A model-driven approach to quantify migration patterns: individual, regional and yearly differences

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Summary

1. Animal migration has long intrigued scientists and wildlife managers alike, yet migratory species face increasing challenges because of habitat fragmentation, climate change and over-exploitation. Central to the understanding migratory species is the objective discrimination between migratory and nonmigratory individuals in a given population, quantifying the timing, duration and distance of migration and the ability to predict migratory movements.

2. Here, we propose a uniform statistical framework to (i) separate migration from other movement behaviours, (ii) quantify migration parameters without the need for arbitrary cut-off criteria and (iii) test predictability across individuals, time and space.

3. We first validated our novel approach by simulating data based on established theoretical movement patterns. We then formulated the expected shapes of squared displacement patterns as nonlinear models for a suite of movement behaviours to test the ability of our method to distinguish between migratory movement and other movement types.

4. We then tested our approached empirically using 108 wild Global Positioning System (GPS)-collared moose *Alces alces* in Scandinavia as a study system because they exhibit a wide range of movement behaviours, including resident, migrating and dispersing individuals, within the same population. Applying our approach showed that 87% and 67% of our Swedish and Norwegian subpopulations, respectively, can be classified as migratory.

5. Using nonlinear mixed effects models for all migratory individuals we showed that the distance, timing and duration of migration differed between the sexes and between years, with additional individual differences accounting for a large part of the variation in the distance of migration but not in the timing or duration. Overall, the model explained most of the variation (92%) and also had high predictive power for the same individuals over time (69%) as well as between study populations (74%).

6. The high predictive ability of the approach suggests that it can help increase our understanding of the drivers of migration and could provide key quantitative information for understanding and managing a broad range of migratory species.

Key-words: animal movement, moose, net squared displacement, nonlinear mixed models, spatial ecology

Introduction

Migration is part of a species' life-history strategy and has wide ranging consequences for individual reproduction and survival (Stearns 1992) and in turn population dynamics. Migratory strategies have been studied in species ranging from birds and mammals to fish, amphibians and insects (Lundberg 1988; Dingle 1996; Alerstam, Hedenström & Åkesson 2003; Grayson & Wilbur 2009). However, anthropogenic impacts are growing and animals face increasing challenges to follow their migration routes because of habitat fragmentation, exploitation and climate change (Both *et al.* 2006; Sanderson *et al.* 2006; Bolger *et al.* 2008), making it important for wildlife management and conservation to quantify their spatio-temporal movement patterns to be able to secure their seasonal ranges (Harris *et al.* 2009).

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Ecological research has used five main variables to quantify migration and to distinguish between migratory and other movement: (i) the proportion of a population that migrates, (ii) the distance individuals migrate, (iii) the timing (onset, termination) of migration, (iv) the duration and (v) the fidelity to a specific site (Ball, Nordengren & Wallin 2001; Nelson, Mech & Frame 2004; Alerstam, Hake & Kjellen 2006; Jonzén, Hedenström & Lundberg 2007; Brodersen *et al.* 2008, Gillis *et al.* 2008). Migration has been observed and studied at multiple spatial scales (Fryxell & Sinclair 1988; Dingle 1996), but a uniform scale-independent approach to analyse individual migration patterns based on spatio-temporal data and ecological theory has not been developed (Bauer *et al.* 2009). New technological advances in tagging and following animals, such as global positioning system (GPS) tracking, now make it possible to collect high-resolution data in space and time on many less easily observable species, and on species migrating over large distances, such as ungulates, pelagic sea birds and fish (e.g. Nelson, Mech & Frame 2004; Rutz & Hays 2009; Sims *et al.* 2009; Wakefield, Phillips & Matthiopoulos 2009). In this paper, we propose a novel method to (i) distinguish migration from other movement behaviours, especially dispersal, home range and nomadic behaviour, and (ii) quantify the three main variables of migration (distance, timing and duration) in a single, integrated frame work. This method is scale-independent and is therefore applicable to movement patterns of a wide range of species and data.

To distinguish from other movement patterns and to quantify migration, we used a single measurement, the net squared displacement (NSD), which measures the straight line distances between the starting location and the subsequent locations for the movement path of a given individual. The NSD, as its related mean, is a statistic of fundamental importance for movement research as it provides a synthetic measure of key properties of movement paths (Turchin 1998; Nouvellet, Bacon & Waxman 2009). Here, we show that the NSD can provide valuable information also for migration studies. We expect the following behaviour of NSD when applied to migration (see also Kolzsch & Blasius 2008). At the winter site, we expect the NSD of a given migratory animal to be stable, with values close to zero as animals remain stationary inside their winter ranges. As spring approaches, we expect animals to migrate to their summer ranges, and thus a rapid increase in NSD. Once individuals have reached the summer ranges, we expect a relatively stable NSD (second stationary phase), indicated by an asymptote in the s-shaped curve. During the second movement phase (autumn migration), a reverse s-shaped curve appears where the NSD is expected to decrease and again reach zero as the animal moves back to the winter range where it remains until the next movement phase. Given these patterns, summarized in Fig. 1, we can use NSD in this study to develop a set of hypotheses. We test them using competing models to distinguish between different movement patterns and quantify the distance, timing and duration of migration.
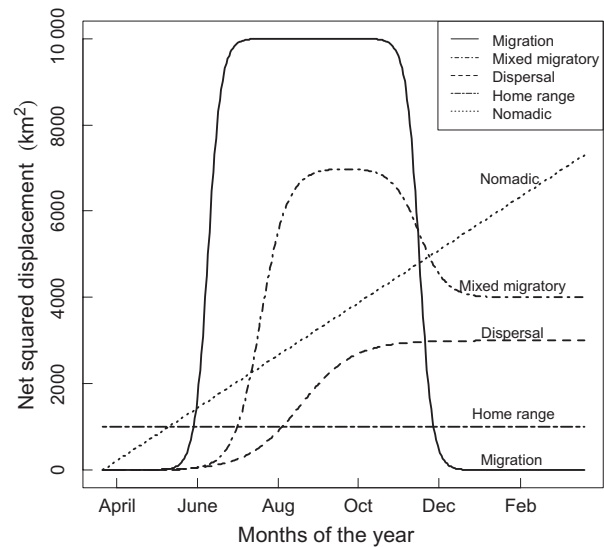

Fig. 1. Demonstration of the five movement types: Migration (solid line: $\delta_s = \delta_a = 10\,000$, $\theta_s = 80$, $\theta_a = 240$, $\varphi_s = \varphi_a = 5$); mixed migratory (dotted dashed line: $\delta_s = 7000$, $\delta_a = 3000$, $\theta_s = 120$, $\theta_a = 240$, $\varphi_s = \varphi_a = 10$); dispersal (dashed line: $\delta = 3000$, $\theta_s = 50$, $\varphi_s = 20$); home range (twodash line: intercept = 1000, slope = 0); nomadic (dotted line: intercept = 0, slope = 20).

Research has shown that for an animal moving according to a random walk, the expected squared distance, rather than the linear distance, increases linearly with time (Turchin 1998; Börger, Dalziel & Fryxell 2008). It is also known that for animals restricting their movement to stable home ranges, the form of the NSD curve over time will be asymptotic (Moorcroft & Lewis 2006; Börger, Dalziel & Fryxell 2008). It has recently been suggested that the functional form of NSD patterns of dispersers will be a sigmoid curve (L. Börger, T. McIntosh, M. Ryckman, R.C. Rosatte, J. Hamr, J.M. Fryxell, unpublished). Thus, NSD has recently received increased attention in the random walk and animal movement theory and combines characteristics of movement trajectories in a single synthetic measurement (Turchin 1998; Moorcroft & Lewis 2006; Börger, Dalziel & Fryxell 2008).

In this study, we first simulate the NSD in a random walk framework to see how our predictions fit the theory of animal movement and especially how NSD patterns vary under assumptions of resident, dispersal, migratory and random walk ('nomadic') behaviour. Then we classify individual movement behaviour as migratory, dispersing, resident, or nomadic, by fitting competing models to each individual NSD and comparing the models using information-theoretic methods (Burnham & Anderson 2002). In the next step, we use the migratory individuals to develop an objective and repeatable method to estimate the population-level migration parameters (distance, timing and duration), as well as to quantify and decompose the variation within and between individuals and between years in a nonlinear mixed effects model framework (Pinheiro & Bates 2000).

We used moose (*Alces alces*) as our empirical study system. Moose have been observed to shift between resident,

dispersing and migratory behaviours, with only a part of a given population migrating, and migration distances differing between individuals (Hundertmark 1998; Ball, Nordengren & Wallin 2001; Hjeljord 2001). Furthermore, the consistency of an individual moose movement strategy across years has never been quantified. Therefore, the movement behaviour of moose is ideal to explore the usefulness of the proposed method compared to a species with more consistent movement patterns.

Material and methods

STUDY AREA

The 108 GPS-collared moose for this study were distributed between 63°N 10°E and 67°N 20°E in Norway and Sweden (Fig. 2). The study area ranges from inland boreal forest in the eastern part (mostly Sweden) to the North-Atlantic coast in Norway. The low alpine area at the border between Norway and Sweden is partly covered by mountain birch forests (*Betula sp*) and partly above the woodland limit. The inland boreal forest is characterized by regenerating monocultures of Scots Pine (*Pinus silvestris*). The forest cover west of the alpine area (mostly in Norway) is dominated by Norway spruce (*Picea abies*) and to a lesser extent Scots pine on less productive land. Birch often dominates at the woodland limit. Coniferous forests in Sweden and Norway are typically managed by modern forestry practices, generating a patchwork of even-aged forest stands.

DATA

We immobilized moose from a helicopter using a dart gun to inject a mixture of an anaesthetic and a tranquilizer (ethorphine and xylazine; Arnemo *et al.* 2006). We equipped each moose with a GPS/Global System for Mobile communications (GSM) collar including a traditional VHF–beacon (Vectronic Aerospace GmbH, Berlin, Germany). In the Swedish study area, moose were immobilized during four capture events: November 2004, 2005, 2006 and February/March 2007. In the Norwegian study area, moose were captured during February–March or November 2006 and February–March 2007. Collars weighed approximately 1·2–1·5 kg with an estimated battery lifetime of 3 years. Each collar acquired a position every 0·5–2 h and stored them internally for later download using the GSM network in Europe. Locations with two consecutive movements of more than 10 km distance for hourly intervals were removed as these were most likely location errors.

From the moose locations recorded, one position per day and moose closest in time to 12·00 h was extracted to study the seasonal patterns of movement (diurnal patterns were not of interest in this study). Location data were included for the years 2005/06, 2006/07 and 2007/08. To be able to develop the migration model and test the predictive ability of the model, we created three subdata sets. First, moose were assigned to be Norwegian and Swedish depending on their first capture location (Fig. 2). Second, the Swedish moose were divided into two data sets. The first Swedish data set consisted of 77 individual moose (66 females, 11 males) recorded for 1 year. This data set, called the Swedish base data set, consisted of 28 108 positions and was used to develop the model. The second Swedish data set consisted of 7676 positions for 14 females. These individuals are a subset of the 77 individuals of the first data, for which a second year of data was available. The 14 Swedish females were used to test the temporal predictive power of the base data for the same individuals in different years. The Norwegian data set consisted of 31 moose (22 females, 9 males) and a total of 11 315 positions. This data set was used to test the predictive ability of the model based on the Swedish base data set in a different location.

CALCULATING NET SQUARED DISPLACEMENT

The first step to obtain the NSD from the GPS location data was to calculate the net distance, which is the straight line distance in kilometres between the first location, given the coordinates north $N(t)$ and east $E(t)$, and the subsequent locations $N(t + n)$ and $E(t + n)$; n is the total number of locations of the movement path of an individual in a given year (Turchin 1998). The first position was set to 21st March, when moose are still in their winter ranges (Ball, Nordengren & Wallin 2001). The distances between the location obtained on the 21st March and
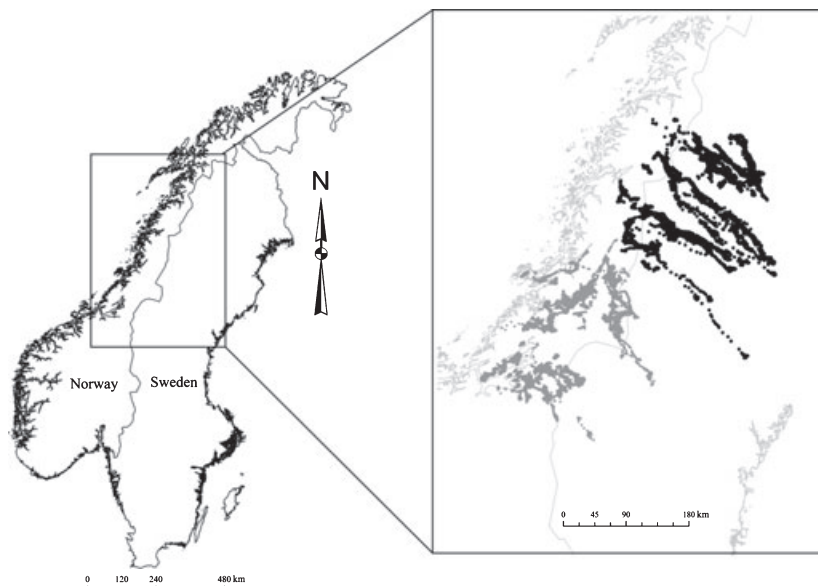

Fig. 2. Distributions of moose locations. Moose captured in Norway are given in grey and moose captured in Sweden in black.

the subsequent locations for each moose and year were then squared, which resulted in the measurement of square kilometres for the NSD. We calculated the NSD for each individual and year using the adehabitat package version 1.6 (Calenge 2006) in the open-source programme R for statistical computing (R Development Core Team 2009, R version 2.9.0).

MOVEMENT MODELS

The simplest model for the NSD patterns of migrants (eqn 1) is a double sigmoid or s-shaped function, which is repeated within a year, leading to an exact return to the departure locations (e.g. winter range, spring migrations, summer range, autumn migration, winter range).

$$NSD = \frac{\delta}{1 + \exp\left(\frac{\theta_s - t}{\varphi_s}\right)} + \frac{-\delta}{1 + \exp\left(\frac{\theta_a - t}{\varphi_a}\right)} \qquad \text{eqn 1}$$

where δ is the asymptotic height, θ_s and θ_a are the timing at which the migration reaches half its asymptotic height in spring and autumn, respectively, φ_s and φ_a models the timing elapsed between reaching half and $\frac{1}{1+e^{-1}} \cong \frac{3}{4}$ of migration in spring and autumn, respectively, and t as number of days since 21st March for each year. The different parameters for spring and autumn allow the timing and speed of migration to differ between spring and autumn. All model parameters have a clear biological interpretation: the asymptotic height δ is the distance of migration between the winter and the summer range; the inflection point θ is the timing of migration, i.e. the time at which the curve reaches half its asymptotic height; and the scale parameter φ models the duration of migration. At between ¼ and 3/4 of the migration period, moose are moving at their fastest speed; thus, the curve shows essentially linearity. Therefore, we use twice the time φ as half of the duration of migration as between ¼ and 3/4 of the migration period. The double sigmoid function is an extension of the logistic curve model as provided by Pinheiro & Bates (2000, p 274).

Often, animals return to the same geographical area but not to the exact location of the preceding year, leading to a different distance moved between the start and the return areas. To model moose not returning to exactly the location of departure, but to a nearby area (called mixed migratory strategy), we let the asymptote vary between spring and autumn $\delta_s \neq \delta_a$ in eqn 2).

$$NSD = \frac{\delta_s}{1 + \exp\left(\frac{\theta_s - t}{\varphi_s}\right)} + \frac{-\delta_a}{1 + \exp\left(\frac{\theta_a - t}{\varphi_a}\right)} \qquad \text{eqn 2}$$

where the asymptote δ can vary according to patterns in spring and autumn.

For a dispersal strategy, we used a logistic model to model moose that disperse from the initial location and settle in a new area (Pinheiro & Bates 2000 p274, L. Börger, T. McIntosh, M. Ryckman, R.C. Rosatte, J. Hamr, J.M. Fryxell revised for resubmission).

$$NSD = \frac{\delta}{1 + \exp\left(\frac{\theta - t}{\varphi}\right)} \qquad \text{eqn 3}$$

where δ is the asymptotic height, θ is the timing at which the migration reaches half its asymptotic height, φ models the timing elapsed between reaching half and 3/4 of migration and t as number of days since 21st March for each year.

To test if the NSD data would be best described by a simple home range model, we fitted an intercept model to the data

$$NSD = c \qquad \text{eqn 4}$$

where c is a constant. Such a model reflects a lack of large changes in NSD over time, indicating that the moose is stationary within a restricted area during the entire year. The same results were obtained by using an asymptotic regression model, which is a more adequate home range model (Börger, Dalziel & Fryxell 2008). The constant model is more parsimonious because only one parameter is estimated (c), in comparison with two parameters in an asymptotic model.

The last model was a linear equation:

$$NSD = \beta \times t \qquad \text{eqn 5}$$

where β is a constant and t the number of days since 21st March for each year, which we take here as a simple example of a nomadic individual. This was a simple linear model with zero intercept, allowing moose to increase in distance throughout the year relative to the starting location.

SIMULATED MOVEMENT BEHAVIOUR

To exemplify our theoretical framework, we start the analysis by fitting space use models to simulated random walk data. We simulated all five movement types (nomadic, home range, dispersal, migration and the mixed dispersal-migration movement) for 365 time steps (corresponding to the year tracking duration of the moose in our study). The nomadic movement type was simulated with a random walk (scaled to show realistic median step lengths around 400 m for moose). For home range movement, we used an 2-D Ornstein–Uhlenbeck process (with symmetric attraction (0·05) and noise (325) matrices leading to realistic median step lengths around 400 m and home range radii around 2,000 m for moose). An Ornstein–Uhlenbeck process is a random walk towards an attractor, in this instance the origin, which results in the emergence of a stable home range. For the dispersal movement, we simulated the home-range using an Ornstein–Uhlenbeck process. At time step 71 (onset of spring), the transient phase started, using a Brownian bridge of 30 time steps towards the settlement located 70 km away (which corresponds roughly to the mean migration distance of moose). The Brownian bridge model estimates the probability of occurrence given a set of locations, the time between them and the mobility of the specific study object (Bullard 1999; Horne *et al.* 2007). The settlement phase was again simulated using an Ornstein–Uhlenbeck process with the attraction point located at the new area at 70 km distance. In the migration simulation, we modified the dispersal process with an additional Brownian bridge of 30 steps at time step 275 back to the origin, where we simulated a third seasonal home range with a Ornstein–Uhlenbeck process. Finally, for the mixed movement, we simulated a migration movement, where the second displacement of the attractor is not back to the origin, but mid-way between the origin and the second attractor. We used the implementations of the random walk, Ornstein–Uhlenbeck process and Brownian bridge in the R library adehabitat (Calenge 2006). For each movement type, we ran 100 simulations, hence a total of five movement types times 100 simulations each consisting of 365 time steps. The outcome of the simulation models is exemplified in Fig. 3.

STATISTICAL ANALYSIS OF MOVEMENT BEHAVIOUR

Given the nonlinearity in the hypothesized shape of the NSD curves, we used nonlinear models for the analysis (Pinheiro & Bates 2000). The advantage of using nonlinear models is that competing *a priori*
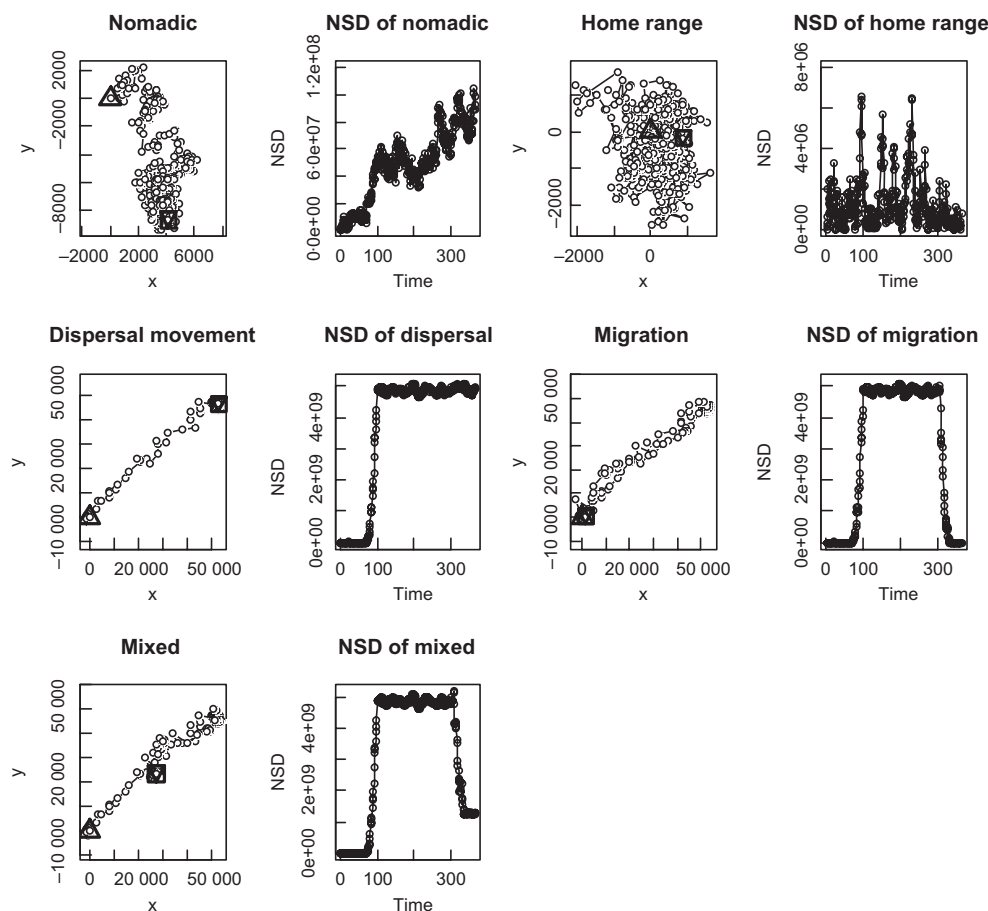
Fig. 3. Net squared displacement patterns from simulated random walk data. See Methods for more detail.

models (derived from hypotheses) can be translated into parameters that have a direct biological interpretation. Furthermore, in general fewer parameters are estimated for nonlinear models than for linear models (e.g. polynomial) and thus the fitted model is more parsimonious, and nonlinear models provide more reliable predictions than linear models outside the parameter range (Pinheiro & Bates 2000).

We analysed the simulated data and the NSD data of individual moose with nonlinear least squares models (*nls* function in R) fitted to each individual moose and simulated data set separately. Nonlinear least squares allow specifying the form of the function according to the hypothesis set above and thus five different models (migration, mixed migration, dispersal nomadic, home range) were fitted to the data. Model parameters were constrained to fall within realistic parameter space, i.e. $\delta > 0$ and $0 < \theta < 365$. All five models were compared, and the best model was selected using an information theoretic approach (Akaike Information Criteria, AIC, Burnham & Anderson 2002). AIC weights were calculated for each individual (Appendices S1 and S2) to take into account that for some moose the data may lend similar support to different movement models. Akaike weights give the probability that a model is the best model, given the data and the set of candidate models (Burnham & Anderson 2002). Given the complexity and specific functional form of the migratory, mixed migratory and dispersal model, the data might not support the model and thus convergence is not reached. As there is no support for the model in cases of nonconvergence, we set AIC to zero.

To quantify the migration parameters at the population level, we included all moose identified by the method above as migra-

tory into a mixed effects nonlinear model (nlme package version 3.1-89; Pinheiro & Bates 2000; sample code in Appendix S3). Individual moose ID was added as a random effect to avoid pseudo-replication and to include individual variation in the parameters that estimate the migration function. We also tested for the most parsimonious random effects structure, including individual differences in the distance, duration and timing of migration (Pinheiro & Bates 2000). We included the sex of the moose and the year as fixed effects to study population-level differences of moose movement behaviour. We identified a set of 17 models to test hypotheses based on the biology of the species, such as the need for females to be constrained to be at calving grounds in the spring and the joint rut of both sexes. Yearly differences were hypothesized to be apparent for all parameters and we tested explicitly the timing of migration to be constrained by rutting and calving more than environmental effects, such as the start of the spring and autumn.

PREDICTIBILITY OF MIGRATION PATTERNS

Setting apart a certain proportion of data for model validation or using cross-validation methods are customary approaches used in ecological research. We used an integrated approach to fully evaluate the predictive ability of the models (i) within individuals over time; (ii) between individuals from the same capture area (Sweden); and (iii) between individuals from different capture areas, i.e. the Norwegian and Swedish moose.

To assess the predictive ability within individuals over time, we first extracted the predicted values at the individual level from the mixed effects model based on the Swedish base data set for the first year. We then calculated the squared correlation (analogue to R^2 in linear regression analysis) between the predicted values for the first year of data and the data from the following year for the same moose in the base data and in the second Swedish data set. The derived squared correlation thus provides an estimate of how repeatable the movement patterns are between years for the same individual.

To make predictions on the population level, we calculated the predicted values for different years and sexes from the migration model using the Swedish base data set. We then calculated the squared correlation between the predicted values for a specific year and sex from the Swedish base data set and compared these with the data from the second Swedish data set and the Norwegian data set. Only females were considered at the population level because of limited data for males.

Results

MOVEMENT BEHAVIOUR

The results of fitting the five different statistical models (mixed migratory, migratory, dispersal, home range, nomadic) to the simulated movement data showed that the two migration patterns and the dispersal pattern were mostly correctly classified (99% for mixed migratory, 83% for migratory, 90% for dispersal). All misclassified migratory movements (17%) fell in the other migration category: mixed migration. Dispersal misclassification was low, with 10% misclassified as mixed migratory. The nomadic movement type's realized NSD shows large variability in their behaviour and was categorized as dispersal for nearly half of the cases. Similarly, the simulated home range data were in about one-third of the cases (36%) categorized as dispersal. The movement type with the highest proportion of misclassifications is the nomadic type with 49% categorized as dispersal. See Table 1 for an overview.

The same approach was then applied to real data where we divided moose movement patterns into five different movement behaviours – mixed migratory, migratory, dispersal, resident and nomadic. We found that 87% ($n = 67$) of the Swedish moose and 67% ($n = 21$) of the Norwegian moose were migratory, defined here as regular seasonal return movements. Of these, more than half of the moose (52%,

$n = 40$) in the Swedish base data set returned to the same area, compared to only 32% of the Norwegian moose ($n = 10$). The remaining migratory moose (55% of all individuals; $n = 27$ Swedish, $n = 11$ Norwegian) returned in winter to a similar geographical area, but not close to the same location used during the previous winter (here we call this a mixed strategy). Using AIC weights as a proxy for the relative support of a movement model given the AIC of the alternatives, the results show for the Swedish moose that slightly higher support was found for the mixed migratory behaviour (AIC_{weight}, Swedish: 0·50, Norwegian 0·39), followed by the migratory one (AIC_{weight}, Swedish 0·38, Norwegian 0·32).

The remaining moose did not migrate: 8% ($n = 6$) of the Swedish moose and 16% ($n = 5$) of the Norwegian moose in our study dispersed to a different location and did not return to their initial starting point the year before, whereas 4% ($n = 3$) and 3% ($n = 1$) stayed in their home range and 1% ($n = 1$) and 10% ($n = 3$) showed a nomadic movement pattern (Appendices S1 and S2). In comparison with the two migratory patterns, there was considerably less support for the dispersal, home range and nomadic behaviour (AIC_{weight}, Swedish 0·07, 0·04, 0·01; Norwegian 0·16, 0·03, 0·10, respectively). See Appendices S1 and S2 for detailed information.

MIGRATION PARAMETERS AND SEX AND YEAR DIFFERENCES

The most parsimonious model included variation of sex and year for the distance, timing of spring and autumn migration and duration of spring migration. It also included differences between years in the autumn duration but no difference between the sexes in this parameter (Appendix S4, model M17). Of the 67 Swedish moose that followed a migratory or mixed strategy, the estimated migration distance for females was 60, 107 and 114 km in 2005/2006, 2006/2007 and 2007/2008, respectively (Fig. 4, summary in Table 2). Males migrated further than females, but overlapping confidence intervals indicate large variation around these estimates and a competing model without sex differences in the migration distances receives some support ($AIC_{weight} = 0·24$, Appendix S4) compared to the model with sex differences in the migration distance ($AIC_{weight} = 0·48$, Appendix S4). Distance estimates did not differ between spring and autumn

Table 1. Each row gives the simulated movement types (nomadic, home range, dispersal, migration and mixed dispersal-migration) and the proportion classified for these movement types fitted to the net squared displacement. Numbers in bold represent the matching movement types from the fitted model and the simulated data

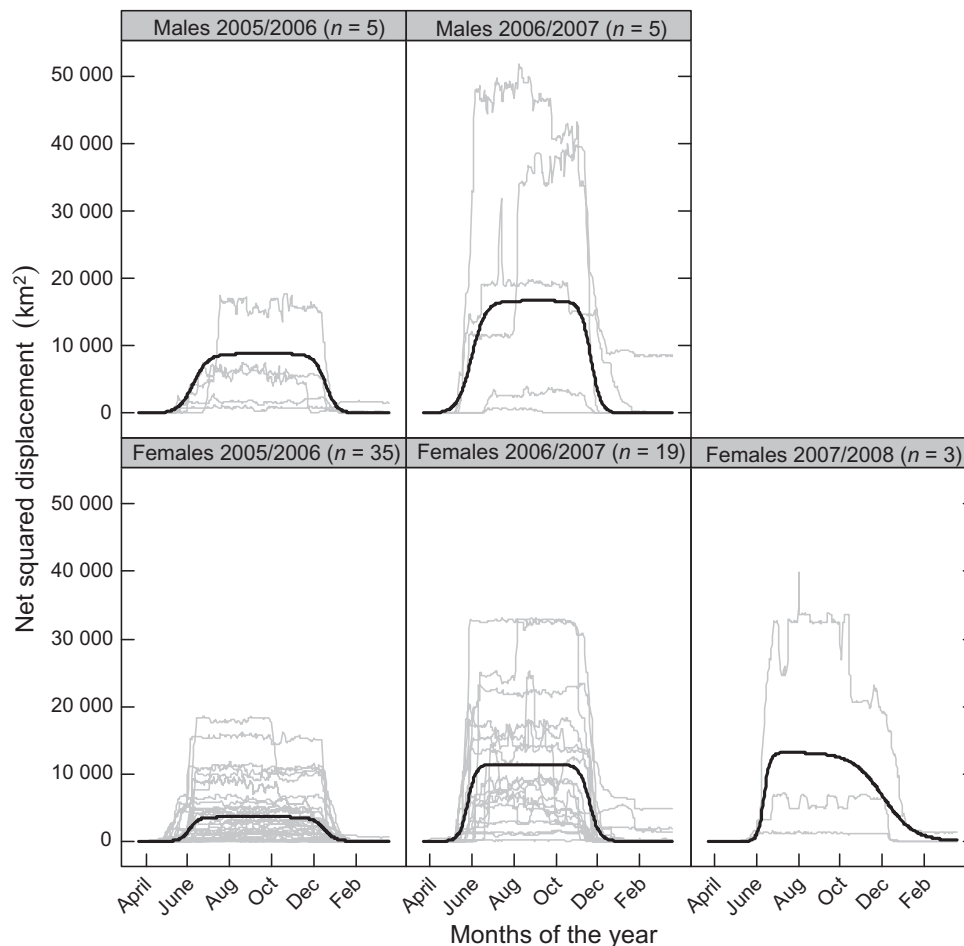|	MixedMigratory	Migratory	Dispersal	HomeRange	Nomadic
MixedMigratory	**0·99**	0·01	0	0	0
Migratory	0·17	**0·83**	0	0	0
Dispersal	0·10	0	**0·90**	0	0
HomeRange	0·09	0·06	0·36	**0·42**	0·07
Nomadic	0·13	0·04	0·49	0·03	**0·31**

Fig. 4. The population-level nonlinear mixed effects model for net squared displacement of the 69 moose in the Swedish base data set. The sample size *n* represents the number of individual moose trajectories in each panel of the plot. Day 1 is the 21st March.

Table 2. Estimated migration parameters (95% confidence intervals) for the Swedish moose population. The fixed effect estimates for the nonlinear mixed effects model are shown. Distance (km) represents the asymptotic height (δ), the timing of migration (θ) where the curves reaches half its asymptotic height, and duration (φ) is the time spent on half of the migration. Parameters relate to eqn 1 in the methods. The duration of autumn migration did not differ between males and females

Migration parameter	2005/2006		2006/2007		2007/2008	
	Females	Males	Females	Males	Females	Males
Distance (km)	60 (31–79)	94 (58–119)	107 (89–122)	129 (106–149)	114 (63–150)	135 (88–171)
Timing (Date)						
Spring	4/6 (3/6–4/6)	9/6 (8/6–10/6)	26/5 (25/5–27/5)	31/5 (31/5–1/6)	12/6 (11/6–12/6)	17/6 (16/6–18/6)
Autumn	17/12 (16/12–18/12)	19/12 (18/12–20/12)	19/11 (19/11–20/11)	21/11 (21/11–22/11)	3/12 (1/12–4/12)	4/12 (3/12–6/12)
Duration (Days)						
Spring	13 (12–14)	21 (20–23)	12 (11–13)	20 (19–21)	9 (7–10)	17 (15–19)
Autumn	17 (15–18)		15 (14–15)		45 (42–48)	

migration. We did not test for an interaction between sex and year because no data were available for males in the last year (2007/2008).

The timing of migration differed between years and sex. Females reached half of their spring migration distance between 26th May and 12th June in the years 2005–2007, whereas males arrived 5 days later in all years. During the autumn migration, females reached half of their migration distance between 19th November and 19th December. Males reached the same point 2 days later in all years. As for migration distance, we could not test for an interaction between year and sex.

Spring migration (half distance) lasted between 9 and 13 days in the years 2005–2007 for females and 8 days longer in all years for males. Autumn migration tended to last longer, between 15 and 45 days for both females and males (2005–2007, Table 2, see Methods for definitions). The duration of autumn migration did not differ between males and females. Overall, the variation explained by differences between years and sexes accounted for 37% of the total variation.

In addition to differences between years and sex, the distance of migration varied between individuals, but there was no additional individual variation in the duration and timing of migration. By taking into account additional individual differences, the model for the migratory moose explained 92% of the total variation in movement behaviour.

PREDICTABILITY OF MIGRATION PATTERNS

The predictability analysis within the Swedish individuals revealed that on average 69% of individual movement patterns in a given year can be predicted based on movement patterns for the same individuals during the previous year. The variation in predictability was generally high across individuals (range: 36–95%, Appendix S5), indicating that some individuals showed relatively low consistency in their migration behaviour while others showed similar migration patterns between years.

Population-level predictability from Swedish moose in 1 year to a different set of Swedish moose within the same year and capture area was 73% (range: 30–97%) for females in 2006/2007 and 74% (range: 30–88%) for females in 2007/2008. To assess the predictability across sites, the NSD of 13 female Norwegian moose classified as migratory were included in the analysis. The analysis showed that 45% of the NSD could be predicted from Swedish females in the same year. The variation across individuals ranged between 1% and 86%. Predictability for males was not assessed at population level because of small sample size.

Discussion

Many species restrict their movements to a limited and stable range during a given period of their life, which is commonly called the home range of an individual (Burt 1943; Börger, Dalziel & Fryxell 2008; Van Moorter *et al.* 2009). Two major life-history events disrupt the pattern of stable space use: dispersal and migration. We present a modelling approach to objectively distinguish between migration and other movement strategies, particularly dispersal, home range and nomadic behaviour, by using a multi-model selection approach. A clear categorization of animal movement strategies is doubtful, and therefore we suggest using Akaike weights to quantify the likelihood of a given model to be the best model relative to other models (Burnham & Anderson 2002). Hence, instead of categorizing the movement strategy we show how mixed strategies can be described and how likely it is that a particular animal follows a set of movement strategies. Using simulations, we showed that our nonlinear models were able to categorize simulated data drawn from theoretical movement theory. The main aim of the study, to be able to separate migratory (including mixed migratory) movement from other movement patterns (dispersal, nomadic, home range), was achieved with high certainty for the simulated data (100–87% correctly classified). The method showed uncertainty in classifying nomadic and home range behaviour with both categories being misclassified as dispersal to a considerable degree. The simulated data also showed that the method is biased towards describing migratory individuals as mixed migratory. The mixed migratory behaviour can be seen as more flexible migration behaviour as individuals do not need to return to their exact position.

Fitting the models to GPS-collared moose data showed that 87% and 67% of the Swedish and Norwegian moose, respectively, follow a migratory pattern. These results are in line with earlier research where 88% and 60% of the moose were categorized as migratory (Canada: Mauer 1998; Sweden: Ball, Nordengren & Wallin 2001). Furthermore, we show that models that allow moose not to return to exactly the same location as the year before was more parsimonious and received slightly higher support ($AIC_{weights}$) in the Swedish and Norwegian moose. For the Norwegian moose, considerable support is also given to dispersal behaviour where moose do not return at all but find a new location to move to after the summer. This is in line with the simulated data, where a movement was to some degree classified as dispersal when it was simulated as home-range or nomadic behaviour. Our results not only confirm earlier findings of a wide range of movement patterns observed for moose in the field (Hundertmark 1998; Ball, Nordengren & Wallin 2001; Hjeljord 2001) but also quantify these in an objective and repeatable way.

The migration model presented in this study was able to quantify the population-level migration distances from the original starting point accurately with 92% of the total variation in the NSD data explained. Despite recent achievements in understanding migration, the ability to predict migration is still limited (Bauer *et al.* 2009). Our method contributes to understanding the predictability of migration of the same individual, with on average 69% of the NSD variation explained from 1 year to the next. Individuals returning to a given site are observed in a variety of species, for example albatrosses *Thalassarche melanophrys* (Phillips *et al.* 2005), and are of major importance for conservation planning (Thirgood *et al.* 2004). Here, we quantified that around 74% of the NSD in a given year can be explained by modelling other individuals in the same population and year. Life-history data on individual moose will likely increase the predictability as we expect moose at earlier stages and experience to be more variable in their behaviour than older moose with a successful movement history.

Across regions the predictive power was somewhat lower with 45% of NSD explained when aiming to predict

Norwegian moose migration patterns from Swedish moose. Norwegian moose start slightly earlier and migrate less far, but the overall pattern of migration is similar to the Swedish moose. It is suggested from studies on northern-temperate cervids that migration takes place along an altitudinal gradient to increase energy intake (Demarais & Krausman 2000; Mysterud *et al.* 2001). Accordingly, differences in the landscape topology east and west of the mountain divide might explain the differences in migration patterns between the Swedish and Norwegian moose. In the east, the altitudinal change is less abrupt and thus moose have to move further to get to lower altitude during winter, whereas in the west this can be achieved within short distances. We therefore predict that future models, using landscape features and other environmental data as covariates, will explain more of the spatial variation in movement pattern observed between Swedish and Norwegian moose.

Yearly differences in the timing and duration of migration were identified in this study. In an earlier study, autumn migration in moose was found to be related to snow accumulation (Hundertmark 1998), whereas the triggering factors in spring are less clear (Hjeljord 2001). In red deer *Cervus elaphus*, Pettorelli *et al.* (2005) found an earlier start of migration in years with an earlier onset of spring measured using the normalized difference vegetation index, and possibly a similar mechanism may apply for moose. Using our model approach will provide an objective way to test these predictions.

A second influential fixed effect was the sex of the individual with male moose migrating consistently greater distances than females. The opposite trend has been observed in albatrosses (Phillips *et al.* 2005) and hermit thrushes (*Catharus guttatus faxoni*, Stouffer & Dwyer 2003) where females travelled further than males. The estimates for the different years in our moose model are derived from different individuals and we were not able to separate sex, cohort and environmental effects. Multi-year data for the same individual would help to identify the relative roles of the environment, the cohort and the individual. The timing of migration also varied between the sexes with female moose starting to migrate earlier than males. Possibly, this is because females are constrained by calving, which for Scandinavian moose show much variation in time but are mainly taking place at the end of May and the first 2 weeks of June (Saether & Heim 1993; Solberg *et al.* 2007).

The timing and duration did not vary between individuals, but did vary between years. Thus, our results suggest that the timing and duration of migration is mostly determined by environmental differences between years and less by individual characters. Given different experience and life-history, we expected the timing and duration of migration to depend on the individual. In the most parsimonious model, migration distance (asymptotic height) explained a considerable amount of variation between individuals, which indicates that individual moose make different decisions on how far they go. Thus, moose that walk further, but over the same time period, move at a faster speed to cover a longer distance.

Research on intraspecific variation in behaviour is increasing, and studies of temperament have recently been performed on a variety of animals, including mammals (e.g. Réale *et al.* 2000). Estimates of individual temperament can be directly incorporated into our modelling framework to test their ability to explain individual differences in migration. Given our results showing a large influence of individual variability, this should be an interesting direction for future research.

Why individuals differ in behaviour and why it is consistent over time is still rather unclear. Biro & Stamps (2008) hypothesized that personal traits are correlated with productivity (growth, reproduction) where the most bold and active individuals are the more productive. This suggests that individual variation in migration patterns might have consequences for viability and population dynamics. By using an objective approach, our method can contribute to the understanding of what limits migratory populations by linking estimates of the timing, duration and distance of migration to vital rates. For example, Hebblewhite & Merrill (2007) found predation risk in migratory elk *C. elaphus* to be highest during the migratory phase, and L. Börger, T. McIntosh, M. Ryckman, R.C. Rosatte, J. Hamr, J.M. Fryxell (revised for resubmission) showed that the distance and timing of dispersal both were strongly related to individual variation in long-term survival. A combination of movement path analysis and the analysis of disturbed and undisturbed habitats is needed to increase our knowledge on the causes and mechanism of population limitations.

Migration patterns vary among and within species, and have been described as partial when part of the population migrates (Lundberg 1988) and differential if migration distances vary within a species (Cristol, Baker & Carbone 1999). To determine whether an individual migrates and how far it migrates, studies have used the initial and the new capture or resighting locations as the starting and end point of migration, respectively (Lundberg 1988). A similar approach is to use the proportion of different age and sex classes at the different capture locations and seasons to determine which age and sex classes migrate and to what extent (e.g. Brodersen *et al.* 2008; Gillis *et al.* 2008). In ungulates, the degree of overlap of summer and winter home ranges has been used to distinguish between migratory and nonmigratory patterns (Ball, Nordengren & Wallin 2001; Nelson, Mech & Frame 2004). Bergman, Schaefer & Luttich (2000) have used comparisons of movement paths with expected patterns from correlated random walk to determine migratory and nonmigratory movement patterns. Johnson *et al.* (2002) used nonlinear models to distinguish between intra- and inter-patch movements. Dettki & Ericsson (2008) calculated the NSD to distinguish between migrating and nonmigrating individuals but did not apply nonlinear models. Here, we use features of existing approaches to develop a framework that incorporates random walk theory with nonlinear models to

understand key parameters of migration studies and the proportion of migratory individuals in a population.

The uniform framework for migration presented here is a parsimonious and objective way to study migration and requires few assumptions about seasonality of migration, but instead derives these parameters from a combination of models. Only three parameters were needed to describe a baseline migration pattern using nonlinear mixed effect models: the distance, timing and duration of migration, which showed good predictive ability of time and space. In line with the movement ecology paradigm proposed by Nathan *et al.* (2008), our approach facilitates the identification of different movement phases, such as stable range use or migration phases, which according to the paradigm should be at the beginning of each movement analysis.

Acknowledgements

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Supporting Information

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

Appendix S1. The AIC weights for the models describing a mixed strategy (MixedMigratory), a migratory strategy (Migratory), a dispersal strategy (Dispersal), home-range (HomeRange) and nomadic (Nomadic) strategy for the Swedish moose (base data).

Appendix S2. The AIC weights for the models describing a mixed strategy (MixedMigratory), a migratory strategy (Migratory), a dispersal strategy (Dispersal), home-range (HomeRange) and nomadic (Nomadic) strategy for the Norwegian moose.

Appendix S3. Example R code for migration analysis.

Appendix S4. Candidate models from which the model with the lowest AIC was found.

Appendix S5. The variation (%) explained by the non-linear mixed effect model from 1 year to the next and the number of individuals that fall within each category ($n = 14$).

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