

# A framework for modelling range shifts and migrations: asking when, whither, whether and will it return

Eliezer Gurarie<sup>\*,1</sup>, Francesca Cagnacci<sup>2,3</sup>, Wibke Peters<sup>2,4</sup>, Christen H. Fleming<sup>1,5</sup>, Justin M. Calabrese<sup>1,5</sup>, Thomas Mueller<sup>6,7</sup> and William F. Fagan<sup>1</sup>

<sup>1</sup>Department of Biology, University of Maryland, College Park, MD 20742, USA; <sup>2</sup>Biodiversity and Molecular Ecology Department, IASMA Research and Innovation Centre, Fondazione Edmund Mach, San Michele all'Adige, Italy;

<sup>3</sup>Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA, USA; <sup>4</sup>Wildlife Biology Program, College of Forestry and Conservation, University of Montana, Missoula, MT, USA; <sup>5</sup>Conservation Ecology Center, Smithsonian Conservation Biology Institute, National Zoological Park, Front Royal, VA, USA; <sup>6</sup>Biodiversity and Climate Research Centre, Senckenberg Gesellschaft für Naturforschung, Frankfurt, Germany; and <sup>7</sup>Department of Biological Sciences, Goethe University Frankfurt, Frankfurt, Germany

## Summary

1. Many animals undertake movements that are longer scaled and more directed than their typical home ranging behaviour. These movements include seasonal migrations (e.g. between breeding and feeding grounds), natal dispersal, nomadic range shifts and responses to local environmental disruptions. While various heuristic tools exist for identifying range shifts and migrations, none explicitly model the movement of the animals within a statistical framework that facilitates quantitative comparisons.

2. We present the mechanistic range shift analysis (MRSA), a method to estimate a suite of range shift parameters: times of initiation, duration of transitions, centroids and areas of respective ranges. The method can take the autocorrelation and irregular sampling that is characteristic of much movement data into account. The mechanistic parameters suggest an intuitive measure, the range shift index, for the extent of a range shift. The likelihood based estimation further allows for statistical tests of several relevant hypotheses, including a range shift test, a stopover test and a site fidelity test. The analysis tools are provided in an R package (MARCHER).

3. We applied the MRSA to a population of GPS tracked roe deer (*Capreolus capreolus*) in the Italian Alps between 2005 and 2008. With respect to seasonal migration, this population is extremely variable and difficult to classify. Using the MRSA, we were able to quantify the behaviours across the population and among individuals across years, identifying extents, durations and locations of seasonal range shifts, including cases that would have been ambiguous to detect using existing tools.

4. The strongest patterns were differences across years: many animals simply did not perform a seasonal migration to wintering grounds during the mild winter of 2006–2007, even though some of these same animals did move extensively in other, harsher winters. For seasonal migrants, however, site fidelity across years was extremely high, even after skipping an entire seasonal migration. These results suggest that for roe deer behavioural plasticity and tactical responses to immediate environmental cues are reflected in the decision of *whether* rather than *where* to migrate. The MRSA also revealed a trade-off between the probability of migrating and the size of a home range.

**Key-words:** *Capreolus capreolus*, continuous time movement models, migratoriness, OU process, OUF process, partial migration, roe deer

\*Correspondence author. E-mail: egurarie@umd.edu

## Introduction

Movement events on much longer scales than typical ranging are commonly observed in animal (Dingle & Drake 2007). The most common kinds of long range movements are dispersal, periodic migrations and nomadic movements (Mueller & Fagan 2008; Baguette *et al.* 2013). Such movements can be considered meso-scale movement phase processes (*sensu* Nathan *et al.* 2008) in that they occur at larger temporal and spatial scales than the tactical steps (e.g. of searching, foraging and homing), but are shorter than the lifetime track. Identifying and understanding these processes is of great interest for understanding animals' ecology and evolution (Mueller & Fagan 2008; Nathan *et al.* 2008; Chapman *et al.* 2011; Middleton *et al.* 2013).

Seasonal migration, defined as the movement of individuals from one region to another in response to annual changes in resources in space, most commonly between seasonally determined breeding and feeding grounds (Fryxell & Sinclair 1988; Dingle & Drake 2007), has long been the most intensely studied mesoscale movement process. The dynamics of seasonal migrations can be highly variable and unpredictable, both among and between individuals and populations. Partial migration, which occurs when only a fraction of the population migrates and another fraction remains resident (Dingle & Drake 2007) occurs widely across taxa, including birds (Berthold 2001), fish (Kerr, Secor & Piccoli 2009; Wysujack *et al.* 2009) and many ungulates (Ball *et al.* 2001; White *et al.* 2007; Cagnacci *et al.* 2011; Myrsetrud *et al.* 2011). Theoreticians have explored trade-offs between food availability, risk factors such as predation (Hebblewhite & Merrill 2009) and breeding potential as explanations of partial migration (Kaitala, Kaitala & Lundberg 1993; Taylor & Norris 2007; Griswold, Taylor & Norris 2010; Shaw & Levin 2011).

Most studies of partial migration are concerned with clear distinctions between migrants and non-migrants within a population. In some partially migratory populations, however, migratory behaviour can vary along a gradient from residency to migration within and among individuals and years (Dingle & Drake 2007; Cagnacci *et al.* 2011). Furthermore, seasonally migratory behaviours might best be viewed within a behavioural continuum of space use tactics that includes sedentarism and nomadism (Dingle & Drake 2007; Mueller & Fagan 2008; Börger & Fryxell 2012; Cagnacci *et al.* 2016). Beyond partial migration in a population, additional complexities arise when a migration distance is very short or difficult to detect. Short distance migrations are common in mountainous regions with high landscape diversity, where short planar migration distances correspond to dramatic altitudinal shifts in habitat (LeResche & Rausch 1974; Boyle *et al.* 2011). Intermediate or ambiguous cases, in which seasonal ranges overlap or there are multiple shifts, are particularly hard to characterize into a binary

migratory vs. non-migratory framework of space-use strategies (Cagnacci *et al.* 2016). Given these complexities, there is value in building a mechanistic migration model that shifts the paradigm from a binary identification of migration to a framework for quantifying a degree of migration, or *migratoriness*, within a spectrum of possible behaviours (Cagnacci *et al.* 2016).

Previous efforts to quantify migratoriness have been largely heuristic or descriptive, without recourse to a mechanistic movement model (though see Johnson *et al.* 2002). Standard tools to quantify migration rely on comparing seasonal range estimates (Craighead, Atwell & O'Gara 1972), such as utilization distribution overlap (Fieberg & Kochanny 2005), algorithms to characterize spatial clustering (Cagnacci *et al.* 2011), or a distance measure like net-squared displacement (NSD) (Börger & Fryxell 2012; Spitz, Hebblewhite & Stephenson 2017) (see Cagnacci *et al.* (2016) for a recent review of methods). These techniques, while often effective, are either entirely spatial or, when they do include a temporal component, reduce the spatial component to a single dimension. One recent approach analyses clustering of locations in a space-time cube to identify 'stay regions' (Damiani *et al.* 2016), though this method does not take into account autocorrelation in the process.

In contrast to these mainly spatial approaches, there are several analysis frameworks devoted to behavioural partitioning of the movement process itself, such as multi-state random walk models (Morales *et al.* 2004; Patterson *et al.* 2008), behavioural change point analysis (Gurarie, Andrews & Laidre 2009; Kranstauber *et al.* 2012) and Bayesian partitioning (Calenge 2006) that might be expected to be useful for identifying migrations. These can be effective at partitioning more transitory from more tortuous movements. However, they typically do not incorporate absolute spatial information like centres of attraction (though see McClintock *et al.* 2012; Blackwell *et al.* 2015), a critical weakness that compromises their ability to detect range shifts (Gurarie *et al.* 2016).

Some of the challenges of studying partial migration are similar in many ways to the phenomenological and descriptive challenges involved in analyses of home ranges and territories (Börger, Dalziel & Fryxell 2008; Fieberg & Börger 2012). Strengths and weaknesses of statistical estimators of home ranges such as kernel density estimators and minimum convex polygons have been extensively reviewed (Laver & Kelly 2008; Kie *et al.* 2010; Lichti & Stewart 2011), with a compelling argument made that the appropriate metrics should be driven by the research question (Fieberg & Börger 2012; Fleming *et al.* 2015). A mechanistic, movement-based approach with absolute spatial and temporal information seems like a necessary basis for the study of range shifts and migration.

Here we propose just such a method: the mechanistic range shift analysis, or *MRSA*. The method (i) estimates the spatial and temporal structure of both the ranging process and the range shift, (ii) leads to a continuous

index of range shifting and (iii) provides likelihood-based statistics for estimating confidence intervals and hypothesis testing. As a case example, we applied the method to a movement dataset of roe deer (*Capreolus capreolus*) in the Italian Alps, a population which exhibits a wide variety of range shifting behaviours within and between individuals. While we are primarily motivated by analyses of seasonal migrations, the model can also be applied to dispersal events, multi-staged nomadic type movements or fine scaled behavioural changes.

## Model

### MODEL DESCRIPTION

We conceptualize the location of an animal in time  $\mathbf{z}(t)$  as a possibly autocorrelated fluctuation  $\mathbf{r}(t)$  around a mean process  $\mathbf{m}(t)$ :

$$\mathbf{z}(t) = \mathbf{m}(t) + \mathbf{r}(t)$$

where bold facing indicates 2D vectors representing an animal location on a plane in consistent units in x and y, for example in Universal Transverse Mercator (UTM) easting and northing projections of geographic data.

The mean component describes the range shift, thus its key parameters are the central location of each focal range and the timing (beginning and duration) of each transition. A simple range shifting event with no stopovers can be modelled as one where  $\mathbf{m}(t)$  shifts from one location to another over some transition duration  $\Delta t$  beginning at some time  $t_1$

$$\mathbf{m}(t) = \begin{cases} \mathbf{m}_1 & \text{where } t < t_1 \\ \mathbf{m}_1 + (\mathbf{m}_2 - \mathbf{m}_1) \times (t - t_1) / \Delta t & \text{where } t_1 < t < t_1 + \Delta t \\ \mathbf{m}_2 & \text{where } t > t_1 + \Delta t \end{cases} \quad \text{eqn 1}$$

A process with  $k > 1$  ranges is described by  $4k-2$  parameters ( $\{x, y\}$  locations for each of  $k$  ranges and initiation and duration times for  $k-1$  transitions). We denote the complete set of mean shift parameters as  $\theta_m = \{x_i, y_i, t_j, \Delta t_j\}$ , where  $i \in (1, 2, \dots, k)$  and  $j \in (1, 2, \dots, k-1)$ . A useful measure is the distance from centroid to centroid of a given transition, i.e.  $D_j = |\mathbf{m}_{j+1} - \mathbf{m}_j|$  where the vertical bars indicate the magnitude of the vector. In subsequent analysis, we look at processes with one and two shifts (i.e. two and three ranges), including a return migration model in which the third and first centroids are equal. In principle, any arbitrary mean process with a fixed number of parameters can be similarly modelled and analysed.

The ranging term  $\mathbf{r}(t)$  captures the spatial extent of the respective home ranges and features of the autocorrelation in the data. We consider several models for the ranging component, all of which are defined in continuous time, are spatially stationary, and can be meaningfully

characterized by a ‘typical’ area of use, corresponding to the home range area at each of the animal’s central locations. A further, much stronger assumption is that the spatially stationary state is approximately isotropically bivariate normal and similar across all local ranges, though this assumption can be relaxed to incorporate different magnitudes of the  $x$  and  $y$  axis and correlation between the two (i.e. elliptical home ranges).

Three possible ranging models are (i) an uncorrelated two-dimensional white noise (WN), which is the continuous-time equivalent of independent Gaussian residuals, (ii) an Ornstein–Uhlenbeck position process (OU), which contains a first-order autocorrelation on the locations (see Dunn & Gipson 1977; Blackwell 1997 for applications to animal home ranges) and (iii) a hierarchical Ornstein–Uhlenbeck velocity and position process (OUF) which additionally models autocorrelation in the velocities (Fleming *et al.* 2014b). All of these processes can be characterized with respect to a circular area within which observations are expected to occur with 95% probability, a measure consistent with long-standing probabilistic definitions of home ranges (Jennrich & Turner 1969; Dunn & Gipson 1977). We refer to this quantity as the *ranging area*,  $A$ .

The WN process assumes ‘jumps’ with no correlation around some central location with a Gaussian distribution. It is completely specified by the central location and the ranging area, analogous to the mean and single variance, and is consequently denoted:  $\text{WN}(A, \mu_x, \mu_y)$ . The migratory white-noise process – MWN – is then additionally specified by the locations and times of the range shift, e.g.  $\text{MWN}(A, \theta_m)$ , where  $\theta_m$  represents the set of mean locations and transition times.

The OU process generalizes the WN process to allow for spatial autocorrelation by including an additional parameter,  $\tau_z$ , the time-scale of the location autocorrelation. This time-scale can be thought of, roughly, as the time it takes for an animal to move across its range. We denote the OU process as  $\text{OU}(A, \tau_z, \mu_x, \mu_y)$ , and the migratory OU process as  $\text{MOU}(A, \tau_z, \theta_m)$ . The final generalization of spatially constrained movement process is the OUF process (Fleming *et al.* 2014b), which includes a time-scale of autocorrelation of velocities,  $\tau_v$ . The migratory version is denoted  $\text{MOUF}(A, \tau_z, \tau_v, \theta_m)$ . The relationship between these models is summarized in Table 1, further technical details are provided in Appendix S1A, Supporting Information and in Fleming *et al.* (2014a) and Calabrese, Fleming & Gurarie (2016).

Actual movements, of course, are never entirely uncorrelated. Interpreted strictly, the WN and OU models assume jumps of infinite speed, and the OUF model assumes jumps with infinite acceleration. However, observations of locations are often sampled too coarsely to detect autocorrelation in the locations or velocities, in which case the appropriate model can also be uncorrelated. In practice, as shown below in the estimation of the roe deer, mean daily locations – a sufficient scale for

**Table 1.** Table of parameters and definitions. The presence of spatial and/or velocity autocorrelation determines whether the model is a migratory white noise (MWN), MOU or MOUF process respectively

Range location and size parameters				
95% ranging area	$A$			
Centroid of $k$ th range	$\mathbf{z}_k = \{x_k, y_k\}$			
Range shift parameters				
Time of initiation of $k$ 'th range shift	$t_k$			
Duration of range transition	$\Delta t_k$			
Movement parameters				
Time-scale of spatial autocorrelation	$\tau_z$	Model:	MWN	MOU
			0	(0, $\infty$ )
Time-scale of velocity autocorrelation	$\tau_v$		0	0
				(0, $\tau_z$ )
Derived measures				
Distance of range shift	$D =  \mathbf{z}_2 - \mathbf{z}_1 $			
Range shift index	$RSI = (D\sqrt{\pi})/(2\sqrt{A})$			

identifying large scale annual movements – retain no velocity autocorrelation, and the (M)OU or (M)WN models are the appropriate ones to fit.

As a continuous index of the relative extent of a range shift, we introduce a *range shift index* (RSI) defined as the ratio of the distance from the  $x, y$  locations of the range shift centroids to the diameter of ranging area. In terms of  $D$  and  $A$ , it is given by  $RSI = D/(2\sqrt{A/\pi})$ . An RSI of 0 indicates no range shift, 1 corresponds to a case where the two ranging areas are exactly adjacent but with no overlap and increasing values indicate longer migrations.

#### ESTIMATING PARAMETERS

We use likelihood methods to estimate the parameters, which allow us not only to fit models to data but also to perform inference at different levels. Likelihood-based estimates allow us to compare the values of fitted parameters with confidence intervals and likelihood-based tests allow us to select the appropriate level of autocorrelation (WN vs. OU vs. OUF), compare models with and without range shifts, with and without stopovers, and to test site fidelity.

The highest order MOUF process can be recast in terms of a single set of equations:

$$\frac{d}{dt}\mathbf{z}(t) = -\frac{1}{\tau_z}(\mathbf{z}(t) - \mathbf{m}(t|\theta_m)) + \mathbf{v}(t) \quad \text{eqn 2}$$

$$\frac{d}{dt}\mathbf{v}(t) = -\frac{1}{\tau_v}\mathbf{v}(t) + \sigma_f d\mathbf{w}_t. \quad \text{eqn 3}$$

of which the MOU and MWN processes are special cases where  $\tau_v$  or both  $\tau_v$  and  $\tau_z$  are equal to zero respectively. For a movement process  $\mathbf{z}(t) = (x(t), y(t))$  that has been sampled at (arbitrary) times  $T_i$ , a likelihood for the observations  $\{X_i, Y_i\}$  can be written down by separating the

mean component from the OUF variance component (Fleming *et al.* 2014a). This likelihood can then be numerically maximized to obtain estimates and approximate confidence intervals.

For large datasets, simultaneously maximizing the likelihood over all parameters tends to be computationally intensive and slow because it requires iteratively inverting a  $n \times n$  matrix. This process is also sensitive to initial guesses of the parameters, often failing to converge around a global maximum when applied to real data. We therefore use the following procedure to make the estimation both faster and more stable:

1. Obtain initial guesses of the centroids ( $x_i$  and  $y_i$ ) of activity either manually or using  $k$ -means clustering (`kmeans` function in R), setting the number of clusters to the desired number of ranges to estimate, e.g. two clusters for a single shift (or a shift with a return), and three clusters for two shifts.
2. Use these estimates as initial seeds to fit the mean model ( $\hat{\mathbf{m}}(t|\theta_m)$ ) by minimizing the square of the distance between the data and the mean model:  $\arg\min_{\theta_m} |\mathbf{z}(t) - \mathbf{m}(t|\theta_m)|^2$ . If the data are correlated (see next step), confidence intervals are best obtained by bootstrapping the estimates.
3. Compute the residuals ( $\mathbf{r}(t) = \mathbf{z} - \hat{\mathbf{z}}(t)$ ) and estimate the WN/OU/OUF ( $\theta_r = \{A, \tau_z, \tau_v\}$ , as necessary) from the residuals directly. It is during this step that the required level of autocorrelation is determined using Akaike's information criterion (AIC). For the WN model, the variance is simply the (isotropic) estimated variance of the zero mean bivariate normal residual. In the case of regularly sampled data, the OU process is equivalent to a first-order autoregressive (AR(1)) model (Brockwell & Davis 1996). AR models are efficiently estimated using a Kalman filter (Gardner, Harvey & Phillips 1980) (see Appendix S1C for details).
4. Calculate complete likelihoods and AIC values based on these point estimates.

One immediate application of the likelihood is to perform a variety of significance tests with biological interpretations. A *range shift test* compares fitted models with and without a single range shift. This is straightforwardly performed with a likelihood ratio test (l.r.t.) with 4 d.f. corresponding to the estimation of two more range centre coordinates and times of migration. The  $P$ -value of this test quantifies the 'detectability' of a range shift, while the RSI quantifies the 'effect size'. A *stopover test* fits a model with three ranges against a null model of two ranges, potentially picking up stations within a migration (l.r.t. with 4 d.f.). The *seasonal return test* compares a three-range model with unique centroids against a three-range model in which the initial and final centroids are identical (l.r.t. with 2 d.f.). The seasonal return test is consistent with the definition of return migration suggested by Fryxell & Sinclair (1988).

We refer to this integrated approach of fitting range shift models and testing hypotheses as a MRSA. All of



the estimation procedures were encoded in R (R Core Team 2013) with notable use of the *zoo* (Zeileis & Grothendieck 2005), *mvtnorm* (Genz *et al.* 2008) and *minpack.lm* (Elzhov *et al.* 2016) packages. The tools have been compiled into an R package, *marcher* (Migration and Range CHange Estimation in R, Gurarie & Cheraghi 2017). The package is also available in the supplementary materials with an accompanying vignette that includes additional examples of workflow and analysis.

## Applications

### SIMULATION STUDY

To explore the effectiveness of the MRSA, we performed two simulation studies: One to assess the precision and accuracy of the estimates for the three range shift models, and the second to assess the sensitivity of the range shift detection.

In the first study, we simulated 30 tracks lasting 100 days with a ranging area 100 km<sup>2</sup>, shifting at time 45 for 10 days a distance of 20 km (i.e. RSI = 1.77). We simulated 10 each of a MWN, MOU( $\tau_z = 4$ ) and MOUF ( $\tau_z = 4$ ,  $\tau_v = 1$ ) process, respectively, with completely random sampling intervals. We estimated all the MRSA parameters and illustrate the point estimates and standard errors of the time estimates (beginning and end of range shift) and the spatial estimates (area and distance of range shift). We expressly chose a relatively short ( $n = 100$ ) time series of locations with random sampling intervals, that is a typically challenging data set to analyze, to assess the robustness of the MRSA.

The second study was designed to assess the sensitivity of the MRSA by examining processes with more subtle range shifts (from RSI = 0, i.e. no migration, to RSI = 1) and applied the 'range shift test' described above. We compared these outcomes to a test based on the NSD (more details on our implementation of the NSD provided in Appendix S1D). We simulated the data similarly to the simulations above, with 100 observations of shifts that commenced at time 45 and lasted 10 time units, with an important distinction being that the times were regularly sampled in order to better accommodate the NSD method. For each of four values of RSI (0, 0.25, 0.5 and 1) and each of two models [MWN and MOU( $\tau_z = 4$ )], we simulated 100 tracks and counted the number of times each test determined that a range shift was significant at an  $\alpha$  level of 0.05.

### ITALIAN ROE DEER STUDY

#### Study species and area

We used the MRSA to analyse data collected on a group of European roe deer collared and tracked in the Monte Bondone-Monte Stivo mountain range in the Italian Alps (Fig. 1). The area (approximately 10 000 ha) is

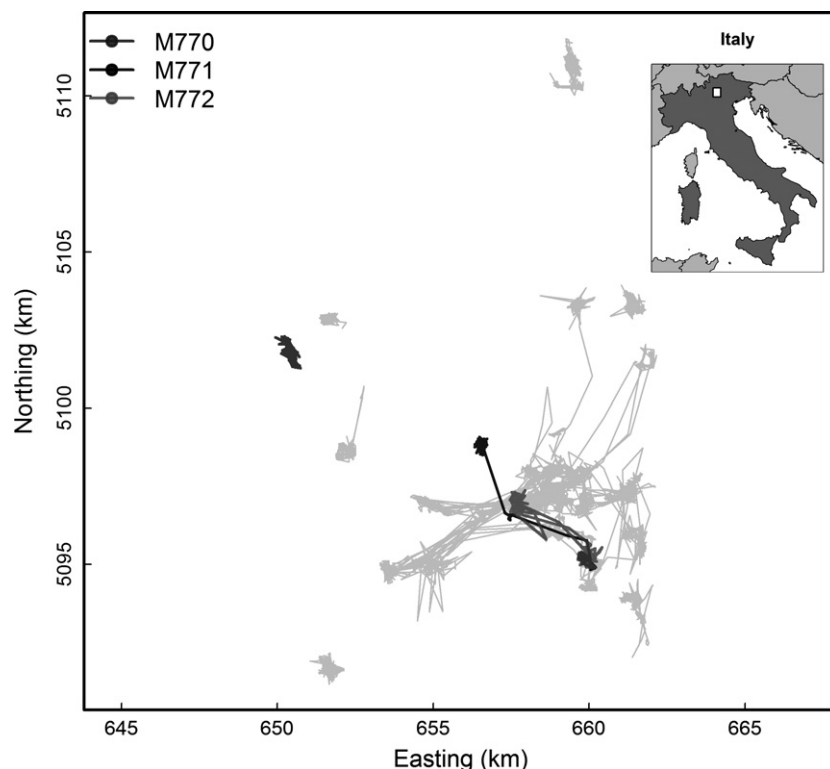
characterized by a high environmental, morphological and geological complexity, with pronounced vegetational transitions over short distances, from Mediterranean scrubwood to alpine pastures, with elevation ranges from 400 m in the main valleys to 2100 m at the highest rocky peaks. The region is likewise marked with strong seasonality with considerable spatial and inter-annual variation in snowfall and temperatures.

European roe deer are small cervids present in a wide variety of European environments, with the Alpine environment representing an altitudinal limit of the roe deer's distribution (Holand 1998). Throughout the year, roe deer alternate between two main behavioural and physiological seasons: the reproductive season in spring and summer, when this species is mainly solitary, and the winter season, when small family groups can be observed (Hewison 1998). As with other populations of roe deer at the extremes of the distribution range, this population is partially migratory, i.e. a portion of the individuals performs seasonal migrations, while others remain in one ranging area throughout the year (Mysterud 1999; Ramanzin, Sturaro & Zanon 2007). The migratory behaviour itself can be variable, ranging from two clearly established seasonal ranges, to intermediate spatial behaviours such as commuting between several ranges or intermittent migratory routes (Cagnacci *et al.* 2011). Because of the complexity and heterogeneity of the behaviour of these roe deer, they provided a challenging and rich dataset for applying and interpreting the MRSA.

#### Roe deer analysis

A total of 25 roe deer (15 females, 10 males) were captured by 'drives' (i.e. people walking aligned) into standing nets and collared with GPS tracking devices (Authorization 23 September 2004; Wildlife Committee of the Province of Trento). Age at capture was determined by body size, antler and tooth eruption, such that individuals were classified as fawns (<1 year), yearlings (between 1 and 2 years) and adults (>2 years). The majority of analysed animals were adults (18, with 5 yearlings and 2 fawns; one yearling transitioned into adult status while being monitored). GPS collars collected 6 fixes per day, with some exceptions implemented to conserve batteries (4 fixes per day in winter months) or capture behavioural details (2 fixes per h for 1 day each month). In several cases, trajectories were interrupted because of collar failures or sensitivity to limited skyview.

The average number of observations per calendar day was 4.9 (SD 3.6). Because we were not interested in circadian patterns of behaviour, we reduced the data to daily average locations using the centroid of all locations on a given calendar date. As an ancillary convenience, this reduced sample sizes and averaged away some observation error in the GPS location. On the daily time-scale we did not expect, and did not detect, any autocorrelation in the velocities. Together with the regularization of the data, this



**Fig. 1.** Roe deer GPS tracks (grey lines) in the Italian Alps (white box in inset). The three deer illustrated in Fig. 4 are in the darker grey tones. Units are in UTM zone 32T. [Correction added after online publication on 9 June 2017: Figure 1 legend changed to refer to black and white version]

allowed us to use the discrete time AR equivalence of the OU model (Appendix S1C) for estimating the parameters of the residual process. A potential drawback to the daily averaging is the introduction of a downward bias: if animals move across their entire home range over the period of a day, the daily average will cluster near the centre of the range than all the locations. To estimate this bias, we compared 95% kernel density estimates of the ranges of the complete data and the coarsened data (Worton 1995) using the *ADEHABITAT* package in R (Calenge 2006). The ratio of the resulting areas was on average 0.96 (SD 0.07), suggesting that the introduced bias was minor.

We first performed individual range shift analysis to portions of three roe deer tracks (coloured tracks in Fig. 1). The tracks were selected to highlight three different kinds of questions that can be asked via l.r.t. For the first deer (M770), the seasonal range shift, if it all present, is weakly expressed and identifying the timing and the centroids is not obvious. We perform the range shift test against a null hypothesis of no range shift. The second deer (M771) performs a very clear fall migration with a potential stopover, which we test with the stopover test. For the third deer (M772), we looked at an entire year of data, during which a clear fall and spring migration occur, and test the fidelity of the deer's return with a seasonal return test.

We then fit two-range shift models to portions of the data delineated by days of year 50–200 (19 February to 19 July) to detect spring range shifts, and between days 150 and 400 (30 May and 4 February) to detect fall range shifts. These dates were chosen in part as meaningful with respect both to the seasons and the physiological cycle of roe deer described above. However, they were also chosen

with a wide (and overlapping) time span in order to improve the quality of the estimates of the home ranges before and after a potential range shift. All tracks were subsetted to these intervals, such that some individuals with over 2 years of data had up to five analysed subsets. Where the algorithm was able, we obtained all range shift parameter estimates (with confidence intervals), range shift indices and *P*-values for a l.r.t. of range shifting. We summarized the results for *post hoc* analysis, comparing the occurrence of range shifting (determined by the  $\alpha = 0.05$  significance test), and exploring the relationships between duration, distance and ranging area while controlling for factors including year, sex and age. *Post hoc* analyses were performed with linear mixed effects models with individuals as random effects (using the *nlme* package in R; Pinheiro *et al.* 2013) and permutation-based regression (using *LMPERM*; Wheeler 2010).

Finally, for those individuals who exhibited consecutive seasonal range shifts, we applied the seasonal return test to examine site fidelity among the migrants.

## Results

### SIMULATION RESULTS

Tracks simulated from each of the three models in the first simulation study (upper panels in Fig. 2) indicate how increased correlation can make apparent ranging areas smaller due to the process not having enough time to attain stationarity (Fleming *et al.* 2015). Less obvious is the potential blurring of the timing of the beginning and ending of a range shift. Despite this and the short

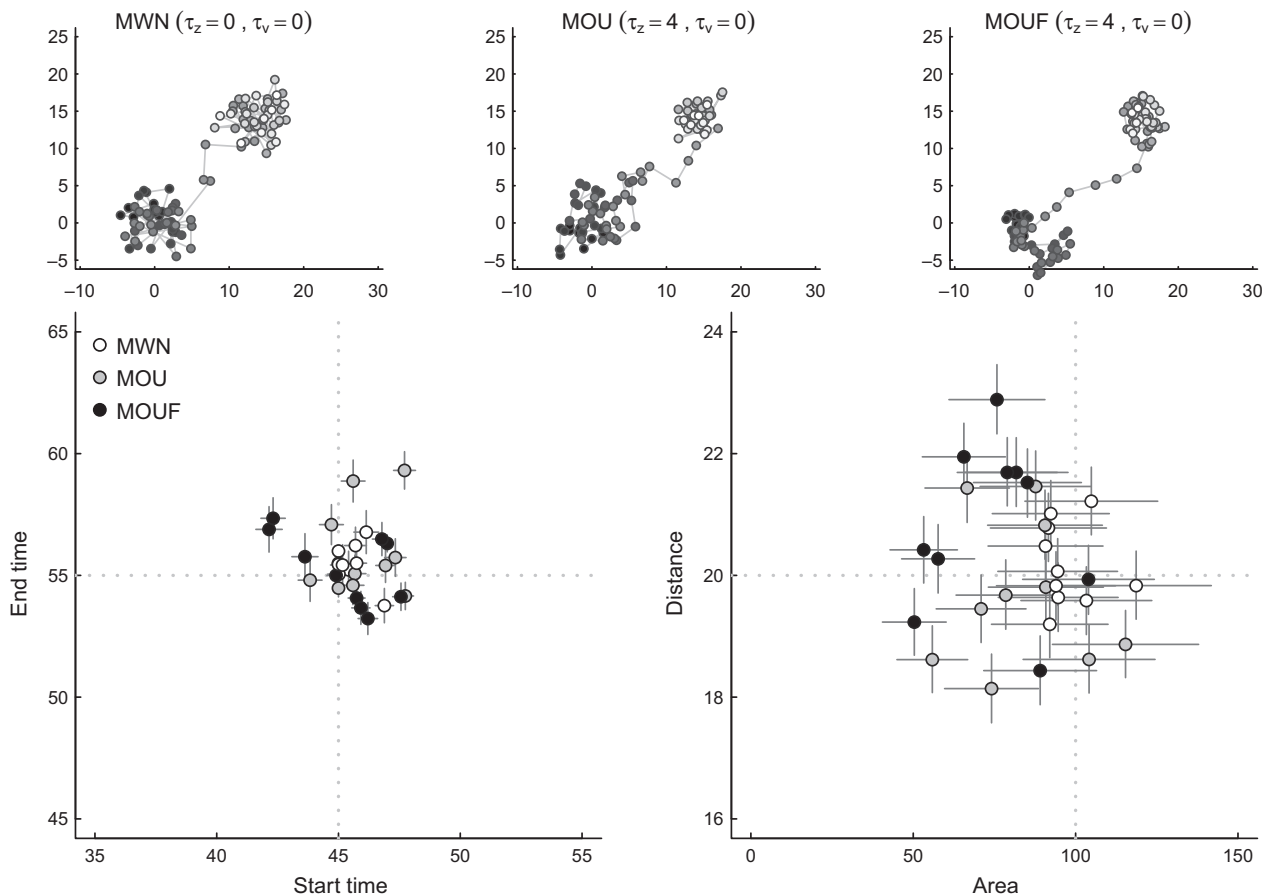
time series and irregular sampling of the simulations, most estimates were accurate (lower panels in Fig. 2). The average of the time parameter (initiation and duration) point estimates were very close to the true values of 45 and 55 for all three models ( $t_1$  means: 45.0, 45.5 and 44.7 for MWN, MOU and MOUF respectively;  $t_2$  means: 55.0, 55.5 and 54.8), with, however, higher standard errors across point estimates for increasingly correlated models (e.g.  $t_1$  SE: 0.63, 1.35, 1.93). The distance estimates were similarly unbiased with increasing standard errors (respectively, means: 20.2, 19.7, 20.8, SE: 0.22, 0.39, 0.46). The area estimates were unbiased for the MWN (mean = 97.6, SE = 2.9), and slightly downward biased for the more correlated models (MOU, mean 83.5, SE 5.9; and MOUF, mean 74.1, SE 5.7).

The sensitivity analysis suggested that both the MRSA and NSD are similarly sensitive when the movement data are uncorrelated. With no range shift, the number of false positives was just 2 and 6 ( $n = 100$ ) for the MRSA and

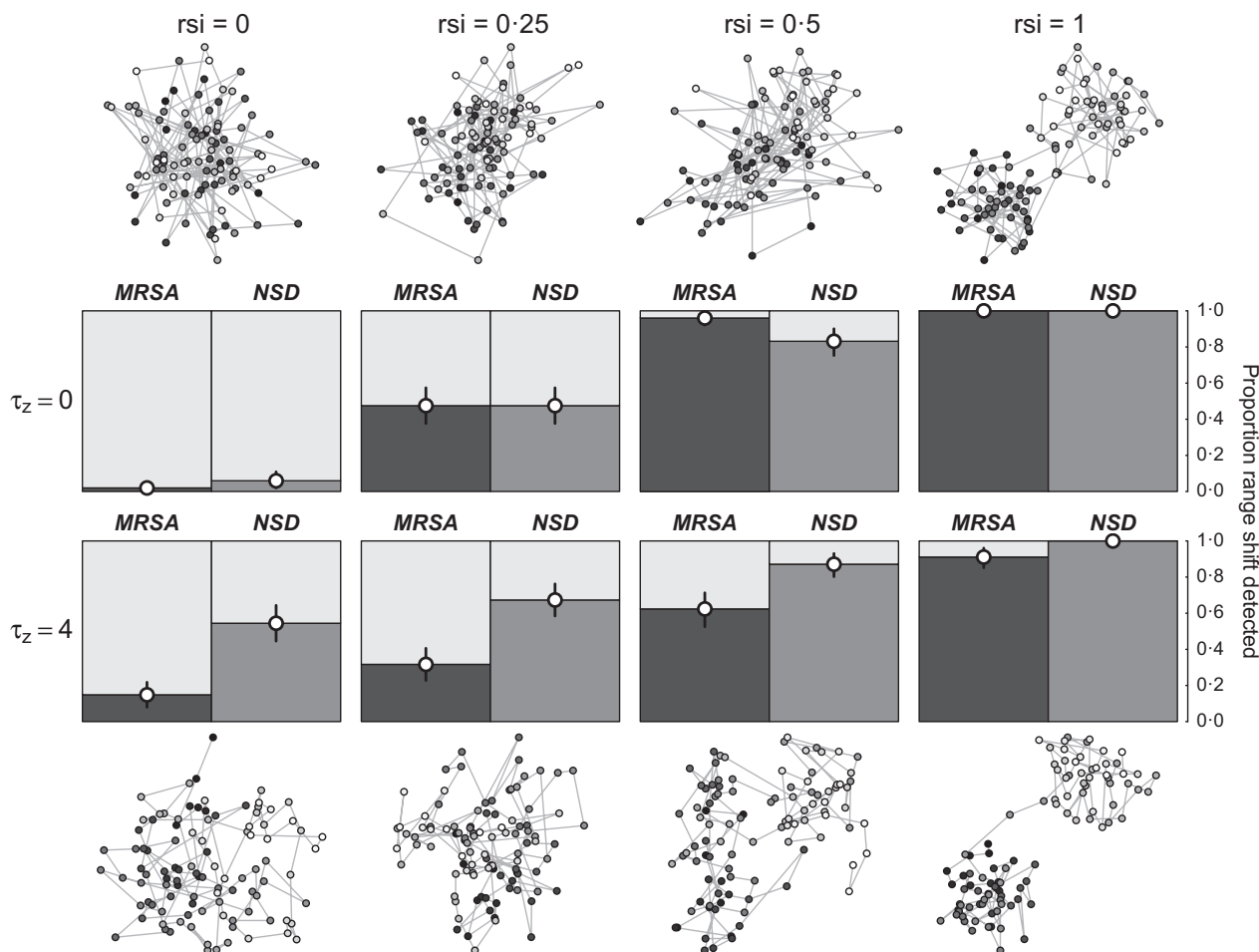
NSD respectively (Fig. 3). For cases with a very weakly expressed range shift ( $RS = 0.25$ ) about half (48 for both) detected the shift, and at  $RSI = 1$ , nearly all analyses (99 and 100, respectively) detected the shift. For the correlated model, the MRSA was slightly more likely to indicate a range shift under the no-shift scenario (15 of 100), but the rate of false positives in the NSD was much higher (55 of 100 simulations for  $RSI = 0$ ). Under the very low shift scenario ( $RSI = 0.25$ ), the MRSA was more conservative than the NSD (32 compared to 68 detected shifts respectively).

#### ROE DEER RESULTS

Parameter estimates, confidence intervals and test statistics for the three deer selected for illustration are summarized in Table 2 and presented visually in Fig. 4. The first deer, M770, underwent a relatively slow (9-day) transition around day 93 (4 April) with wide confidence intervals



**Fig. 2.** Illustration of sample range shift trajectories with different autocorrelations (upper panels) and estimates of parameters for multiple simulations (bottom panels). In all simulations, 100 locations were sampled at random intervals from the respective processes with a range shift of distance 20 occurring between time 45 and 55, with ranging area of 100 units<sup>2</sup> ( $RSI = 1.77$ ). We simulated three processes: a migratory white noise (uncorrelated process, upper left panel, white circles in lower panels), a migratory OU process with position correlation time-scale  $\tau_z = 4$  (middle panel, grey-filled circles), and a migratory OUF process with  $\tau_z = 4$  and velocity time-scale  $\tau_v = 1$  (upper right panel, black circles). Time is reflected in the increasingly lighter colours of the points. The lower left plot shows estimates of the start (x-axis) and end (y-axis) of the range shift, the lower right plot shows estimates of the ranging area and range shift distance. The bars are respective standard errors around the estimates, and true values are represented by the vertical and horizontal dashed lines.



**Fig. 3.** Sensitivity of the MRSA and NSD range shift analysis. The trajectories above and below the bars illustrate range shift processes ranging from zero shift (RSI = 0, left-most panels) to a migration as long as the diameter of the home range (RSI = 1, right-most panels), with an uncorrelated process (position autocorrelation time-scale  $\tau_z = 0$ , upper panels) and a more correlated process ( $\tau_z = 4$ , lower panels). All trajectories consist of 100 regularly sampled locations, with a 10 time-unit migration occurring in the middle of the time period (darker to lighter points indicate progression in time). The pairs of bars represent the proportion of analysis outputs for which the MRSA (left, dark bars) and the NSD analysis (right, lighter bars) determine that a range shift occurred at  $\alpha = 0.05$  significance. The error bars represent 95% confidence intervals based on 100 independent simulations for each parameter combination. For uncorrelated processes, the two methods are largely in agreement, identifying nearly none of the RSI = 0 as undergoing significant shifts, nearly all of the RSI = 1 processes, and about half of the weak RSI = 0.25 processes. The NSD analysis yields a much higher number (over 50%) of false positives in the RSI = 0 case when the data are correlated.

(15 March to 18 April), shifting a home range area of 0.44 km<sup>2</sup> (blue areas in Fig. 4) about 460 m to the south-east. This was among the more weakly expressed range shifts (RSI = 0.61), but the l.r.t. against no migration was still highly significant ( $P < 10^{-16}$ ). The selected autocorrelation was WN, indicating that the movements across the range occur at a scale comparable to or faster than the 1-day interval of sampling. The second deer, M771, performed a much less ambiguous migration on 13 November for 1.2 days, pausing at a stopover 2.4 km away from the initial range until 23 November, and then making a 1.3-day shift another 2.8 km to its final winter range (Fig. 4b). The range area estimate was somewhat smaller for this deer (just 0.3 km<sup>2</sup>), and the autocorrelation time-scale was estimated to be around 1 day. The precision of the estimates for timing were very high (standard errors less than 1 day), and the l.r.t. comparing

against a two-range model was very significant. Finally, the third deer, analysed over a 1-year period from 1 August 2005 to 31 July 2006, migrated on 3 December, moving 2.8 km to the southeast (Fig. 4c), returning the following 15 April. Both migrations were very rapid – point estimates of 1 and 1.5 days respectively. Importantly, a test comparing a fitted model with different summer range locations against a null model where  $\{x_3, y_3\} = \{x_1, y_1\}$  resulted in a  $P = 0.82$ , suggesting that the trip was a true return trip.

The single shift MRSA applied to all the roe deer ( $n = 25$ , 16 female, 9 male), broken into 63 segments (30 spring: 18 female and 12 male; 33 fall: 21 female and 12 male) revealed a high degree of variability in range shifting behaviour among individuals and groups (Fig. 5, see also complete results in Tables A1 and A2 in Appendix S1E). Among all analysed segments, somewhat fewer females (23



**Table 2.** Detailed parameter estimates for range shift analyses performed on three roe deer (see tracks in Fig. 4). For deer 770, a two-range model was fitted, with an AIC selection of a white noise residual process (WMN). The l.r.t. tests whether the range shift (which is relatively weak) is significant. For deer 771, we fitted a three-range model to identify the potential stopover during the migration, and the test compares a model with and without the stopover (i.e. with three or two ranges). For the last deer, we again fitted a three range model but tested to see if there was significant site fidelity for this animal, i.e. if the third range was located at the same location as the first range. The null model in this case was a model with two centroids against a model with three centroids. The high *P*-value is evidence in favour of high site fidelity. For the latter two deer, a position autocorrelated model (MOU) was selected

	Roe deer M770		Roe deer M771		Roe deer M772	
	WMN – 2 range ( <i>n</i> = 134)		MOU – 3 range ( <i>n</i> = 178)		MOU – 3 range ( <i>n</i> = 365)	
Fitted model	Estimate	95% CI	Estimate	95% CI	Estimate	95% CI
<i>A</i> (km <sup>2</sup> )	0.44	0.37–0.52	0.3	0.26–0.35	0.49	0.44–0.54
$\tau_z$ (d)			1.6	1.16–2.02	1.29	0.96–1.74
<i>t</i> <sub>1</sub> (doy)	90.23	73.16–107.3	315.95	315.29–316.62	336.49	336–336.97
$\Delta t_1$ (d)	8.76	0–35.25	1.12	0.09–2.14	0.98	0.05–1.91
<i>t</i> <sub>2</sub>			326.14	326.14–326.14	469.45	468.69–470.21
$\Delta t_2$			1.3	1.3–1.3	1.53	0–3.65
<i>x</i> <sub>1</sub> (UTM)	650.29	650.06–650.53	656.56	656.42–656.7	657.7	657.56–657.83
<i>x</i> <sub>2</sub>	650.46	650.31–650.6	657.47	657.01–657.77	659.83	659.71–659.95
<i>x</i> <sub>3</sub>			659.87	659.71–660.04	657.69	657.56–657.83
<i>y</i> <sub>1</sub> (UTM)	5102.04	5101.8–5102.27	5098.79	5098.64–5098.93	5096.87	5096.74–5097
<i>y</i> <sub>2</sub>	5101.61	5101.46–5101.75	5096.54	5096.06–5096.84	5095.29	5095.16–5095.41
<i>y</i> <sub>3</sub>			5095.17	5095.01–5095.34	5097.04	5096.91–5097.17
<i>D</i> (km)	0.46	0.2–0.8	4.91*	4.7–5.1	2.8	2.6–3.0
RSI	0.61	0.3–1.0	7.87*	7.2–8.7	3.88	3.6–4.2
l.r.t.	Against no migration: 90.8 (2 d.f.) <i>P</i> = 0		Against no stopover: 194 (4 d.f.) <i>P</i> = 0		Against return: 0.39 (2 d.f.) <i>P</i> = 0.82	

\*Distance between and RSI across ranges 1 and 3, ignoring the stopover.

of 39, 59%) than male segments (20 of 24, 83%) exhibited a significant range shift (l.r.t.  $P < 0.05$ ) with a weak difference across sexes ( $\chi^2 = 3.02$ ,  $P = 0.08$ ). Among those with significant range shifts, the median distance of the shift ranged from 0.16 to 5.2 km (median 1.4, inter-quartile range 0.41–3.12). Home range areas were consistently small (median 0.44 km<sup>2</sup>, IQR 0.29–0.70) with no differences between sexes or age groups ( $P > 0.08$ ), consistent with kernel density estimates of the same animals (Morellet *et al.* 2013). Of those animals determined to have performed a significant range shift, the median RSI was 2.48 (IQR: 0.96–4.4), much higher than that of non-significant range shifts (median 0.27, IQR: 0.16–0.40). Durations of transitions were also highly variable (Fig. 5), from less than 1 day to 70 days (median 8.5, IQR: 2.5–10.5).

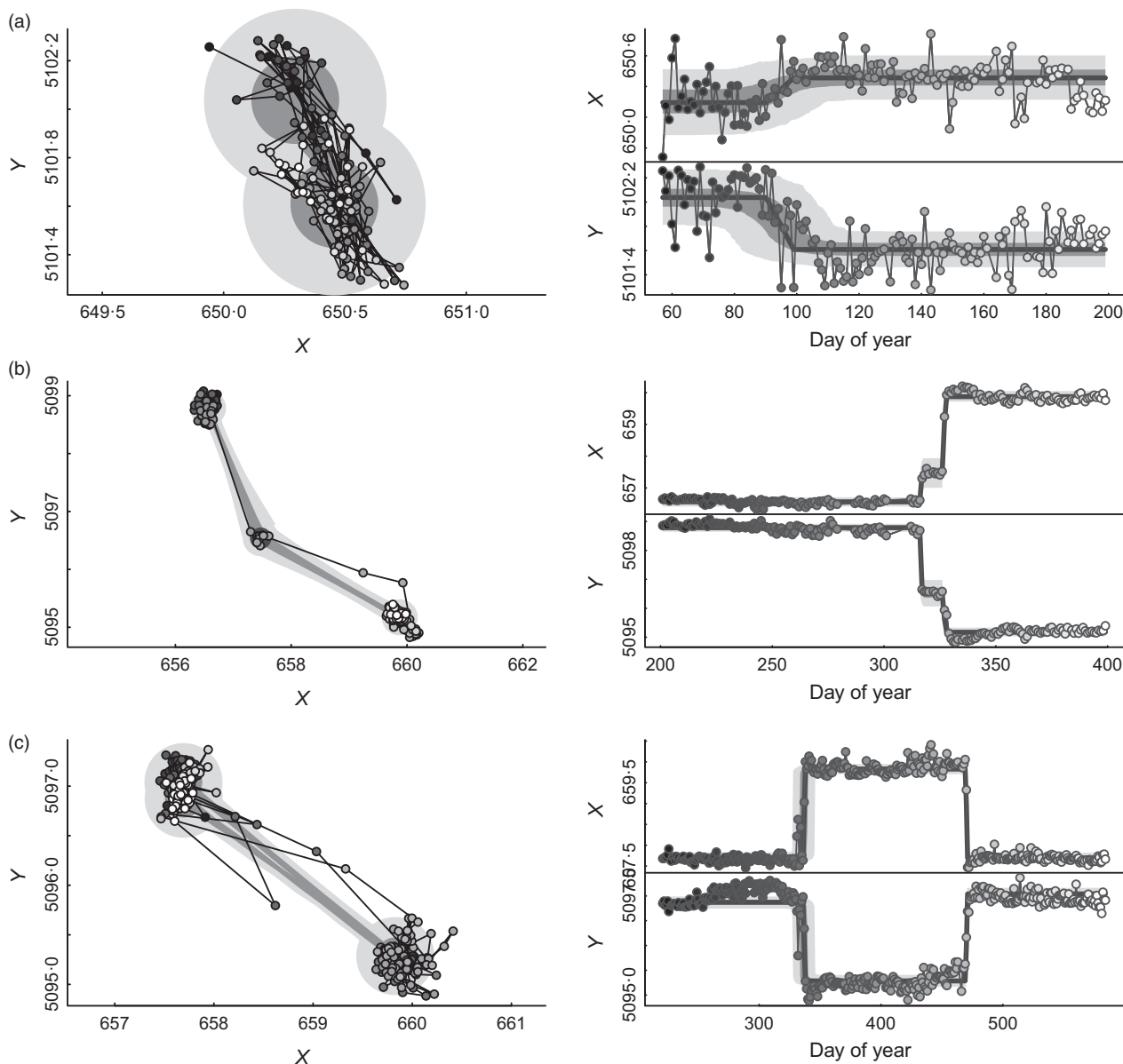
Neither distance, area, RSI nor durations showed any significant patterns with respect to age or sex (all mixed effects model  $P > 0.4$ ). However, ranging area was positively related to migration distance. We fitted a linear mixed effects model of standardized log(area) against standardized log(distance) and range significance (TRUE/FALSE  $P < 0.05$ ) with animal identification (ID) code as a random effect after model selection rejected sex, age and interactions as covariates. The analysis yielded main effects of 0.68 (SE 0.14,  $P < 10^{-4}$ ) for standardized log(distance) and  $-0.9$  (SE 0.3,  $P < 0.001$ ) for the range significance. This means that animals undertaking longer migrations tended to have larger ranging areas, but range shifting individuals had

significantly smaller ranging area than non-shifting individuals (Fig. 6).

An interesting pattern emerged with respect to travel times: of the significant range shifts, longer distance ones tended to be faster than short distance ones: a linear model of log-duration against standardized log-distance yielded an effect of  $-0.51$  ( $P = 0.002$ ), i.e. the expected duration of a 5 km vs. 0.5 km migration were 3.9 and 11.3 days respectively (Fig. 6). Otherwise, neither sex, year nor season were significant predictors of duration ( $P > 0.2$ ).

Many of the spring segments indicated short and non-significant range shifts, especially among females (10 of 16 segments were non-significant, compared to 2 of 12 for males), and most of the range shifts identified between 1 May and 1 September, i.e. in summer, were non-significant (0 of 6 for the females and 3 of 6 for the males), though one yearling male (M773) performed an early, highly significant (RSI = 8.01) range shift in late July, likely a natal dispersal event.

The most striking pattern in the range shifting behaviour was the difference across years (Fig. 5). In the fall of 2005, all the analysed deer performed significant range shifts to wintering grounds, with the shifts occurring primarily in November through December (five females, four males), including several very rapid and relatively long distance (e.g. four individuals migrating 2.8–5.2 km in 4 days or fewer), with only two short, outlying migrations in late September and October. In the following spring (2006), there was considerable movement, with significant



**Fig. 4.** Illustration of model fits to three roe deer, with three different applications. The left panels indicate the  $X$ – $Y$  coordinates, the right pairs of panels are time series of the displacement East–West ( $X$ ) and North–South ( $Y$ ) displacement. In the  $X$ – $Y$  plots, the increasingly dark-shaded blue circles indicate the 95% and 50% estimated area of use, while the bars indicate confidence intervals around the estimate of the migration axis. In the time-series plots, increasingly dark blues reflect the 95%, 50% and point estimate of the centroids of the ranges and the range shift axis. In all plots, locations are shaded from black to white to reflect oldest to newest. The first deer (a) undergoes a slow and relatively short shift. For the second (b), we fitted a three-range model to identify the stopover. In the third (c), the deer undergoes a seasonal migration with a return. See Table 2 for parameter estimates.

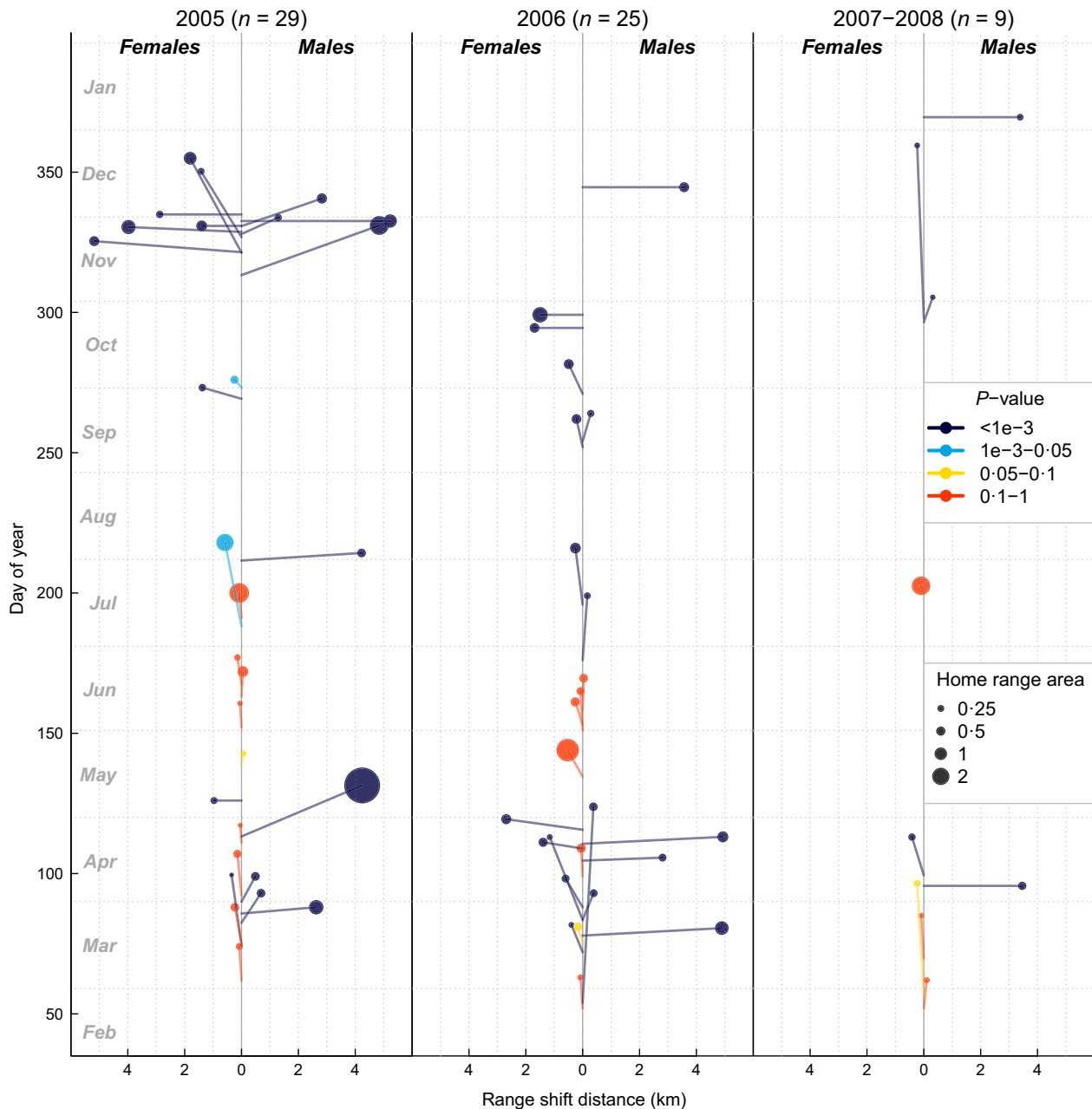
shifts of five females and four males, with, again, four individuals making shifts of over 2 km in under 4 days. In contrast, in late fall of 2006, there was only one significant range shift over 2 km (of a male in November), while other significant range shifts (three female, one male) occurred much earlier (September and October) but were generally much shorter.

Eleven individuals were tracked long enough to observe seasonal range shifts in consecutive seasons. Three of these exhibited at least three shifts, allowing us to test for site fidelity both to summering and wintering grounds. Of the 14 potential round trips, 8 (from six individuals)

exhibited high site fidelity (Table 3). One notable trajectory was that of adult female F792 that migrated to the same wintering ground in the winter of 2005 and 2007, but skipped a migration entirely in 2006, spending the middle winter in its summering range (Table A1 in Appendix S1E and Appendix S1G).

## Discussion

We present a nested family of models that can be used for a versatile and general investigation of range shifting and migratory behaviour. The models have several features

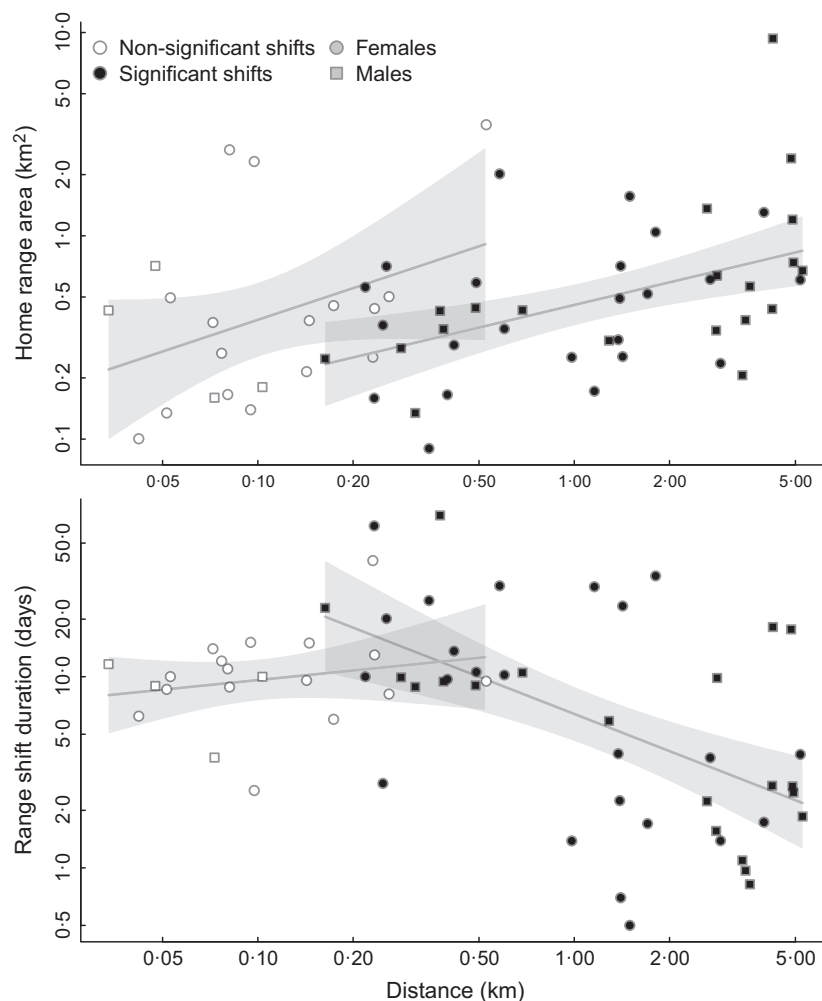


**Fig. 5.** Estimated range shifts for roe deer segments in 2005, 2006 and 2007–2008 pooled together. Each segment represents the beginning and ending of the estimated range shift, the timing along the y-axis and the absolute distance from the initial location along the x-axis. In all panels, females are to the left and males are to the right. Filled circle sizes are proportional to the 95% home range area, and the colours reflect the significance ( $P$ -value) of the likelihood ratio test of range shifting, warm and cold colours indicating non-significant and significant range shifts respectively.

which, together, set them apart from any one of the currently available tools. In particular, the parameterization is biologically meaningful, identifying the timing and distance of range shifts, the spatial extent and locations of the respective ranges, and the temporal scales of autocorrelation. Each of the estimates comes with reliable estimates of confidence intervals, and the whole model fits into a nested likelihood or information criteria framework which facilitates hypothesis testing and model comparisons.

Because the model is described in continuous time, it can be fit to data without particular concern to sampling

regime, as illustrated by the accuracy of the simulation estimates. Irregularity of observations is a nearly universal issue in marine systems (Johnson *et al.* 2008; Gurarie, Andrews & Laidre 2009), but can also influence terrestrial data collection. The time-scale of position autocorrelation is often an important parameter, providing an estimate of the typical time an animal requires to move across its home range. In principle, autocorrelations in velocities can also be estimated, related to the integrated OU process variously described in Alt (1990); Johnson *et al.* (2008); Gurarie & Ovaskainen (2011) and generalized in the OUF



**Fig. 6.** Relationship between ranging area (upper panel) and duration of range shift (lower panel) against distance of range shift, with log–log regression lines and 95% confidence intervals (shaded areas) for significant (filled symbols) and non-significant (empty symbols) shifts. Circles and squares represent females and males respectively.

**Table 3.** Site fidelity of return trips to previous ranges using the range shift likelihood ratio test described in the text. In the ‘return’ column, ‘summer’ refers to subsequent fall and spring range shifts (i.e. from summer to winter ranges, back to summer ranges), while ‘winter’ refers to returns back to winter ranges. The significance symbols (\*\*\*, \*\*, -) represent *P*-values below 0.001, 0.01, and above 0.05 respectively. High *P*-values (bold-faced individuals), in this case, suggest strong evidence for a return to a home range with the same centroid as in the previous year

ID	Return	Significance
F767	Summer	**
F768	Summer	***
<b>F784</b>	Summer	-
F784	Winter	***
<b>F792</b>	Summer	-
F792	Winter	-
<b>F797</b>	Winter	-
F800	Summer	***
<b>M771</b>	Summer	-
M771	Winter	-
<b>M772</b>	Winter	-
<b>M774</b>	Summer	-
M775	Winter	***
M787	Winter	***

process in Fleming *et al.* (2014a, b). In contrast to range shifting/migration processes that occur on the movement mesoscale, autocorrelations in velocity occur on a much shorter tactical scale, meaning they can be ignored in most larger scaled applications. However, for short-term displacements, such as night-time foraging behaviour or shifts between feeding grounds, accounting for the autocorrelation in velocities can be informative on its own terms and lead to more accurate estimates of ranging areas even when they are undersampled (Fleming *et al.* 2014b).

As with any statistical methodology, it is important to dwell on the key assumptions of the model. For simplicity of estimation and to minimize the number of parameters, we separated a single mean process (the shift of the centroid) from a ‘random’ process which simultaneously encompasses both range areas and fluctuations around the mean during migration. There is no *a priori* biological reason to assume that seasonal ranges will be of similar size, nor that the residual variation around the migration process might be related to the seasonal range. In the case of the roe deer, the range sizes did not appear to change significantly and the migrations themselves were either so rapid (e.g. between 1 and 3 days long) that any violation



of this assumption was irrelevant. Alternatively, for very slow range shifts, the ranging process itself was hardly disrupted and the residual assumption seemed acceptable. As with many linear Gaussian models, the estimation of the mean process is often fairly robust to violations in residual assumptions. A visual inspection of the residuals (i.e. the estimated mean process subtracted from the raw location data plotted over each dimension against time) should generally be sufficient to identify deviations from normality or homoscedasticity.

Another important assumption is that the stationary distribution of locations within a home range is circularly symmetric and Gaussian. For the roe deer, this assumption seemed generally to hold. It can, however, be relaxed to allow for elliptical (i.e. bivariate normal) distributions by estimating not just a single spatial variance but the  $x$ - $y$ -covariance matrix. As illustrated in the simulation examples, the area estimates were less reliable than the other range shift parameters. Generally, in the study of range shifting and migration, however, ellipticity and the size of home ranges are parameters of less biological interest than the timing, locations and distances of migration.

#### COMPARISON WITH OTHER METHODS

Our approach facilitates the fitting of parameters with direct interpretations to an animal-centric (Lagrangian) movement model. This distinguishes our approach from other methods that rely on space use and overlap of ranges (e.g. Craighead, Atwell & O'Gara 1972; Fieberg & Kochanny 2005; Cagnacci *et al.* 2016), spatial clustering algorithms (Van Moorter *et al.* 2010; Cagnacci *et al.* 2011) or, most recently, spatio-temporal clustering (Damiani *et al.* 2016). These methods have the important advantage of characterizing the home ranges themselves with more structure and detail than in the MRSA; however, they only indirectly identify the timing and duration of the migration process itself, ignore the consequences of autocorrelation, and do not offer a natural statistical framework for estimating uncertainty or model comparison.

The other most commonly applied tool for quantifying migratory behaviour is the NSD method (Börger & Fryxell 2012; extended to migration in Bunnefeld *et al.* 2011), which fits a set of curves corresponding to residency, migration, dispersal and nomadic type movements to the plot of the squared displacement from an initial location. The NSD analysis is useful for broadly profiling a movement track, is more flexible in accounting for more types of behaviours than our implementation of the MRSA, and has been importantly generalized for hierarchical, population-level modelling (Singh *et al.* 2012; Bastille-Rousseau *et al.* 2016). The agreement between the NSD analysis and the MRSA was generally high, with the important exception of correlated data leading to a higher rate of false positive identifications for the NSD. This is not unexpected: Type I errors are a common consequence of not

accounting for correlation. The mechanism which accounts for both position and velocity correlation essentially makes the MRSA more conservative under a hypothesis testing framework. A more fundamental difference between the two methods is that the NSD fits a derived quantity rather than modelling the movement process itself.

In a recent review of methods for classifying migrations, Cagnacci *et al.* (2016) illustrated inconsistencies between the range overlap, spatial clustering and NSD methods, in particular when dealing with more ambiguous cases of range shifting and migration. When using these tools to classify roe deer migrations, the overall rate of agreement between methods was between 40% and 80%, depending on the total proportion of migrants in the populations (i.e. the highest rates of agreement occurred when migration was obligatory in that specific population). Furthermore, all three lack the ability to identify 'an obvious process shift between migratory and non-migratory behaviour' (Cagnacci *et al.* 2016). The simple piecewise linear shape of the mean process in our models is specifically designed to address that particular issue by focusing the estimation on the location and timing of the centroid shift. Thus, even relatively subtle or slow shifts that would likely be difficult to detect with other methods (e.g. in the upper panels of Fig. 4) can be identified with the MRSA.

In order to compare the results obtained by the MRSA and a geometric approach, we applied a spatio-temporal clustering procedure (Van Moorter *et al.* 2010; Cagnacci, *et al.* 2011, 2016) (see details in Table A3 in Appendix S1F). Agreement was very high between the two methods for unambiguous, long-range migrations, but about half of those segments that were classified as non-migratory by the clustering algorithm contained a significant range shift according to the MRSA. All of these cases corresponded to very short migrations, mostly with overlapping ranges (i.e.  $RSI < 1$ ), underscoring the higher sensitivity of the mechanistic framework of the MRSA compared to purely spatial measures.

#### APPLICATION TO ROE DEER DATA

The Bondone roe deer are characterized by small home ranges and short migration distances over highly structured terrain. Our primary goal in applying the MRSA to these deer was to quantify the variability among individuals in a population that does not lend itself easily to categorization. The diversity of behaviour is clearly illustrated in Fig. 5. Some deer tended to perform unambiguous, relatively rapid seasonal migrations, with a high degree of site fidelity between summer and wintering sites. Others shifted the centroid of their range slowly, over a period of weeks or even months. Many did not significantly shift their range at all in certain years. The most striking pattern was the considerably fewer number of migrants in the fall of 2006, likely due to the mildness of that winter season. Because the distances migrated were so short, many of the roe deer performed exploratory trips to the eventual

candidate sites of migration, typically a week or more before eventually taking the trip, apparently deciding whether or not to perform the migration. This scouting behaviour (a topic for future study), together with the strong interannual variability of our results, suggests that roe deer behaviour is rather plastic (or, to use the term of Dingle & Drake 2007, 'facultative'), with individuals making decisions to migrate based on tactical information about local conditions. This variability contrasted strongly with the high degree of site fidelity (Table 3), suggesting that the main decision the roe deer were making was *whether* and *when* to make the trip, whereas the *whither* was strongly predetermined by previous experience. Responses to proximate cues have been shown to trigger migrations in several ungulates, including white-tailed deer (*Odocoileus virginianus*) responding to snow melt (Sabine *et al.* 2002), zebras (*Equus burchelli*) responding to precipitation (Bartlam-Brooks *et al.* 2013) and snow cover depth in moose (*Alces alces*) (Singh *et al.* 2012).

Another interesting result is the inverse relationship between migratoriness and ranging area. A home range can be considered as an area comprising resources to optimize animals' performance on a lifetime (or at least, multi-seasonal) temporal scale (Burt 1943; Gaillard *et al.* 2010). Residency (a lack of range shift/migration) and range shifting are clearly alternative tactics in roe deer, as in other ungulates (Singh *et al.* 2012). A mixture of both classes of movement have been identified as an evolutionarily stable strategy (Kokko 2011). Simplistically, in a highly heterogeneous environment, a larger residence area may contain a diversity of suitable environments and conditions, compensating for a clean shift between two alternative and well diversified environments (Mueller & Fagan 2008). This set of hypothetical assertions could be tested by comparing the resource quality of home ranges in migrating and non-migrating individuals (Peters *et al.* 2017).

The MRSA provides a set of animal-centric biological parameters which can be meaningfully analysed with an array of standard tools to test hypotheses to explain behavioural variability, an active topic of further research for this and other ungulates. The roe deer are mainly independent, short-distance migrants, in contrast to other ungulates that engage in long-distance, mass migrations. By isolating 'residual' movements from ranging and migratory models, interactions between individuals and environmental covariates and interactions among individuals (i.e. collective behaviours) can yield deeper insights into the cognitive mechanisms of migration (Delgado *et al.* 2014; Dalziel *et al.* 2016).

#### GENERAL IMPLEMENTATION

In analysing the roe deer, we attempted to automate the analysis as much as possible, dividing the year into periods that encompass the spring and fall migrations as consistently as possible across years. While this automation largely worked, it is important to note that to best obtain

reliable estimates, it was necessary to tune some of the estimation settings by hand, most notably the range of analysis window. In particular, the exploratory trips that many of the roe deer took 'confused' the fitting algorithms. These excursions were therefore trimmed from the analysis window (hence, the variation in the time spans of analysis in Tables A1 and A2 in Appendix S1E). Once provided a relatively clean portion of data, the algorithm was robust to different initial conditions given for estimating the initiation and transition duration. Considering the complexity of the roe deer data, we felt that this limited amount of biologically informed pre-processing was acceptable.

For a certain kind of study, e.g. to obtain the relevant timings and ranges for a population with considerable synchrony in migration, a fully automated analysis of individuals would certainly be feasible. However, as a general principle, we feel it is important for users of parameter fitting tools to exercise judgement and knowledge of the system by setting ranges or seeding initial values for the parameters to be estimated. As a further general principle, simulation-based sensitivity analyses are important for assessing the detectability of effects.

The range shift analysis framework can be extended in several straightforward ways. The mean function, currently a piece-wise linear model, can take any form, not only linear segments between multiple ranges but also following some mean path along a known corridor, or between known means (Dalziel, Pourbohloul & Ellner 2013). The model can be extended to account for asymmetric and different-sized home ranges. It is possible to include covariates into the parameters to test hypotheses related to environmental drivers. One might fit an entire population of tagged individuals into a hierarchical framework wherein individual variation would be a random effect and range shift parameter values would be fixed effects, with, for example, some dependence on environmental covariates or group membership. In a recent application of an OU range-shifting model to coastal movements of sea otters (*Enhydra lutris*) (Breed, Golson & Tinker 2017), for example, the authors introduce environmental covariates (wind and waves) as explanatory variables for the probability of transitioning between identified ranges, thereby adding an additional mechanistic layer. In many cases, individual movement data are so rich, and behaviours so complex, that *post hoc* analysis of the parameters (as in our roe deer analysis) can also yield important population-level insights.

#### Authors' contributions

All authors contributed to the conception of the work, with E.G., C.F., J.C. and W.F. developing the statistical concept and E.G., F.C., W.P. and T.M. developing the ecological context and implications; E.G. and C.F. worked out the modelling framework and code; F.C. and W.P. were responsible for collecting and collating the roe deer data; E.G. drafted the article with contributions from F.C., W.P. and W.F.; W.P. also tested and reviewed the code. All authors contributed to critical revisions of the article and provided final approval of the text.

## Acknowledgements

The field work in Italy was partially supported by the Research Fund of the Autonomous Province of Trento (grant no. 3479 to F.C.: BECO-CERWI – Behavioural Ecology of Cervids in Relation to Wildlife Infections) and by EU grant GOCE-2003-010284 EDEN. The roe deer data are part of the EURODEER collaborative project (<http://www.eurodeer.org>). The analysis was supported by NSF bioinformatics grants ABI 1062411 (E.G., W.F., J.C., T.M. and C.F.) and ABI 1458748 (E.G., J.C., W.F. and C.F.). E.G. was additionally supported by a NASA 'Animals on the Move' grant (NNX15AV92). T.M. was funded by the Robert Bosch Foundation. F. Cheraghi is gratefully acknowledged for help in compiling the marcher package. An anonymous reviewer and V.A. Drake provided helpful comments on earlier drafts. The authors declare no conflicts of interest.

## Data accessibility

The roe deer data have been archived in the context of another study in (De Groeve *et al.* 2015, <https://doi.org/10.5061/dryad.h4f7p>). One roe deer track is included in the accompanying MARCHER R package. The code required to replicate the simulations and estimations is provided in the package and its accompanying vignette, provided as supplementary materials, on CRAN (Gurarie & Cheraghi 2017) and as a live development version on GitHub at <https://github.com/EliGurarie/marcher>.

## References

- Alt, W. (1990) Correlation analysis of two-dimensional locomotion paths. *Biological Motion: Proceedings of a Workshop Held in Königswinter Germany* (eds W. Alt & G. Hoffmann), pp. 254–268. Springer-Verlag, Berlin, Germany.
- Baguette, M., Blanchet, S., Legrand, D., Stevens, V. & Turlure, C. (2013) Individual dispersal, landscape connectivity and ecological networks. *Biological Reviews*, **88**, 310–326.
- Ball, J.P., Nordengren, C., Kjell, W. *et al.* (2001) Partial migration by large ungulate: characteristics of seasonal moose *Alces alces* ranges in northern Sweden. *Wildlife Biology*, **7**, 37–49.
- Bartlam-Brooks, H.L., Beck, P.S., Bohrer, G. & Harris, S. (2013) In search of greener pastures: using satellite images to predict the effects of environmental change on zebra migration. *Journal of Geophysical Research: Biogeosciences*, **118**, 1427–1437.
- Bastille-Rousseau, G., Potts, J., Yackulic, C., Frair, J., Ellington, E. & Blake, S. (2016) Flexible characterization of animal movement pattern using net squared displacement and a latent state model. *Movement Ecology*, **4**, 1.
- Berthold, P. (2001) *Bird Migration: A General Survey*. Oxford University Press, New York, NY, USA.
- Blackwell, P. (1997) Random diffusion models for animal movement. *Ecological Modelling*, **100**, 87–102.
- Blackwell, P., Niu, M., Lambert, M. & LaPoint, S. (2015) Exact Bayesian inference for animal movement in continuous time. *Methods in Ecology and Evolution*, **7**, 184–195.
- Börger, L. & Fryxell, J. (2012) Quantifying individual differences in dispersal using net squared displacement. *Dispersal Ecology and Evolution* (eds J. Clobert, M. Baguette, T. Benton & J. Bullock), pp. 222–228. Oxford University Press, Oxford, UK.
- Börger, L., Dalziel, B. & Fryxell, J. (2008) Are there general mechanisms of animal home range behavior? A review and prospects for future research. *Ecology Letters*, **11**, 637–650.
- Boyle, W., Guglielmo, C., Hobson, K. & Norris, D. (2011) Lekking birds in a tropical forest forego sex for migration. *Biology Letters*, **7**, 661–663.
- Breed, G.A., Golson, E.A. & Tinker, M.T. (2017) Predicting animal home-range structure and transitions using a multistate Ornstein-Uhlenbeck biased random walk. *Ecology*, **1**, 32–47.
- Brockwell, P.J. & Davis, R.A. (1996) *Introduction to Time Series and Forecasting*. Springer, New York, NY, USA.
- Bunnefeld, N., Börger, L., van Moorter, B., Rolandsen, C., Dettki, H., Solberg, E. & Ericsson, G. (2011) A model-driven approach to quantify migration patterns: individual, regional and yearly differences. *Journal of Animal Ecology*, **80**, 466–476.
- Burt, W. (1943) Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy*, **24**, 346–352.
- Cagnacci, F., Focardi, S., Heurich, M., Stache, A., Hewison, A., Morellet, N., Kjellander, P., Linnell, J., Mysterud, A., Neteler, M., Delucchi, L., Ossi, F. & Urbano, F. (2011) Partial migration in roe deer: migratory and resident tactics are end points of a behavioural gradient determined by ecological factors. *Oikos*, **120**, 1790–1802.
- Cagnacci, F., Focardi, S., Ghisla, A., van Moorter, B., Gurarie, E., Heurich, M., Mysterud, A., Linnell, J., Panzacchi, M., Nygard, T., Merrill, E., Rolandsen, C. & Hebblewhite, M. (2016) How many routes lead to migration? Re-establishing the link between definitions, methods and movement ecology. *Journal of Animal Ecology*, **85**, 54–68.
- Calabrese, J., Fleming, C. & Gurarie, E. (2016) ctmm: an R package for analyzing animal relocation data as a continuous-time stochastic process. *Methods in Ecology and Evolution*, **7**, 1124–1132.
- Calenge, C. (2006) The package adehabitat for the R software: tool for the analysis of space and habitat use by animals. *Ecological Modelling*, **197**, 1035.
- Chapman, B., Brönmark, C., Nilsson, J.A. & Hansson, L.A. (2011) The ecology and evolution of partial migration. *Oikos*, **120**, 1764–1775.
- Craighead, J., Atwell, G. & O'Gara, B. (1972) Elk migrations in and near Yellowstone National Park. *Wildlife Monographs*, **29**, 3–48.
- Dalziel, B.D., Pourbohloul, B. & Ellner, S.P. (2013) Human mobility patterns predict divergent epidemic dynamics among cities. *Proceedings of the Royal Society B: Biological Sciences*, **280**, 20130763.
- Dalziel, B.D., Corre, M.L., Côté, S.D. & Ellner, S.P. (2016) Detecting collective behaviour in animal relocation data, with application to migrating caribou. *Methods in Ecology and Evolution*, **7**, 30–41.
- Damiani, M., Issa, H., Heurich, M. & Cagnacci, F. (2016) Introducing 'presence' and 'stationarity index' to study partial migration patterns: an application of a spatio-temporal clustering technique. *International Journal of Geographical Information Systems*, **30**, 907–928.
- De Groeve, J., Van de Weghe, N., Ranc, N., Neutens, T., Ometto, L., Rota-Stabelli, O. & Cagnacci, F. (2015) Data from: Extracting spatio-temporal patterns in animal trajectories: an ecological application of sequence analysis methods. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.h4f7p>
- Delgado, M.d.M., Penteriani, V., Morales, J.M., Gurarie, E. & Ovaskainen, O. (2014) A statistical framework for inferring the influence of conspecifics on movement behaviour. *Methods in Ecology and Evolution*, **5**, 183–189.
- Dingle, H. & Drake, V. (2007) What is migration? *Bioscience*, **57**, 113–121.
- Dunn, J. & Gipson, P. (1977) Analysis of radio telemetry data in studies of home range. *Biometrics*, **33**, 85–101.
- Elzhov, T.V., Mullen, K.M., Spiess, A.N. & Bolker, B. (2016) *minpack.lm: R Interface to the Levenberg-Marquardt Nonlinear Least-Squares Algorithm Found in MINPACK, Plus Support for Bounds*. R package version 1.2-1. Available at: <https://CRAN.R-project.org/package=minpack.lm>
- Fieberg, J. & Börger, L. (2012) Could you please phrase "home range" as a question? *Journal of Mammalogy*, **93**, 890–902.
- Fieberg, J. & Kochanny, C.O. (2005) Quantifying home range overlap: the importance of the utilization distribution. *Journal of Wildlife Management*, **69**, 1347–1359.
- Fleming, C., Calabrese, J., Mueller, T., Olson, K., Leimgruber, P. & Fagan, W. (2014a) Non-Markovian maximum likelihood estimation of autocorrelated movement processes. *Methods in Ecology and Evolution*, **5**, 462–472.
- Fleming, C.H., Calabrese, J.M., Mueller, T., Olson, K.A., Leimgruber, P. & Fagan, W.F. (2014b) From fine-scale foraging to home ranges: a semi-variance approach to identifying movement modes across spatiotemporal scales. *The American Naturalist*, **183**, E154–E167.
- Fleming, C., Fagan, W., Mueller, T., Olson, K., Leimgruber, P. & Calabrese, J. (2015) Rigorous home range estimation with movement data: a new autocorrelated kernel density estimator. *Ecology*, **96**, 1182–1188.
- Fryxell, J. & Sinclair, A. (1988) Causes and consequences of migration by large herbivores. *Trends in Ecology & Evolution*, **3**, 237–241.
- Gaillard, J.M., Hebblewhite, M., Loison, A., Fuller, M., Powell, R., Basille, M. & Van Moorter, B. (2010) Habitat–performance relationships: finding the right metric at a given spatial scale. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 2255–2265.
- Gardner, G., Harvey, A.C. & Phillips, G.D.A. (1980) Algorithm AS154. An algorithm for exact maximum likelihood estimation of autoregressive-moving average models by means of Kalman filtering. *Applied Statistics*, **29**, 311–322.
- Genz, A., Bretz, F., Miwa, T., Mi, X., Leisch, F., Scheipl, F. & Hothorn, T. (2008) *mvtnorm: Multivariate Normal and t Distributions*. R package



- version 1.0–5. Available at: <http://CRAN.R-project.org/package=mvt> norm
- Griswold, C.K., Taylor, C.M. & Norris, D.R. (2010) The evolution of migration in a seasonal environment. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 2711–2720.
- Gurarie, E. & Ovaskainen, O. (2011) Characteristic spatial and temporal scales unify models of animal movement. *The American Naturalist*, **178**, 113–123.
- Gurarie, E., Andrews, R.D. & Laidre, K.L. (2009) A novel method for identifying behavioural changes in animal movement data. *Ecology Letters*, **12**, 395–408.
- Gurarie, E., Bracis, C., Delgado, M., Meckley, T., Kojola, I. & Wagner, M. (2016) What is the animal doing? Tools for exploring behavioral structure in animal movements. *Journal of Animal Ecology*, **85**, 69–84.
- Gurarie, E. & Cheraghi, F. (2017) *marcher: Migration and Range Change Estimation in R*. R package version 0.0-2. Available at: <https://CRAN.R-project.org/package=marcher>
- Hebblewhite, M. & Merrill, E.H. (2009) Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. *Ecology*, **90**, 3445–3454.
- Hewison, A.J.M. (1998) Social organisation of European roe deer. *The European Roe Deer: The Biology of Success* (eds R. Andersen, P. Duncan & J. Linnell), pp. 189–220. Scandinavian University Press, Oslo, Norway.
- Holand, Ø. (1998) Roe deer in northern environments: physiology and behaviour. *The European Roe Deer: The Biology of Success* (eds R. Andersen, P. Duncan & J. Linnell), pp. 117–138. Scandinavian University Press, Oslo, Norway.
- Jennrich, R.I. & Turner, F.B. (1969) Measurement of non-circular home range. *Journal of Theoretical Biology*, **22**, 227–237.
- Johnson, C., Parker, K., Heard, D. & Gillingham, M. (2002) A multiscale behavioral approach to understanding the movements of woodland caribou. *Ecological Applications*, **12**, 1840–1860.
- Johnson, D.S., London, J.M., Lea, M.A. & Durban, J.W. (2008) Continuous-time correlated random walk model for animal telemetry data. *Ecology*, **89**, 1208–1215.
- Kaitala, A., Kaitala, V. & Lundberg, P. (1993) A theory of partial migration. *American Naturalist*, **142**, 59–81.
- Kerr, L., Secor, D. & Piccoli, P. (2009) Partial migration of fishes as exemplified by the estuarine-dependent white perch. *Fisheries*, **34**, 114–123.
- Kie, J., Matthiopoulos, J., Fieberg, J., Powell, R., Cagnacci, F., Mitchell, M., Gaillard, J. & Moorcroft, P. (2010) The home-range concept: are traditional estimators still relevant with modern telemetry technology? *Philosophical Transactions of the Royal Society of London. Series B*, **365**, 2221–2231.
- Kokko, H. (2011) Directions in modelling partial migration: how adaptation can cause a population decline and why the rules of territory acquisition matter. *Oikos*, **120**, 1826–1837.
- Kranstauber, B., Kays, R., LaPoint, S.D., Wikelski, M. & Safi, K. (2012) A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. *Journal of Animal Ecology*, **81**, 738–746.
- Laver, P. & Kelly, M. (2008) A critical review of home range studies. *Journal of Wildlife Management*, **72**, 290–298.
- LeResche, R. & Rausch, R. (1974) Accuracy and precision of aerial moose censusing. *The Journal of Wildlife Management*, **2**, 175–182.
- Lichti, N. & Stewart, R. (2011) Estimating utilization distributions with kernel versus local convex hull methods. *Journal of Wildlife Management*, **75**, 413–422.
- McClintock, B., King, R., Thomas, L., Matthiopoulos, J., McConnell, B. & Morales, J. (2012) A general discrete-time modeling framework for animal movement using multistate random walks. *Ecological Monographs*, **82**, 335–349.
- Middleton, A., Kauffman, M., McWhirther, D., Cook, J., Cook, R., Nelson, A., Jimenez, M. & Klaver, R. (2013) Animal migration amid shifting patterns of phenology and predation: lessons from a Yellowstone elk herd. *Ecology*, **94**, 1245–1256.
- Morales, J.M., Haydon, D.T., Frair, J., Holsinger, K.E. & Fryxell, J.M. (2004) Extracting more out of relocation data: building movement models as mixtures of random walks. *Ecology*, **85**, 2436–2445.
- Morellet, N., Bonenfant, C., Börger, L., Ossi, F., Cagnacci, F., Heurich, M., Kjellander, P., Linnell, J., Nicoloso, S., Sustr, P., Urbano, F. & Mysterud, A. (2013) Seasonality, weather and climate affect home range size in roe deer across a wide latitudinal gradient within Europe. *Journal of Animal Ecology*, **82**, 1326–1339.
- Mueller, T. & Fagan, W. (2008) Search and navigation in dynamic environments - from individual behaviours to population distributions. *Oikos*, **117**, 654–664.
- Mysterud, A. (1999) Seasonal migration pattern and home range of roe deer (*Capreolus capreolus*) in an altitudinal gradient in southern Norway. *Journal of Zoology*, **247**, 479–486.
- Mysterud, A., Loe, L., Zimmerman, B., Bischof, R., Veiberg, V. & Meisingset, E. (2011) Partial migration in expanding red deer populations at northern latitudes a – role for density dependence? *Oikos*, **120**, 1817–1825.
- Nathan, R., Getz, W., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. & Smouse, P. (2008) A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 19052–19059.
- Patterson, T., Thomas, L., Wilcox, C., Ovaskainen, O. & Matthiopoulos, J. (2008) State-space models of individual animal movement. *Trends in Ecology & Evolution*, **23**, 87–94.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team (2013) *nlme: Linear and Nonlinear Mixed Effects Models*. R package version 3.1-113. Available at: <http://CRAN.R-project.org/package=nlme>
- Peters, W., Hebblewhite, M., Mysterud, A. et al. (2017) Migration across the realized ecological niche in space and time by a large herbivore. *Ecological Monographs*. <https://doi.org/10.1002/ecm.1250>.
- R Core Team (2013) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: <http://www.R-project.org/>
- Ramanzin, M., Sturaro, E. & Zanon, D. (2007) Seasonal migration and home range of roe deer (*Capreolus capreolus*) in the Italian eastern Alps. *Canadian Journal of Zoology*, **85**, 280–289.
- Sabine, D., Morrison, S., Whitlaw, H., Ballard, W., Forbes, G. & Bowman, J. (2002) Migration behavior of white-tailed deer under varying winter climate regimes in New Brunswick. *The Journal of Wildlife Management*, **66**, 718–728.
- Shaw, A. & Levin, S. (2011) To breed or not to breed: a model of partial migration. *Oikos*, **120**, 1871–1879.
- Singh, N., Börger, L., Dettki, H., Bunnefeld, N. & Ericsson, G. (2012) From migration to nomadism: movement variability in a northern ungulate across its latitudinal range. *Ecological Applications*, **22**, 2007–2020.
- Spitz, D.B., Hebblewhite, M. & Stephenson, T.R. (2017) ‘MigrateR’: extending model-driven methods for classifying and quantifying animal movement behavior. *Ecography*. doi:10.1111/ecog.02587.
- Taylor, C. & Norris, D. (2007) Predicting conditions for migration: effects of density dependence and habitat quality. *Biology Letters*, **3**, 280–284.
- Van Moorter, B., Visscher, D., Jerde, C., Frair, J. & Merrill, E. (2010) Identifying movement states from location data using cluster analysis. *Journal of Wildlife Management*, **74**, 588–594.
- Wheeler, B. (2010) *lmPerm: Permutation tests for linear models*. R package version 1.1-2. Available at: <http://CRAN.R-project.org/package=lmPerm>
- White, P., Davis, T., Barnowe-Meyer, K., Crabtree, R. & Garrott, R. (2007) Partial migration and philopatry of Yellowstone pronghorn. *Biological Conservation*, **135**, 502–510.
- Worton, B. (1995) Using Monte Carlo simulation to evaluate kernel-based home range estimators. *Journal of Wildlife Management*, **59**, 794–800.
- Wysujack, K., Greenberg, L., Bergman, E. & Olsson, I. (2009) The role of the environment in partial migration: food availability affects the adoption of a migratory tactic in brown trout *Salmo trutta*. *Ecology of Freshwater Fish*, **18**, 52–59.
- Zeileis, A. & Grothendieck, G. (2005) zoo: S3 Infrastructure for Regular and Irregular Time Series. *Journal of Statistical Software*, **14**, 1–27.

Received 4 February 2016; accepted 12 March 2017

Handling Editor: Luca Börger

## Supporting Information

Details of electronic Supporting Information are provided below.



**Data S1.** Source bundle for the marcher package v. 0.0-2. Also available on CRAN (<https://cran.r-project.org/web/packages/marcher/index.html>) and in a development version on GitHub (<https://github.com/EliGurarie/marcher>).

**Data S2.** Vignette to the marcher package documenting and illustrating analysis workflow and comparison to net-squared displacement (NSD) analysis.

**Appendix S1.** Includes more technical derivations and details of the models, complete results of the roe deer analysis, explanation of NSD implementation, and comparison to clustering results.