernel density UD (Worton 1989). BA is a function of the product of the probability surfaces of overlapping UD (Fieberg & Kochanny 2005). This index quantifies the degree of similarity among probability surface estimates on a scale from 0 (perfectly disjoint UDs) to 1 (complete overlap). We used the `kerneloverlap` function of the `R` package `adehabitat` (Calenge 2006; href smoothing factor). We identified the time window with the minimum overlap between successive UDs for each yearly trajectory of an individual independently.

In the second step of the procedure, we established whether a certain value of minimum overlap corresponded to allopatric seasonal ranges, or residence. Specifically, we defined a threshold value as the median of minimum overlap between seasonal ranges across the population. If the minimum seasonal overlap of an individual was above the defined threshold, we considered the yearly individual trajectory as 'resident'. If the minimum overlap was below the threshold, we further distinguished between migratory trajectories and 'no-return' movements, for example dispersal events or nomadic behaviour. To do so, we looked at the overlap between successive winter ranges. In cases of very high values (i.e. >50%: return phase), we defined the yearly individual trajectory as 'migratory', or as 'no-return' movements otherwise. We also defined a 'no-return' movement when the minimum overlap corresponded to a combination of time windows with only two seasonal ranges. We defined the threshold value at the population level to account for differences in movements across landscapes that can correlate with migration distance (Cagnacci *et al.* 2011), and hence seasonal range overlap. We arbitrarily chose a lower limit to the threshold, (BA = 0.15) for clear allopatric seasonal ranges.

For the yearly trajectories of individuals identified as migratory, we measured the distance of migration as the Euclidean distance between geographic centroids of the 90% winter and summer UDs, timing of migration as the starting date of the time window defining the summer range and residence time in summer range as the duration in days of that time window.

SPATIO-TEMPORAL SEPARATION OF SEASONAL CLUSTERS

The cluster approach was based on the assessment of spatio-temporal separation of seasonal clusters as defined in Cagnacci *et al.*

(2011; but see also Van Moorter *et al.* 2010). We applied a supervised cluster procedure to identify the two main clusters of locations for the yearly individual trajectory. Each cluster was assigned to a 'season' (winter and summer), according to the median Julian date (SAS 2010, PROC CLUSTER; see Cagnacci *et al.* 2011 and Appendix S2 for a more detailed explanation of the procedure and the SAS code). Then, we computed the maximum time of continuous residence in each cluster that we plotted rescaled for both clusters. A yearly trajectory of an individual was considered to be migratory if the maximum time of continuous residence in both winter and summer clusters was above a threshold value. Here, we considered that a reasonable threshold to discriminate between short visits and continuous, 'seasonal' staying in each cluster was 1 month (Appendix S2, Fig. S2.1: frequency distribution of the seasonal staying). In this way, migratory behaviour was defined explicitly by both *spatial* and *temporal* separation in the use of clustered locations. Distance of migration was computed as the Euclidean distance between the centroid of seasonal clusters; timing of migration was defined as the transition between winter and summer ranges; and residence time in summer range was defined as the maximum continuous residence in the summer cluster. Note that this approach does not distinguish between migration and 'no-return' movements.

NET SQUARED DISPLACEMENT

We used the NSD method to identify the movement pattern of yearly trajectories of individuals following Bunnefeld *et al.* (2011) and Börger & Fryxell (2012). In the first step, using the `nlme` package in `R`, we fitted nonlinear mixed effects models (corresponding to residency, migration and dispersal or nomadic behaviour; see Bunnefeld *et al.* 2011) to the population of yearly trajectories of individuals and used the Concordance Criterion (CC) to evaluate the goodness-of-fit of the best model for each individual trajectory (Börger & Fryxell 2012). In the second step, we fitted a nonlinear mixed effects model to the individual trajectories with the same movement pattern (i.e. residency, migration and dispersal or nomadic behaviour: see above) to obtain both individual and population-level parameter estimates. We noticed, however, that when few individual trajectories were following the same movement pattern, it was likely that models did not converge. In this case, we adopted the Bunnefeld *et al.* (2011) approach by fitting the aforementioned nonlinear models to each individual trajectory separately, using the `nls` function in `R`. We recorded which competing model was selected as best fit, that is, corresponding to residency, migration and dispersal or nomadic behaviour (the latter two are 'no-return' movements). When the migration model (a double sigmoid; Appendix S3) was chosen as best fit, the distance of migration was given by the parameter δ (asymptotic height), the timing of migration by the parameters Θ_s and Θ_a , and the residence in the summer range by $\Theta_a - \Theta_s$. We provide extensive details on the procedure in Appendix S3 (S3.1–S3.7), including the `R` script (`R` package `nlme`; Pinheiro *et al.* 2015).

COMPARISON BETWEEN METHODS

Because we did not have a 'true' reference value, we could not evaluate the 'absolute performance' of methods in classifying individual trajectories as migratory/non-migratory. Rather, we assessed the consistency among methods. To do so, we defined a

binomial classification for pairs of methods (1 for consistent, 0 for inconsistent classification) where the sample units were yearly trajectories of individuals (Table S2). We used generalized linear models with binomial distribution of residuals to test the dependence of consistent classification on methods in interaction with the population. Specifically, we compared candidate models (Table S3) by means of the Akaike Information Criterion (AIC) to evaluate whether the probability of consistent classification of migration was due to differences between methods, populations, both methods and populations, or none of the two. For those cases that were consistently classified as migrants by all methods, we compared the estimates of the migration distance and the residence time in summer ranges by means of one-way repeated-measures ANOVA. The analyses were performed in R 2.15.0 (R Development Core Team, 2013). Finally, we represented the timing of migration as determined by different methods by considering the time of spring and autumn migration across years as a circular variable, where the year is represented on the trigonometric circle with a phase of 365 and the 1st of January at 0 radians. For each method, we obtained the average dates of spring and autumn migration, which are represented by a vector with angle equal to the average of all angles (individual dates of migration), and length ρ comprised between 0 and 1. ρ is inversely proportional to the standard deviation of angles and expresses the synchrony among migration dates of individuals: if all dates are the same, then $\rho = 1$; if dates are distributed at random, then $\rho = 0$.

Results

OVERLAP

The minimum home range overlap could be computed for all roe deer and reindeer, whereas some individual red deer (both Germany and Norway) had to be excluded because their seasonal ranges were too small (i.e. bounded to winter feeding station areas; 17 and 30%, respectively;

Table 2), preventing estimation of overlap in adehabitat. The threshold value of minimum overlap to distinguish residency from migratory or 'no-return' movements was 32 and 22% for roe deer (Germany and Norway, respectively), 21 and 15% for red deer (Germany and Norway) and 15% for reindeer. This method estimated all red deer and 83% of reindeer in Norway to be migratory (Table 2, Table S2), whereas all other populations were identified as 'partially migratory'. Specifically, half of red deer in Germany were classified as migrants, and a smaller proportion of roe deer both in Germany and Norway. For the latter species, several 'no-return' movements were distinguished from migration, plus one case in red deer in Germany and two reindeer cases (Table S2). We show an example of the detection of minimum overlap through shifting time windows for two yearly trajectories of red deer in Fig. 2. In both panels a (left) and b (right), the combination of time windows with minimum overlap identified by the algorithm is pictured in the middle figure. One deer (ID = 20, Germany; Fig. 2a) was classified as a migratory case. This animal was on its winter range between February and April (blue polygon), and then migrated and stayed on the summer range between April and November (orange polygon). Finally, it returned back to the winter range between November and February (yellow polygon). The latter has a minimum overlap with the summer range below the threshold (21%), but fully overlaps the winter range of the previous year, thus showing the return phase typical of migratory behaviour. The top and bottom panels in Fig. 2a represent the seasonal range overlap in two other sequences of time windows: in the top panel, the 'second winter' interval starts too early and includes portions of the summer range; in the bottom panel, the summer interval ends too late and includes por-

Table 2. Summary of migratory occurrence and related metrics for each deer population by different classification methods. Methods are overlap of seasonal home ranges (overlap); spatio-temporal separation of clusters of locations (cluster); and Net Squared Displacement (NSD)

Method	Species, Population	No. of cases	Migration cases n (Prop)	Distance of migration (m) Mean (SD)	Residence time in summer (days) Mean (SD)
Overlap	Roe deer, Germany	29	11 (0.38)	1420 (840)	90 (70)
Cluster	Roe deer, Germany	29	13 (0.45)	3925 (7025)	134 (58)
NSD	Roe deer, Germany	29	16 (0.55)	1709 (1672)	174 (79) ^a
Overlap	Roe deer, Norway	22	5 (0.23)	6008 (6720)	72 (50)
Cluster	Roe deer, Norway	22	14 (0.64)	20 856 (30 414)	117 (43)
NSD	Roe deer, Norway	22	11 (0.50)	11 764 (10 682)	195 (57) ^a
Overlap	Red deer, Germany	15	8 (0.53)	4158 (2601)	165 (43)
Cluster	Red deer, Germany	18	11 (0.61)	6730 (8218)	128 (46)
NSD	Red deer, Germany	18	11 (0.61)	3578 (2936)	187 (44) ^a
Overlap	Red deer, Norway	16	16 (1.0)	20 985 (14 009)	148 (75)
Cluster	Red deer, Norway	21	21 (0.91)	25 744 (29 406)	164 (24)
NSD	Red deer, Norway	23	22 (1.0)	25 800 (18 432)	119 (17) ^a
Overlap	Reindeer, Norway	10	10 (0.83)	48 011 (9324)	150 (60)
Cluster	Reindeer, Norway	12	12 (1.00)	43 144 (6321)	109 (25)
NSD	Reindeer, Norway	11	10 (0.92)	52 864 (9522)	135 (19) ^a

^aFor NSD, summer residence is expressed as $(\Theta_a - \Theta_s)$, that is, timing at which the migration reaches half its asymptotic height in autumn and spring, respectively.

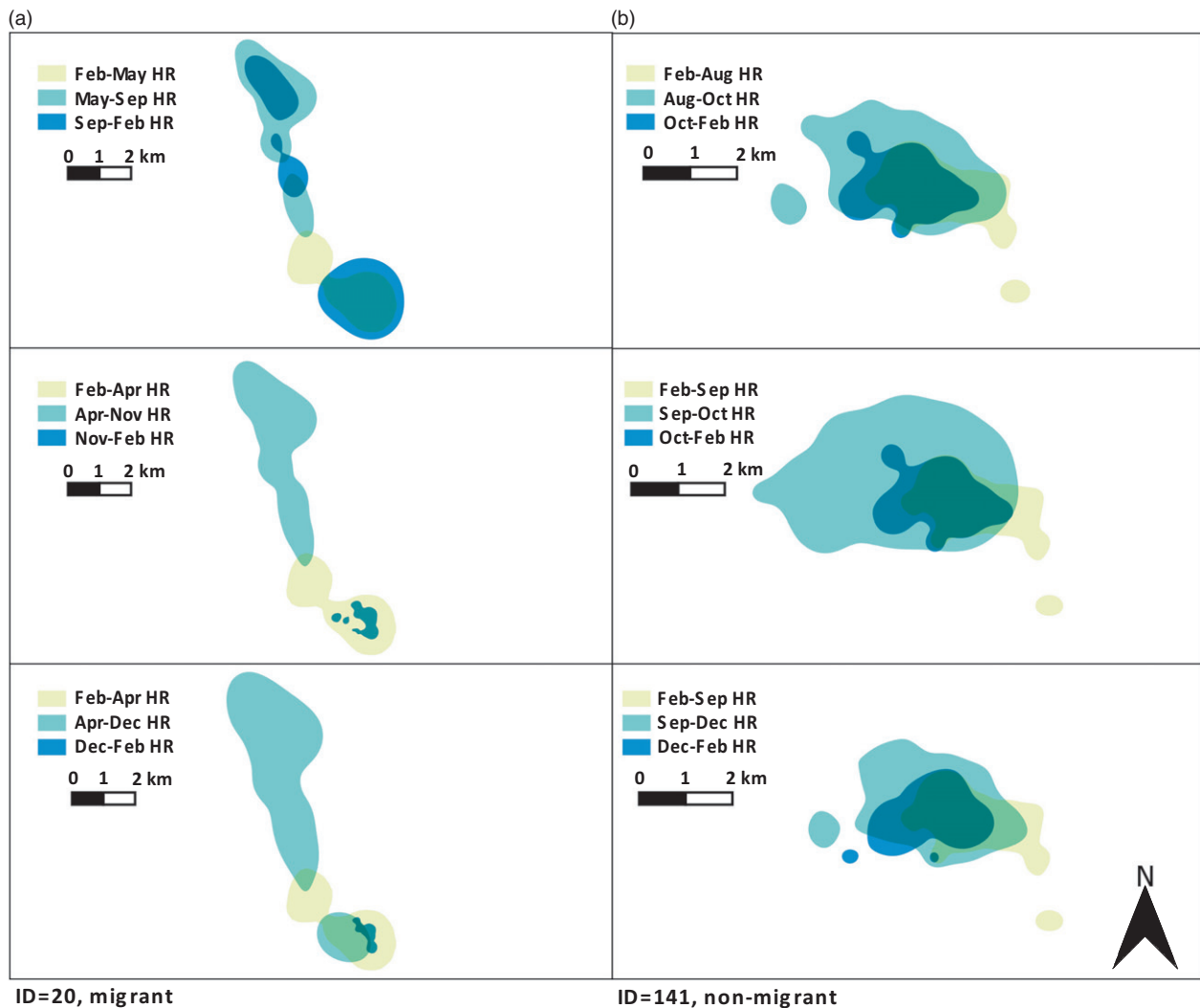


Fig. 2. Seasonal home ranges (UD90) computed for different combinations of sequential periods, and their overlap, for two individual red deer from Germany (a, left panels: ID = 20, classified as migrant; b, right panels: ID = 141, classified as non-migrant). In a, the seasonal home ranges based on the sequential periods February–April, April–November and November–February (middle panel) are clearly separated (minimum overlap between sequential periods <21%), thus indicating separation of seasonal ranges. Conversely, the seasonal ranges based on the first and last periods (top and bottom panels) are largely overlapped, indicating a return to the same winter range. On the basis of these two results, Method 1 classified ID = 20 as migrant. In b, seasonal home ranges do not separate for any combination of sequential periods. The panel in the middle represents the minimum overlap, which exceeds 21%. Thus, the method overlap classified ID = 141 as non-migrant. Note that the minimum overlap case for ID = 141 (middle panel) is due to a temporary home range expansion.

tions of the winter range. Consistently, the automated procedure (Appendix S1) selected the middle panel as the correct minimum overlap. The middle panel in Fig. 2b (ID = 141) shows a larger seasonal range based on the intermediate time interval, thus leading to minimum overlap across all combinations, but without leading to a value below the threshold and a clear separation between seasonal ranges.

CLUSTER

Because cluster definition is independent of time, clusters identify *spatial separation only* between ranges (Fig. 3). The temporal separation in the use of clusters is observed with the following step in the procedure, that is by plot-

ting the *maximum continuous residence time* rescaled as yearly proportions in each seasonal cluster, one against the other (Fig. 4). These plots summarize the *variability* of space use across seasons by the individual animals of a species. The spread of points *within* a population indicates the prevalent seasonal space-use pattern as migration, partial migration or residency.

The spread of points *across* populations indicates the *plasticity* of a species along the residency to perfect migration continuum. In our sample of individuals, reindeer were obligatory migrants with equal time spent in summer and winter clusters (with the exception of two individuals). Similarly, all red deer in Norway showed a clear migratory behaviour. On the contrary, half of the red deer were classified as migrants in Germany. Among those, few spent a

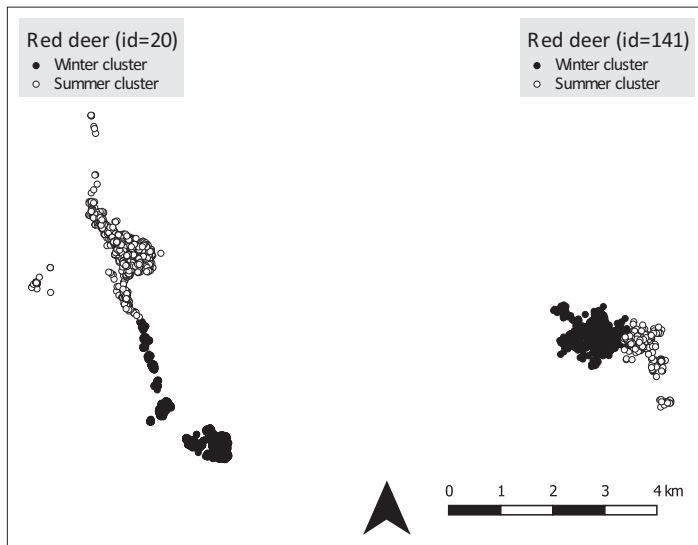


Fig. 3. Seasonal clusters for two individual red deer (same as Fig. 2: ID = 20 and ID = 141, Germany), obtained with the method Cluster. The first animal presents two clearly spatially separated seasonal clusters, whereas the second one does not, despite showing a preferential seasonal use for parts of the home range. Moreover, the maximum residence time exceeded the threshold value of 1 month in both clusters for the first animal (maximum residence time in summer: 180 days; Table S2), but not the second. Thus, the method cluster classified ID = 20 as migrant, while ID = 141 as non-migrant.

similar amount of time in both clusters, whereas most individuals spent most time in one of the two clusters only (Fig. 4). Finally, roe deer showed a different migratory pattern between Norway and Bavarian Forest, although both populations were partially migratory. In the first population, migratory individuals resided continuously in either winter or summer range, while in the second population, some migratory individuals tended to commute between ranges and stabilize in either range for a much shorter time.

Finally, the cluster approach does not distinguish between migration and 'no-return' movements. A way to account for that would be to identify the migration trajectories and their directionality between clusters (Cagnacci *et al.* 2011).

NET SQUARED DISPLACEMENT

The NSD method selected the migration model in almost all cases for reindeer and red deer populations in Norway, and in about half of the cases for all other populations (Table 2, Appendix S2). The same individual red deer examples described above (Figs 2 and 3: Germany ID = 20 and ID = 141) are shown in Fig. 5. The migration model was selected as the best one in both cases, but with very different values of CC. In particular, for ID = 141, CC = 0.1, in a scale from 0 to 1, indicating that NSD could not reliably classify this trajectory.

Notably, several cases were classified as 'no-return' movement in fitting a linear (nomadic) or single sigmoid function (dispersal), which is similar to the results from the overlap method (Table S2). In case of missing convergence of models, we applied the procedure in Bunnefeld *et al.* (2011), although we note that, alternatively, convergence of the mixed effects models might have been obtained by changing the control parameters of the nlme function (Pinheiro *et al.* 2015).

COMPARISON BETWEEN METHODS

A very high match between all methods was obtained in classifying reindeer and red deer in Norway where most individuals were classified as migrants (Fig. 6). The percentage of matching individual classifications for partially migratory populations was instead much lower, with no clear pattern except that the cluster vs. NSD approach matched less often than the other two comparisons. Notably, this was not due to classification of one method biased towards migration or non-migration, because all methods clearly identified partial migration in those populations (Table 2). Instead, the inconsistency among methods emerged at the individual level (Table S2) in the case of partial migration. This observation is confirmed by the best fit of the generalized linear model explaining probability of matching classification between pairs of methods: the model selection indicated that the main factor was the population, with reindeer and red deer, Norway, much more likely to be consistently classified as migrants than in other populations (Table S3). Thus, consistent classification between methods likely identifies stereotyped migration or non-migration cases, whereas inconsistencies probably identify less-stereotyped cases, such as trajectories with a mixed migratory behaviour.

When migration was consistently predicted by all methods (Fig. 6, Table S2), the estimates of the distance of migration did not differ significantly between methods (one-way repeated-measures ANOVA: $F = 2.19$, d.f. = 2.982, $P = 0.12$) nor did the residence time in summer range ($F = 0.51$, d.f. = 2.74, $P = 0.60$).

Finally, the plot of timing of migration (Fig. 7) indicated a very similar pattern for all populations in terms of differences between methods. NSD estimated migration date in spring and in autumn much sooner than other methods, as both cluster and overlap estimates are derived from the 'ar-

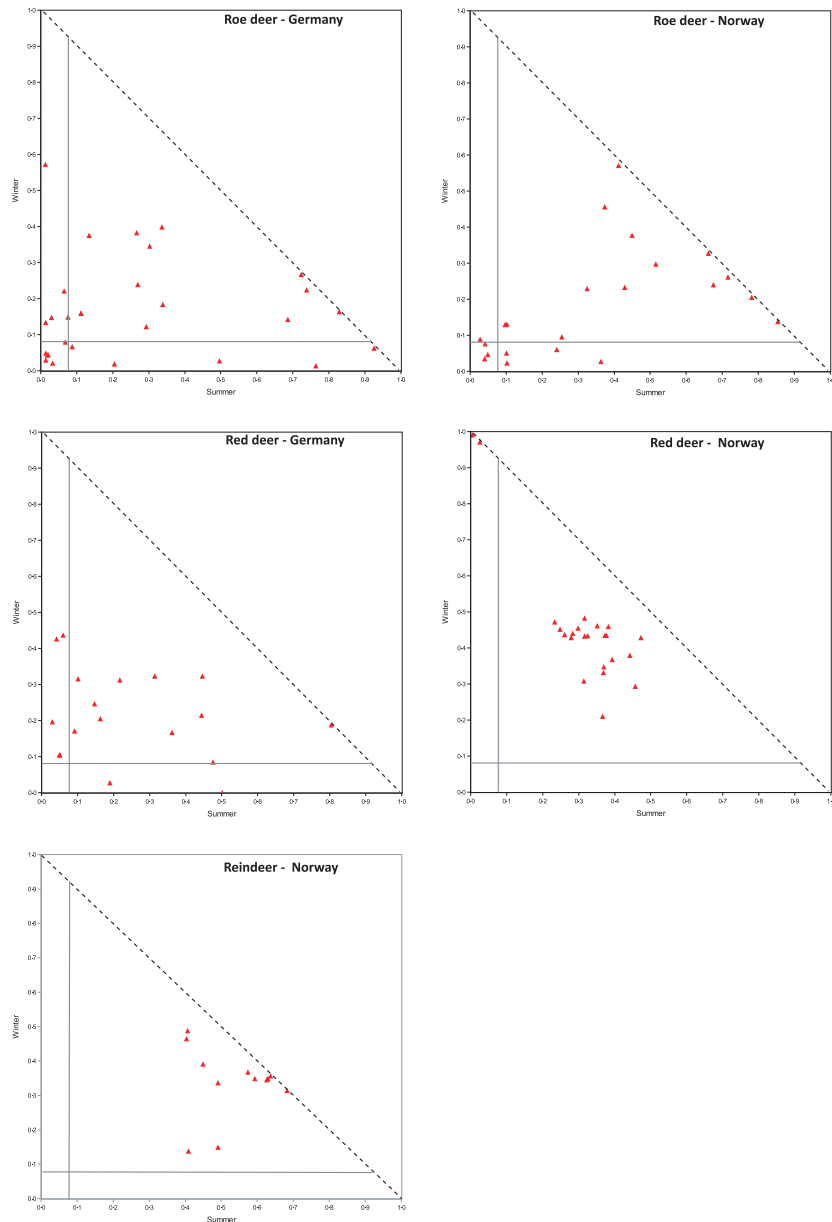


Fig. 4. Maximum residence time in winter (y-axis) and summer (x-axis) clusters, as determined by the spatial separation of locations (method cluster), for each individual of the studied populations (Table S2). The values of residence time are rescaled as proportion of the year. The dashed line represents the limit of possible values (i.e. sum up to 1), so that individuals further away from the line take longer to migrate. The spread of points of all individuals quantifies partial migration, and the residency-to-migration continuum. We considered 1 month (yearly proportion = 0.087, grey lines in the graph), as a threshold continuous time to spend in each cluster, to discriminate between migrants and non-migrants. We expect obligatory migrants to spend an extensive period of continuous time in both ranges (central portion of the graph), whereas resident individuals would use the whole home range at the same time (portion of the graph close to the origin). However, several other tactics are possible and can effectively be detected on the graphs. For example, the use of separated ranges on multiple periods (commuting behaviour: intermediate portion of the graph), or use of one of the two ranges as a 'seasonal refuge', that is for a very limited time only (cases close to the axes).

rival' date in the summer range. Despite these differences, dates of migration varied across species and populations. For example, in spring reindeer migrated sooner than red deer in Norway, but autumn migration seemed to happen at the same time across these two species. Red deer in Norway migrated sooner than in Germany (but not according to NSD). Finally, roe deer showed a consistent migration date in Norway and Germany in spring, but not in autumn.

Discussion

Migration is movement by individuals that can be scaled up and described for a population (Dingle & Drake 2007; Fig. 1). In this paper, we showed that methods consistently classified and characterized migratory behaviour at the population level, but not necessarily at the individual level (Table 2 vs. Table S2; see also Fig. 6). If

a population were detected as fully (or almost fully) migratory by one method, the probability of consistent classification of individual trajectories by other methods was very high. In contrast, the classification of partial migration by methods among individuals was much more inconsistent across methods. However, in both cases, all methods were consistent in identifying the population-level strategy. This generality may seem trivial, but it has significant consequences for applying the methods to ecological questions: identifying migration was an easy task for complete migration at the individual level, and obligatory migration at the population level because it is a neat and stereotypic spatial behaviour. In contrast, it was harder to detect and characterize the unique migratory behaviours of partial migrants. Remarkably, this was not strictly dependent on the species, or on the distance that animals migrated. The same species in two different popu-

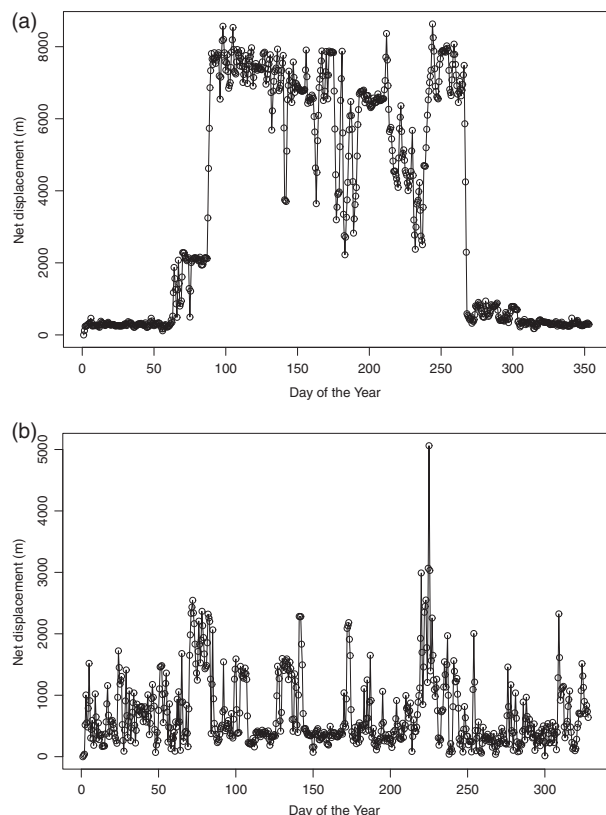


Fig. 5. Net displacement of two individual red deer over 1 year (same as Figs 2 and 3; a: ID = 20 and b: ID = 141, Germany). The migration model was selected as best one in both cases, but with very different values of Concordance Criterion (CC). In particular, for ID = 141 CC = 0.1, in a scale from 0 to 1, indicating that NSD could not reliably classify this trajectory.

lations showed varying proportions of individuals being classified as migratory among methods (e.g. red deer in Norway and Germany).

Our results strongly support the hypothesis that partial migration not only manifests itself as 'a portion' of indi-

viduals migrating, but also with varying patterns of intermediate or inconsistent migratory behaviours (Dingle & Drake 2007; Cagnacci *et al.* 2011). Partial migration is now considered the rule, rather than the exception, across several species and animal populations (Chapman *et al.* 2011). Intermediate space-use strategies between residency and complete migration, such as commuting behaviour, use of stop over sites or use of spatially separated refuges only in extreme occurrences, are common in partially migratory populations (Ball, Nordengren & Wallin 2001; Cagnacci *et al.* 2011). Intermediate behaviours of space use might therefore be evidence of a 'residency-to-migration' continuum (Ball, Nordengren & Wallin 2001; Dingle & Drake 2007). Under the current climate and land-use changes, animal populations are likely to shift along such continuum. For example, in this study, we have compared two populations of red deer, one (Norway) showing complete migration, the other partial migration with less-stereotyped migratory patterns (Germany), according to all methods. Considerable changes in winter conditions or plant phenology in Norway might result in the future in a shift towards partial migration (Mysterud 2013). Notably, the same plasticity might be found also at the individual level, with animals switching between migration and residency across years (Fieberg, Kuehn & DelGiudice 2008), for example in dependence of winter severity (Cagnacci *et al.* 2011). As such, it is important to understand the mechanisms underlying intermediate migratory behaviours in the residency-to-migration continuum. Indeed, one ideally should adopt a conceptual framework of such a continuum, instead of 'forcing' methods to identify stereotyped movement patterns. To our knowledge, a continuous metric that quantifies this variation along the migration gradient is not currently available (but see Damiani, Issa & Cagnacci 2014; Damiani *et al.* 2015; E. Gurarie, pers. comm.).

An interesting result of our comparison is the statistical concordance among methods in characterizing stereotyped

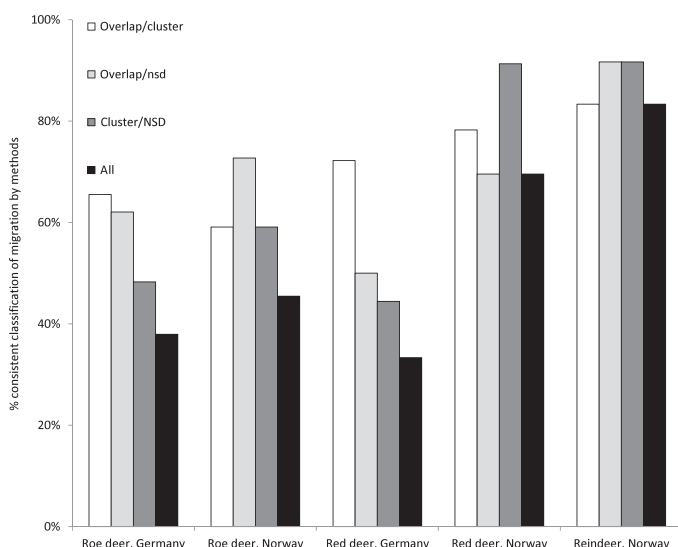


Fig. 6. Percentage of consistent classification of yearly individual trajectories as migratory/non-migratory, by pairs of methods, and all three methods. Methods: overlap (seasonal home range overlap); cluster (spatio-temporal separation of seasonal clusters of locations); Net Squared Displacement (NSD). We found no effect of the type of method on probability of consistent classification as migrant or non-migrant, but a strong effect of populations. In particular, those population with the higher number of migration cases were more likely to be consistently classified by at least two methods.

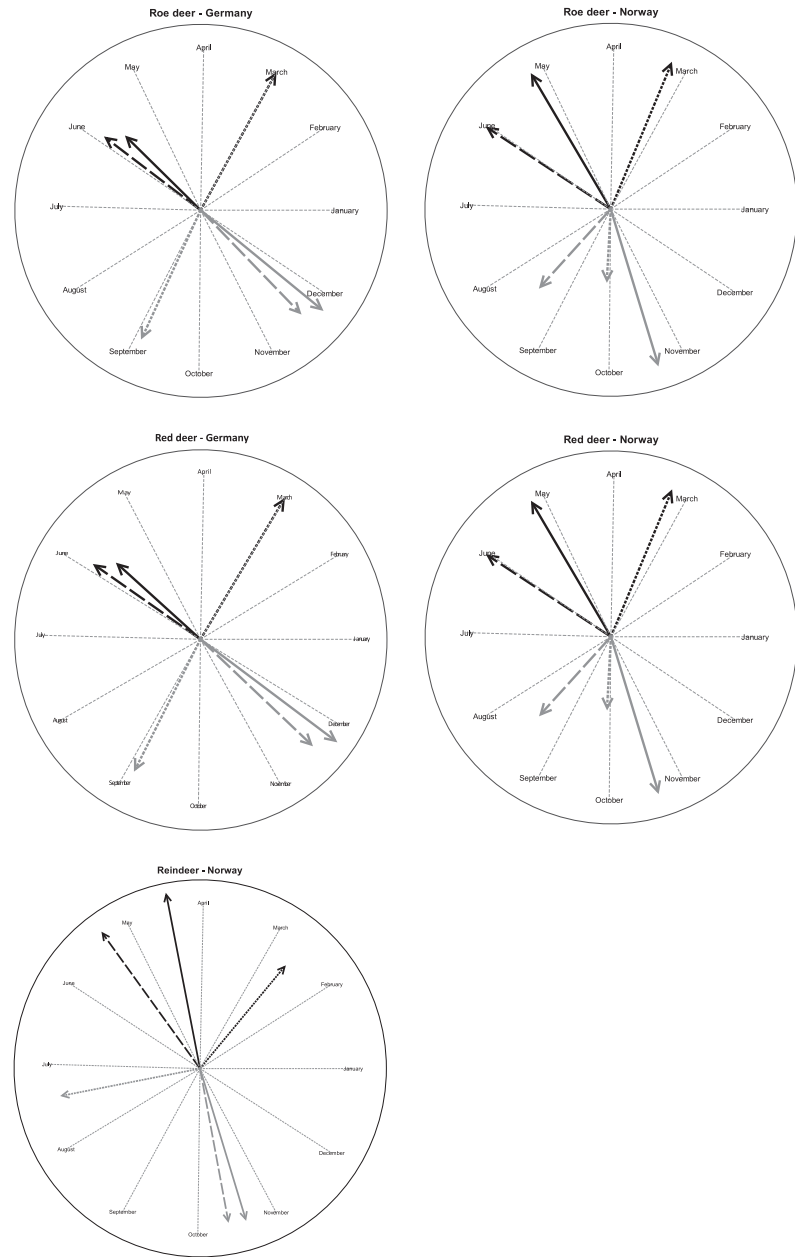


Fig. 7. Comparison of the timing of seasonal migration obtained with different methods (overlap: dashed-line arrows; cluster: solid-line arrows; Net Squared Displacement (NSD): dotted-line arrows), for the studied species/populations, in spring (black arrows) and autumn (grey arrows). We expressed the Julian dates of migration as angles and used circular statistics to assess synchrony of migration. The arrows point to the average migration date of each population, in spring–summer and fall–winter, in a circle with 1st of January at 0 radians. The length of the resultant vector (ρ , comprised between 0 and 1) is inversely proportional to the standard deviation of migration dates across individuals, therefore indicating the degree of migration synchrony among individuals. When $\rho = 1$, then individuals in a population migrate all in the same day, and the arrow touches the trigonometric circle. When $\rho = 0$, migration dates are distributed at random.

migration trajectories (distance, summer residence). Although this might not be surprising, the methods indeed used disparate approaches.

One probably inevitable limitation of all the methods is the need to fix some parameters *a priori*. First, we arbitrarily defined the date of initial monitoring. In general, timing of migration in vertebrates can be extremely variable, and dependent on a variety of factors, both external and endogenous. We fixed the initial time of monitoring on 15th February, considering this as an early enough date to catch spring migration in Boreal hemisphere for deer species. However, later initial dates were included up to 15th April, not to exclude data sets of animals marked later in the season. In the overlap method, the date of initial monitoring affects the time window of the first sea-

sonal home range. The system of shifting time windows to identify successive seasonal ranges, defines the temporal phases of migration in a standardized way, partially independent from the monitoring schedule. The same applies to NSD that however strictly depends on the definition of the starting point, so that if migration started *before* the date of initial monitoring, some unexpected results can be obtained (see the negative or very large or missing values of timing of migration in Table S2). Our conclusion here is that there is no general rule to set the initial sampling date because timing and, even more importantly, variability of timing of migration depends on species and environmental context (see Cagnacci *et al.* 2011; this study). We suggest to set the initial date on previous species-specific knowledge, that is biological–ecological criteria,

and test sensitivity to earlier initial dates. The cluster method is less dependent on initial date than the other two methods because locations are ‘assigned’ to clusters according to a purely spatial criterion (but see missing values in timing of migration for late migrations, Table S2).

Temporal resolution of UD is another parameter to be fixed and similar to the threshold for continuous residence time spent in each cluster to determine temporal separation of clusters. In both cases, we chose 1 month because we studied long-lived vertebrates. This may not be appropriate for other species. Again the choice depends on previous knowledge of a species if available or sensitivity analyses have to be carried out with different resolution of time intervals.

A similarity between overlap and NSD was the possibility to classify other movement behaviours in addition to migration, which we synthetically defined as ‘no-return’ movements. Indeed, most cases identified as ‘no-return’ movements by the overlap method were also distinguished from migration by NSD. The same cases were instead classified as ‘migration’ by cluster because a spatio-temporal separation between clusters was recognized; however, the ‘return phase’ could not be automatically detected (Table S2). Interestingly, the flexibility of overlap and NSD in classifying multiple movement behaviours comes from two very different features. Overlap is spatially explicit and based on a very simple measure, that is, overlap of successive ranges at variable time intervals. Because animals would range over a certain area in a given time interval, most movement behaviours can lead to expected predictions. For example, in residents, a very high overlap among successive ranges is expected. In contrast, migrants have a low overlap between successive seasons, but high overlap between the same seasons across years is expected (but see Fieberg, Kuehn & DelGiudice 2008, and above). Dispersal behaviour would correspond to low overlap between successive seasons, and also between the same seasons in two successive years. Finally, in the case of nomadic behaviour, a low overlap between successive ranges is expected at all times. In contrast, NSD is a mechanistic method based on fitting NSD to pre-defined nonlinear models, corresponding to specific movement patterns. NSD provides in this sense a unifying movement modelling framework that includes migration (Börger & Fryxell 2012). Notably, the use of the CC to evaluate model fitting (Börger & Fryxell 2012) provides the goodness-of-fit of the best selected model, and therefore a measure of how much the data are described by a specific movement pattern.

With our comparison of methods used to quantify migration, we showed that the chosen approach affects the identification of migratory behaviour. Identifying and ‘monitoring’ migratory events is becoming of paramount applied importance for conservation in the current scenario of climate (Harris *et al.* 2009) environmental (Mysterud 2013; Panzacchi *et al.* 2015) and migratory rate change (Middleton *et al.* 2013), which can hamper ecosystems

function (Bauer & Hoyer 2014). We showed that different methods may result in inconsistent conclusions. However, we also suggest that inconsistent classification of migration cases reveals less-stereotyped behaviours along the residency-to-complete migration continuum. Arguably, this may be the most important result of our analysis, and an impetus to developing new metrics accounting for migratory plasticity. Ideally, an ‘index of migratoriness’ should be able to catch the spatio-temporal variability of the migratory behaviour, such as separation and use of seasonal ranges, travelling distance and characteristics of the migratory trajectories Damiani *et al.* (2015). In other words, an ‘index of migratoriness’ would be directed towards deriving a continuous index for a migration continuum based on definitions 9–17 in Table 1 and Fig. 1 (movement patterns and spatial outcome of migration). Also, an ‘index of migratoriness’ would quantify migratory patterns of individuals, but could also be used to scale-up at the population level (Fig. 1; Mueller & Fagan 2008).

Alternatively, other prospective metrics may attempt to summarize the ecological determinants of migration, or the external context where the migration occurs (Fig. 1). The external context potentially can be shaped as the geographic space, particularly in terms of spatial heterogeneity and temporal predictability of resources (Mueller & Fagan 2008; Teitelbaum *et al.* 2015; definitions 6–8 in Table 1), or as the ecological space, or realized niche (Laube, Graham & Böhning-Gaese 2015).

Under the current state of knowledge, we suggest several key points to take into consideration when classifying migratory behaviour. First, we recommend using at least two methods to identify migration occurrence, for example one based on spatial-explicit measures (overlap or cluster), the other on model selection (NSD). Secondly, the three methods we used here have parameters that can help resolve single doubtful cases, by studying the sensitivity of results to their modulation. Thirdly, our results suggest ecologists should not ‘discard’ animals that are difficult to classify, because they may represent an important proportion of the population. Describing and hence understanding their less-stereotyped migratory behaviour may help uncovering new components of the migration complexity. Process-based methods (see Bauer & Klaassen 2013, for a review), such as fractal analysis (Nams 2005), behavioural change point analysis (Gurarie, Andrews & Laidre 2009; Gurarie *et al.* 2015), mechanistic models based on biased and correlated random walks (McClintock *et al.* 2012), may help investigate the behavioural ‘profiling’ of a track, especially in less-stereotyped cases.

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Data accessibility

- The main data set is available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.rg0v3> (Cagnacci *et al.* 2015).
- The data tables in the format to run the overlap scripts in Appendix S1 are made available as supporting information (Data S1–S3).
- R and SAS codes are accessible and fully commented in Appendices S1–S3. The R code in Appendix S1 is also deposited at <https://bitbucket.org/aghisla/homerange-overlap>.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Deer population and datasets used for the comparison of methods to determine occurrence and metrics of migration.

Table S2. Comparison between different methods to assess occurrence of migratory behaviour and related characteristics, for each individual of the studied populations.

Table S3. Model selection for probability of consistent classification of migration occurrence between methods (Generalised Linear Model with binomial error distribution; $n = 375$).

Data S1. GPS locations of the studied individuals, formatted to be recalled by the script in Appendix S1.1.

Data S2. All possible combinations of the shifting time windows for method ‘overlap’.

Data S3. All possible combinations of the shifting time windows joined to individuals, for method ‘overlap’.

Appendix S1. Procedure and R software script (R Development Core Team 2013) for computing UD minimum overlap of animal locations grouped by different time intervals.

Appendix S2. Procedure for the spatio-temporal separation of seasonal clusters, Including SAS (2010) software 9.3 script.

Appendix S3. Net Squared Displacement analysis procedure, including R script.