

Quantifying individual differences in dispersal using net squared displacement

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17.1 Introduction

Quantifying individual differences and the phenotypic correlates of dispersal are of considerable interest for obtaining a better understanding of the mechanisms of dispersal (Bowler and Benton 2005; Clobert *et al.* 2009; Morales *et al.* 2010). The aim of this chapter is to present a new approach for modelling animal dispersal, based on net squared displacement statistics combined with a non-linear hierarchical modelling framework. It allows efficient construction of accurate population redistribution kernels, quantification of individual differences in dispersal, and testing hypothesized correlates of the latter (Börger *et al.* unpublished manuscript).

The chapter is organized as follows. Firstly, we explore the theoretical basis for using net squared displacement as a statistical modelling approach. This is followed by a simulation study to investigate the data requirements and power of the proposed method, ending with general conclusions.

17.2 Theoretical considerations

17.2.1 Net squared displacement as a synthetic measure of animal movement rate

Consider an organism, or in general any object, moving for a certain interval of time t . The straight-line, or Euclidian, distance from the start to the end point is called the net displacement and the square of this value is the net squared displacement (NSD; Turchin 1998). The NSD is a single time-dependent distance statistic which is fundamental for quanti-

fying movements of organisms or particles (Codling *et al.* 2008; Nouvellet *et al.* 2009; Skellam 1951; Turchin 1998), and in general random processes (Uhlenbeck and Ornstein 1930).

The mean (i.e. expected) value of the NSD over time is called the mean net squared displacement (MSD). MSD estimates can be obtained as the average over multiple recording sessions, or as the average over a given time unit for single-trajectory data (Elliott *et al.* 2011; Turchin 1998). In the simplest case of a freely moving Brownian particle over longer timescales (the so-called diffusive regime) the MSD will increase linearly with time (t):

$$MSD = 4Dt \quad (\text{Equation 17.1})$$

where D is the diffusion constant (multiplied by four for two-dimensional movements, by two for movements in one dimension) and t denotes the time since start, whereas over very short timescales the value increases as a quadratic function of time due to inertial forces, called ballistic motion (Einstein 1905; Langevin 1908; Li *et al.* 2010; Moorcroft and Lewis 2006; Turchin 1998; Uhlenbeck and Ornstein 1930). In general, the form of the MSD over time may deviate from a linear pattern due to movement constraints or external forces; thus a more general equation for the MSD over time is the power-law formulation (Codling *et al.* 2008; Metzler and Klafter 2000; Turchin 1998):

$$MSD = Dt^\alpha \quad (\text{Equation 17.2})$$

When $\alpha > 1$ the motion is called super-diffusive, sub-diffusive if $\alpha < 1$, and normal diffusion for $\alpha = 1$.

The inferior limit to sub-diffusion occurs when movements are constrained by an external boundary or when animals remain always in the same area, called the home range (reviewed in Börger *et al.* 2008). In this case, it can be shown (Turchin 1998) that the MSD initially will increase linearly over time as for diffusion (Equation 17.1), but the rate of increase will decrease over time and reach a steady-state constant value:

$$MSD = \frac{3D^2}{c^2} \quad (\text{Equation 17.3})$$

where c is an advection coefficient quantifying the strength of the tendency to return to the home range centre (the localizing tendency, see Moorcroft and Lewis 2006; Chapter 10).

Given these results, we can also predict the broad-scale pattern of the MSD over time for dispersal (see Fryxell *et al.* 2008 for a data-driven approach using GAM models). Specifically, dispersal is a three-stage multi-phase process (*sensu* Fryxell *et al.* 2008; Nathan *et al.* 2008); i.e. two stationary space use phases (the departure and settlement phases) separated by an exploratory transience phase (Bowler and Benton 2005; Clobert *et al.* 2004; Van Dyck and Baguette 2005). Thus, the MSD value will be close to zero during the pre-dispersal (or departure) phase, increase linearly over time during the transience phase, and converge to a stationary value at the settlement phase, hence leading to a sigmoid shape for the expected MSD. Note that we consider here only large-scale patterns—for example, short-scale exploratory movements are often observed during the departure or the transience phases (Clobert *et al.* 2009), yet are considered here as temporary deviations from the long-term pattern; see Turchin (1998) for the importance of focusing on the timescale of interest, whilst ignoring shorter time patterns. This approach can be extended to predict the MSD patterns of migratory animals (Kölzsch and Blasius 2008) by considering migration as a combination of two dispersal events, where the second ‘dispersal’ event returns the animal to the point of origin (and thus the MSD decreases again to zero, which leads to an expected double-sigmoid shape), as we consider in detail elsewhere (Börger *et al.* 2011; Bunnefeld *et al.* 2011).

The NSD is thus a single time-dependent movement statistic which encapsulates key statistical

properties of movement processes, allowing to link empirical measures directly with theoretical expectations of its mean (expected) value (the MSD). It circumvents several of the difficulties of traditional random walk analysis based on modelling distributions of step length and turning angle (Nouvellet *et al.* 2009). Importantly, it does not rely on equally spaced, regularly sampled locations, as displacement is modelled as a continuous function of time. Thus, NSD constitutes an ideal probe for assessing the support from the data for alternative movement models (Moorcroft and Lewis 2006; Nouvellet *et al.* 2009; Turchin 1998). In the following section we describe an efficient inferential approach to link models to data, based on non-linear models.

17.2.2 Capturing the functional form of displacement patterns with non-linear models

Animal movements are best understood as lying on a continuum between the extremes of sedentarism and nomadism (Börger *et al.* 2011). In the previous section, we showed that the NSD efficiently captures key statistical properties of movement processes and that the expected value of the displacement over time (MSD) can be derived from theory for different movement processes (e.g. Equations 17.1–17.3). Here we show how a system of non-linear models can be used to link the theoretical expectations to movement data.

A key characteristic of nomadic animals is that they never remain in the same area for a long time. Over larger scales this will lead to a diffusive space use pattern, with a linear increase of the MSD over time (Equation 17.1) or, more generally, a power model (Equation 17.2). Obviously, at even larger scales, the movements may deviate from a linear pattern due to, for example, regional constraints to movements, but we do not consider such complications here. At the other extreme, for sedentary animals restricting their movements within a home range area the MSD value will initially increase linearly but eventually approach a steady-state value (Equation 17.3). Consequently, the change over time of the MSD can be modelled using a simple equation for asymptotic regression through the origin:

$$MSD = \phi[1 - \exp(-\phi_2 t)] \quad (\text{Equation 17.4})$$

where ϕ_1 is the asymptote at the steady-state equilibrium, and ϕ_2 is the logarithm of the rate constant.

Finally, the expected form of the MSD will be sigmoid for dispersers (see previous section) and thus can be modelled using the equation for the logistic curve:

$$MSD = \frac{\phi_3}{1 + \exp\left[\frac{(\phi_4 - t)}{\phi_5}\right]} \quad (\text{Equation 17.5})$$

where ϕ_3 is the asymptote at the steady-state equilibrium (settlement) and thus quantifies dispersal distance; ϕ_4 is a parameter for the inflexion point, in units of time since start (t), and thus models the timing of the transience phase (note that $MSD = \phi_3/2$ at time $t = \phi_4$; i.e. half the dispersal distance has been reached); ϕ_5 is a scale parameter on the time axis governing the shape of the curve—given ϕ_3 and ϕ_4 it determines the time elapsed between reaching half and approximately 3/4 of the asymptote—and thus predicts how long dispersers stay in the transience phase. Specifically, 95% of the dispersal distance will be reached at the following settlement time:

$$t_{settle} = \phi_4 + 3\phi_5. \quad (\text{Equation 17.6})$$

Thus, t_{settle} can be taken as a reasonable estimate of the start of the settlement phase (similarly for the start of the transience phase).

Having derived a set of non-linear MSD equations, maximum likelihood methods within a model selection framework can be used to identify the movement type and estimate model parameters from observational data (for an example applied to migration, see Bunnefeld *et al.* 2011; but see following). In order to quantify also variation between individuals, an efficient approach is to use non-linear mixed effects models, as we detail in the next section.

17.3 The modelling approach: hierarchical non-linear models

17.3.1 Non-linear mixed effects models

Non-linear mixed effects models, a form of hierarchical non-linear model, are an efficient approach to

estimate parameters and make inferences on features underlying profiles of continuous, repeated measurements from a sample of individuals from a given population of interest (Davidian and Giltinan 2003; Pinheiro and Bates 2000). Of particular interest for observational data, such as most movement data, is that mixed effects models are robust to missing or unbalanced data, and that subject-specific estimates for individuals with limited data are improved by ‘borrowing strength’ from information available for other individuals (Pinheiro and Bates 2000).

Non-linear mixed effects models are an extension of linear mixed models and are usually viewed as two-stage (Davidian and Giltinan 2003; Pinheiro and Bates 2000):

Stage 1: Individual-level model.

$$y_{ij} = f(\Phi_{ij}, x_{ij}) + \epsilon_{ij}, i = 1, \dots, M, j = 1, \dots, n_i \quad (\text{Equation 17.7})$$

where f is a non-linear function of an individual-specific parameter vector Φ_{ij} and of the covariate vector x_{ij} ; ϵ_{ij} is a normally distributed noise term, Equations 17.7 and 17.8: M is the number of individuals, and n_i is the number of records for the i th individual. Note that the noise term may include the effects of measurement error as well as of deviations caused by other, short-scale, movement processes. Specifically, the function f is non-linear in one or more components of the individual-specific parameter vector Φ_{ij} , where the latter is modelled in the second stage as:

Stage 2: Population model.

$$\Phi_{ij} = A_{ij}\beta + B_{ij}b_i, b_i \sim N(0, \sigma^2 D) \quad (\text{Equation 17.8})$$

where β is a vector of fixed population parameters (*fixed effects*), b_i is a *random effects* vector associated with the i th individual (and invariant with j), A_{ij} and B_{ij} are design matrices for the fixed and random effects, and $\sigma^2 D$ is a variance-covariance matrix (D characterizes the magnitude of *natural* inter-individual variation; i.e. variation in the elements of Φ_{ij} not accounted for by systematic association with the individual attributes in β , the fixed effects vector). Both the matrices A_{ij} and B_{ij} depend on the individual, and also on the values of some covariates at the j th record (thus also time-varying covariates can be included in the fixed and random

effects). Observations on different individuals are assumed to be independent and the residuals are assumed to be normally distributed and independent of the random effects (but these assumptions can be relaxed, see Pinheiro and Bates 2000; Chapter 8). Two types of predictions are obtained: population predictions, corresponding to random effects equal to zero, and individual-specific predictions, obtained by adding the estimated random effects (which model subject-specific deviations from the population patterns).

Two important issues to consider are determining which effects should be modelled with an associated random component and which should be entirely a fixed effect, and how to use covariates to explain inter-individual parameter variability (Pinheiro and Bates 2000). Regarding the random effects, the preferred approach is to start with all parameters as mixed effects (i.e. allowing for individual variation for all model parameters), then using AIC to compare alternative models. This may not always be possible, due to non-convergence of the full model, or one of the random effects may be very small compared to the others. In such cases, a common approximation is to choose a model without an associated random effect for the component of concern, in order to achieve parsimony and numerical stability in fitting (Davidian and Giltinan 2003). For example, we found that in many instances the dispersal model (Equation 17.5) may be best fitted without including a random effect for the scale parameter (ϕ_s), in order to avoid overfitting. Once the most appropriate random effect structure has been determined, fixed effects covariates are fitted as linear models of the model parameters.

Model parameters can be estimated using several methods (Pinheiro and Bates 2000). We used the likelihood-based methods implemented in the nlme package (Pinheiro *et al.* 2011) for R (R Development Core Team 2011, version 2.12.2), based on maximum log-likelihood.

Given the availability of theoretical models for the expected NSD relationships (Section 17.2), and an efficient modelling approach to estimate time-related variation for each individual, an important consideration can be raised. Traditional approaches focus on MSD patterns, i.e. values averaged over time or between repeated recording sessions in

order to obtain the broad-scale patterns, while averaging out shorter-scale variation due to other sources. For many animal movement studies, however, sufficient data to calculate MSD values are not available, due to logistical constraints. Yet once a model for a theoretical expectation is available, non-linear mixed models offer an efficient approach to identifying the relevant signal even with highly noisy and unbalanced data. This suggests that similar inferences may be obtained by applying the approach to the observed, non-averaged NSD data directly derived from each individual trajectory. In Section 17.4 we investigate this suggestion using a simulation study.

17.3.2 The model selection approach

Given the set of *a priori* models derived from theory linking different movement behaviours to the expected squared displacement patterns (Section 17.2) it would appear that information-theoretic criteria, such as AIC (Burnham and Anderson 2002), could be used to identify the most likely movement type used by the animals under study. However, given that non-linear mixed models make predictions at the population and individual levels, the situation is considerably more complex, and global measures of goodness-of-fit (GOF) at the population level, as AIC or also R^2 , may be insufficient or even grossly misleading in determining the GOF of fitted models (Huang *et al.* 2009). For example, often a sample of individual location data may contain both sedentary and dispersing individuals and thus it is crucial to assess GOF for individual subjects. Huang *et al.* (2009) developed formulae for non-linear mixed models, highlighting especially the advantages of using the concordance correlation (CC) coefficient calculated at the subject-specific level (see equation 7 in Huang *et al.* 2009, p.2421):

$$CC_i = 1 - \frac{\sum_{j=1}^{n_i} (y_{ij} - \hat{y}_{ij})^2}{\sum_{j=1}^{n_i} (y_{ij} - \bar{y})^2 + \sum_{j=1}^{n_i} (\hat{y}_{ij} - \bar{\hat{y}})^2 + n_i (\bar{y} - \bar{\hat{y}})^2} \quad (\text{Equation 17.9})$$

where \bar{y} and $\bar{\hat{y}}$ are the means of the observed (y_{ij}) and predicted (\hat{y}_{ij}) values for individual i and n_i is

the subject-specific number of locations. The concordance criterion measures the level of agreement between the observed and predicted values, and is a combined measure of the degree of accuracy and precision of pairs of values of y_i and \hat{y}_i on the identity line (the concordance line or the 45° line through the origin) and any $CC \leq 0$ indicates lack of fit (Huang *et al.* 2009). To evaluate the GOF of the model, it is important to investigate individual-specific GOF measures and their frequency distribution (Huang *et al.* 2009). Using simulations, we evaluate the adequacy of the different approaches in Section 17.4.

17.3.3 Deriving dispersal kernels from net squared displacement models

The estimated NSD distances are a prediction of the average location of an individual over time. Thus, an efficient way to obtain an equation for dispersal kernels that takes into account the observed individual variability in movements is to estimate the distribution of parameter values for Equation 17.5 that captures the population distribution. Given that in most populations the distribution of dispersal distances is typically characterized by a long tail of large distance values, a robust approach is to calculate the quartiles of the predicted individual displacement distances for each time step and to fit separate non-linear models to each. The obtained parameter estimates are the values predicting where 50% and 100% of the population will be found at each time step.

17.4 Simulation study: evaluating data requirements and power

We used simulations to test whether individual-level dispersal parameters can be estimated using the proposed NSD approach, even in the presence of substantial individual variability. To do so, we simulated daily movements of 140 dispersers over three years, using the *adehabitat* library in R (Calenge 2006, version 1.8.4). Sedentary space-use patterns during the pre-dispersal and settlement phases were modelled using a Ornstein-Uhlenbeck process (Blackwell 1997), as implemented in the

sim.mou function, which simulates the movements of an individual moving randomly but constantly attracted to a central location (Börger *et al.* 2008). Movements during the transience phase were simulated using a correlated random walk as implemented in the *sim.crw* function. The start of the transience phase was randomly selected for each individual between 30 and 515 days after start. The transience phase lasted between 30 and 90 days, selected randomly for each individual and independently from the timing of the transience phase. The last location of the transience phase became the attraction point of the settlement phase Ornstein-Uhlenbeck function and the distance of this location from the start point was taken as the true dispersal distance.

For each simulated movement path we calculated the NSD after start for each location. To investigate the sensitivity of our approach to different measures of MSD, we calculated MSDs over intervals of three, seven, 14, 30, and 90 days (with each value attributed to the mid-time point) and repeated all analyses for each. Similarly, to test if NSD values can be used directly (see Section 3.1) and evaluate the impact of sampling frequency, we also simulated five different sampling regimes (one location every three, seven, 14, 30, and 90 days). We fitted the dispersal model (Equation 17.5) and extracted the estimated individual-level dispersal parameters (using Equation 17.6 for obtaining the estimates of the end and start of dispersal). We repeated this procedure 100 times, for a total 14 000 simulated movement paths and 140 000 models fitted to the ten different MSD and NSD measures.

True simulated dispersal distances varied over two orders of magnitude and the samples contained both individuals dispersing over the first as well as the second year after start. Results were clear (Figure 17.1)—the true values of distance and timing of dispersal were always recovered with high efficiency ($r > 0.95$), with no difference between using NSD or MSD values (e.g. for estimating dispersal distances, it made no difference to use one location every 90 days or one location every three days). Only estimates of the departure and settlement times become inaccurate when the sampling interval is coarser than the true process—see the estimates for the 30- and 90-days sampling regime in Figure 17.1. For

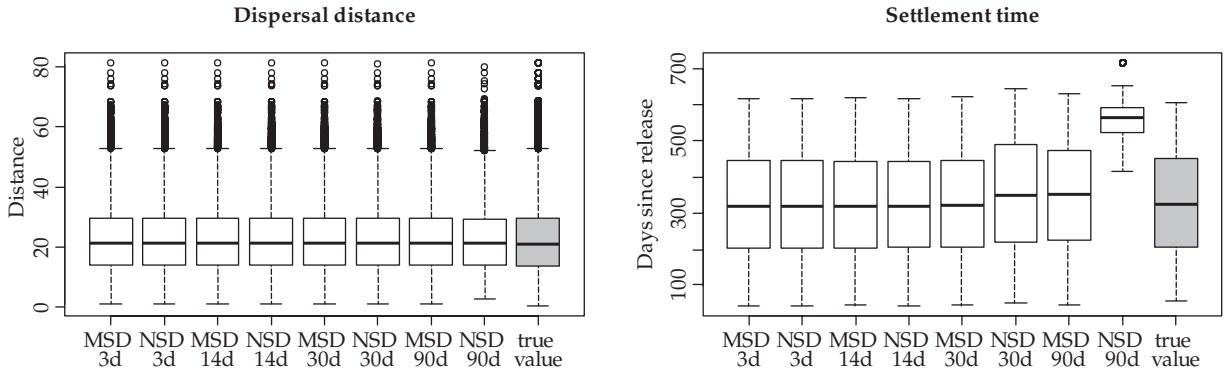


Figure 17.1 Distribution of estimated and true simulated individual-level dispersal parameters (100 simulations of a set of 140 movement paths). Models were fitted to simulated data using five different types of mean net squared displacement statistics (MSD; calculated by averaging the simulated daily net squared displacement values over five different time periods, ranging from three ('MSD3d') to 90 days ('MSD90d') or non-averaged net squared displacement values (NSD) obtained from five different simulated sampling regimes (from one location every three days ('NSD3d') to one locations every 90 days ('NSD90d')). See text for further details.

similar problems associated with too infrequently sampled location data, see Mysterud *et al.* (2011); the impact of these problems will, however, be markedly reduced by using the hierarchical modelling approach (combined with the CC statistic) that we present here (see results following), as compared to the individual-fit approach we presented elsewhere for migration (Bunnefeld *et al.* 2011) and adopted by Mysterud *et al.* (2011).

In order to test the ability to identify the correct movement process, we fitted to the data also the models for sedentary and nomadic animals (Equations 17.1–17.4) and compared all models using both global measures of goodness-of-fit (AIC/BIC, R^2 , and global CC statistics) as well as individual-level measures (individual-level CC_i). In all cases, the dispersal model unambiguously received the highest support, but only the individual-level CC statistics highlighted poor model fit ($CC < 0$) for a small set of simulated data. An inspection of the associated movement paths indicated that the simulated movement paths were peculiar; e.g. the correlated random walk during the transience phase had initially moved far from the start location, but by chance had returned to the departure location before the start of the settlement phase.

To investigate the ability of the approach to separate dispersal from other large-scale movement patterns, we simulated datasets with individuals

moving according to three different movement types: 120 were modelled as dispersers as described, ten always remained within a home range (modelled using an Ornstein-Uhlenbeck process), and ten were nomadic over the whole time period (modelled with a correlated random walk). We also evaluated an alternative model selection approach, by separately fitting the alternative models to each individual location set and evaluating the adequacy of the competing models using the CC, R^2 , and AIC weight statistics calculated for each individual movement path. We repeated this procedure 100 times. Results were clear—classification success using the hierarchical approach combined with the individual-level CC statistic was markedly higher compared to fitting alternative models separately to each single movement path (overall 81% correct space use modes identified; 88% for dispersers, with up to 100% accuracy for single simulations consisting of a set of 140 simulated movement paths).

We lastly evaluated the power of the approach to correctly estimate population-level differences such as sex differences: we simulated a sample of 140 individuals coming from two groups with different mean dispersal distances, timing of dispersal, or both, by modelling individual model parameters for the logistic curve (Equation 17.5) using normal distributions with different means. We simulated three scenarios, with groups differing in mean

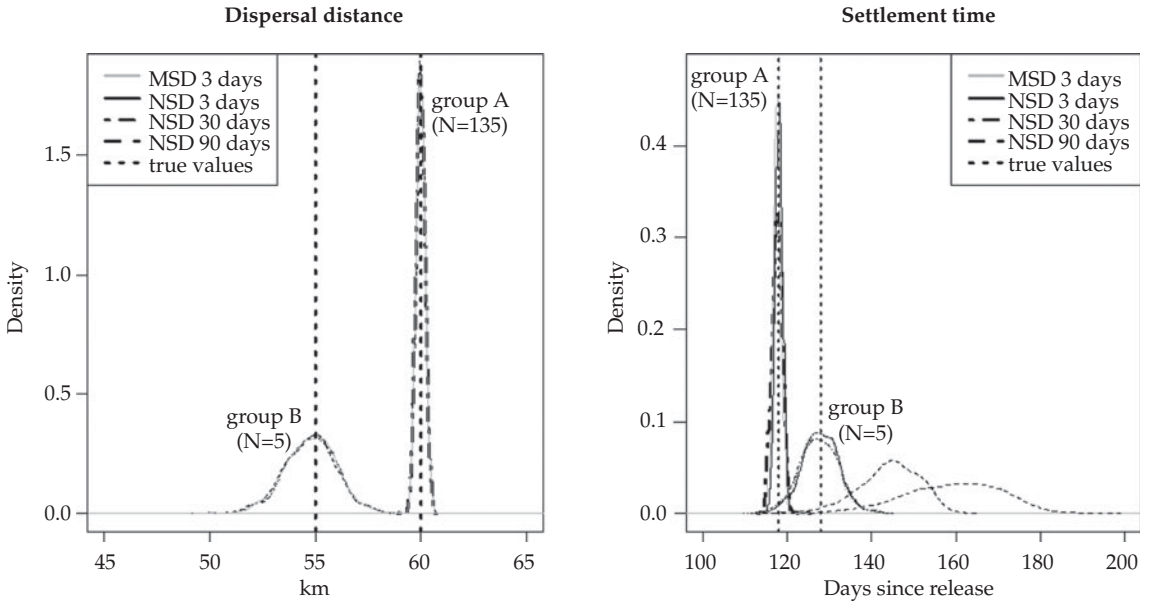


Figure 17.2 Distribution of estimated and true simulated population-level dispersal parameters ($N = 1000$ simulations of a set of 140 dispersers). The aim was to evaluate the power of the approach to estimate true dispersal parameters of two groups of individuals from a same population characterized by fixed mean differences. Results are shown for 1000 simulations of the case of unbalanced sample size (five versus 135 individuals), using four different squared displacement metrics. See text for further details.

dispersal distance (mean = 60 km versus 39 km or versus 55 km, variance = 300 km^2) or/and also timing of dispersal (mean = 100 versus 110 days after start, variance = 10, with 60 km versus 55 km mean dispersal distance, respectively). The scale parameter was always sampled from a normal distribution with mean = 6 and variance = 1. Each simulation consisted of 140 movement paths with equal or unequal sample size between the groups (in the latter case, 130 versus 10 or 135 versus five individuals). We used the individual model parameters to generate the true NSD curves over three years, to which we added two error sources, taken from normal distributions with mean zero and standard deviations of 14 km or 1.7 km, respectively, to simulate stochasticity caused by other movement types and by location error. We calculated NSD/MSD values with different sampling regimes, fitted the dispersal model and extracted the fixed effects population predictions and associated p -values. For each scenario we repeated the simulations 1000 times, for a total of 140 000 simulated NSD patterns.

Results were clear (Figure 17.2). The difference in true mean dispersal distance could be recovered with near certainty even in the most restrictive scenario (five versus 135 individuals) with no appreciable difference even when using only one location every 90 days (and $p < 0.05$ in 99% of the 1000 simulations). Similarly, differences in the timing of dispersal could be detected, except when using too sparsely sampled locations (one location every 30 and, especially, 90 days; Figure 17.2), in accordance with previous simulations. The statistical power, however, was lower, as a significant p -value was obtained only in 58% of the simulations (27% for the 90-days sampling regime). The power increased with better sample sizes between the two groups.

17.5 Conclusions

A problem highlighted by current research is to develop methods to account for the typically high degree of individual variability in dispersal behaviour, in order to develop dispersal kernels of improved predictive ability. We demonstrated that

by modelling NSD patterns within a non-linear mixed effects modelling framework, highly accurate dispersal kernels can be estimated and determinants of individual differences can be tested within the same framework. By including a general theoretical framework for movement studies, we demonstrated how to objectively separate dispersers from non-dispersing individuals. The method works also on sparsely sampled movement data, without requiring equal sampling intervals between locations, and thus might prove applicable for a wide range of taxa.

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