

A statistical framework for inferring the influence of conspecifics on movement behaviour

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Summary

1. The movements of individuals – at almost any scale – are likely to depend on the behaviour of conspecifics. As an example, the movements of dispersing juveniles and their settling decisions may depend on the availability of mates and free territories, that is, both the presence and absence of other individuals. As another example, individuals can use the presence of conspecifics during foraging movements as an indicator of habitat quality.
2. We develop a general statistical framework for identifying and characterizing conspecific influence on movements from tracking data acquired simultaneously from a set of potentially interacting individuals.
3. We model conspecific attraction/repulsion through a functional response in which social behaviour is assumed to depend on proximity to other individuals. The model partitions variation in the functional response into a population component (common to all individuals), variation among individuals (modelled as random intercept-slope) and variation within an individual's trajectory (modelled through temporal autocorrelation).
4. We present a Bayesian approach for the estimation of the model and illustrate its use with simulated movement data generated from a number of contrasting scenarios. We then apply the method to a case study on eagle owl *Bubo bubo* juvenile dispersal, demonstrating that individual movements are generally influenced by the presence of conspecifics, with the level of attraction decreasing with increasing proximity to other individuals. We further show that female eagle owls are more attracted to conspecifics than males, and both males and females are more attracted to females than to males.

Key-words: behavioural rules, condition-dependent dispersal, mixed-effect model, model/data, social information, statistical inference

Introduction

The presence of conspecifics can influence individual movement patterns, with important consequences in many ecological and evolutionary contexts, such as foraging (e.g. Kawaguchi, Ohashi & Toquenaga 2006), mate choice (e.g. Kuussaari *et al.* 1998), habitat selection and space use (e.g. Serrano *et al.* 2003). Depending on the relative costs and benefits of conspecific aggregation, individuals may be attracted to or repulsed from other individuals. The strongest benefit of conspecific attraction is expected to take place at intermediate densities, as at low population densities social cues are typically unavailable, whereas at high population densities, the potential costs of competition may outweigh the benefits from conspecific attraction (Fletcher 2006, 2007). The presence of conspecifics can lead to different behavioural actions, the decision rules behind which can be at least partly inferred from the realized movement patterns (Bode *et al.* 2012). In some cases, individuals may primarily follow their nearest neighbours

(Hemelrijk *et al.* 2008), or they may use local density as a cue (Delgado *et al.* 2010). In many cases, movement strategies are context-dependent and change over time, either gradually or through discrete behavioural switches (Morales *et al.* 2004).

The influence of conspecifics on animal movements has been extensively studied with the help of mathematical models and simulations, especially to understand the underlying mechanisms behind many forms of animal aggregation (e.g. Couzin *et al.* 2002). For example, simple behavioural rules have been shown to lead to patterns of collective motion, which are at least qualitatively similar to those observed for flocking birds, schooling fish or swarming insects (e.g. Couzin *et al.* 2002). Some of these models have been successfully matched to experimental data (e.g. Couzin *et al.* 2011; Herbert-Read *et al.* 2011; Katz *et al.* 2011), but typically not at the temporal resolution at which individuals make their movement decisions. If movement decisions are linked to various types of potentially conflicting motivations (e.g. food searching, predator/competitor avoidance, sampling of potential nesting habitat, or mate search), they may also be made at different temporal resolutions. In addition, even though movement data are intrinsically

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complex, with many levels of structure and heterogeneity, previous models have often assumed fairly simplistic rules (e.g. they usually assumed that all individuals operate according to some behavioural rules; Couzin *et al.* 2002; Eriksson *et al.* 2010; Katz *et al.* 2011), with extensions such as context-dependent interactions having only recently emerged (Guttal & Couzin 2010).

In this article, we develop a simple but general statistical framework for studying whether and how the presence of conspecifics influences animal movement at the individual level. We proceed in two steps, first looking for signals of conspecific influence by comparing the observed movement behaviour to that predicted by a null model. We then use a regression model to partition the variation in the patterns of social information use into components corresponding to density-dependent attraction or repulsion, variation among individuals and variation within individuals. Beside its simplicity, this framework allows incorporating the intrinsic complexity of movement data, and the many levels of structure and heterogeneity in movement behaviour (e.g. across space and time, among individuals, within individuals). We examine the performance of the statistical framework with simulated data and apply the framework to an analysis of eagle owl natal dispersal. The conceptual idea behind the statistical framework is illustrated in Fig. 1.

Materials and methods

NULL MODELS

Whether individuals are attracted to or repulsed from conspecifics can be measured by comparing observed displacements to those predicted by a null model, which describes the expectation in case the movements of the focal individual were not influenced by conspecifics (Fig. 1). Let $\mathbf{z}(t) = (x(t), y(t))$ denote the location of the focal individual at time t . Assuming that two consecutive data points on the location of the focal

individual have been acquired at times t_1 and t_2 , we ask if the observed location $\mathbf{z}(t_2)$ is in some way different from what would be expected from the knowledge of the location $\mathbf{z}(t_1)$ and the null model of movement between the times t_1 and t_2 . In the ideal case, the null model should account for all factors influencing movement behaviour except conspecifics, so that any deviation between the data and the null model could be attributed solely to social factors. While sophisticated modelling approaches for individual movement have been developed (e.g. Patterson *et al.* 2008), the definition of an appropriate null model is a highly non-trivial task to which we return in the Discussion. In the analysis of data generated by simulation models, we simply assume that in the absence of conspecifics, the individual would have taken a movement step with length equal to that of the observed movement step $|\mathbf{z}(t_2) - \mathbf{z}(t_1)|$, but in a totally random direction (uniform in the range from 0 to 2π ; a model often referred to as the *simple random walk*). With this choice, the probability distribution of null locations consists simply of those locations that form a circle around the previous location $\mathbf{z}(t_1)$, the observed location $\mathbf{z}(t_2)$ being one point on the circle (Fig. 1b).

MEASURES OF PROXIMITY AND SOCIABILITY

After deciding on the null model, one next needs to specify how to compare the observed location $\mathbf{z}(t_2)$ with the distribution of null locations. To do so, we defined measures of proximity P and sociability S . We measure proximity P using two alternatives, both of which increase with increasing local density of individuals. Proximity measure 1 (hereafter, *nearest neighbour*) is defined as the negative of the shortest distance to any of the other conspecifics. Proximity measure 2 (hereafter, *density*) is defined as the density (number of individuals per unit area) of conspecifics within a specified radius d from the focal individual. Note that the selection of these indexes (e.g. whether to use the negative of the shortest distance, the inverse of the shortest distance, either of the above for the log-transformed distance, the number of other individuals within a fixed radius and the density of individuals smoothed by a kernel with continuous distance decay) will in most cases be necessarily somewhat arbitrary due to lack of information to which aspect of proximity the individuals respond to. The selection should be based on

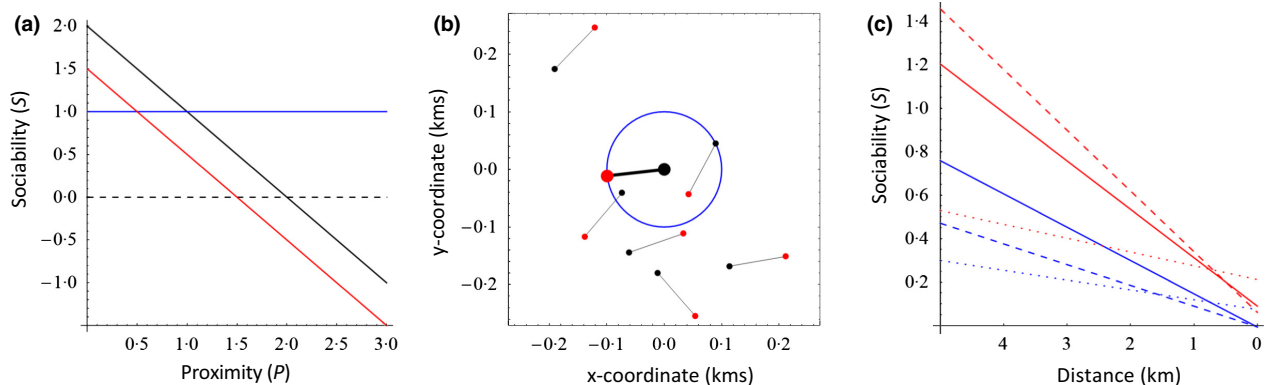


Fig. 1. Panel (a) shows the relationship between current proximity (P) to other individuals and the expected sociability (S) for three hypothetical scenarios: (i) individual attracted to other individuals irrespective of its current proximity (blue line), (ii) individual attracted to conspecifics at low but repulsed at high density (black and red lines) and (iii) individual moving independently of conspecifics (dashed line). Panel (b) illustrates how sociability can be measured from movement data. Large dots represent the focal individual at its initial position (black dot) and after a movement step (red dot). Small dots show the locations of six other individuals. After the movement step, the focal individual is close (39 m) to where one of the conspecifics was initially. The random expectation, averaged over locations within the blue circle, is 69 m; thus, the focal individual showed attraction ($S^{\text{fl}} = 30$ m). Panel (c) shows the median estimates of the functional response for the owl case study. The red and blue lines correspond to the focal owl being a female or male, respectively. The line style indicates how proximity to other individuals is measured: all individuals (continuous line), females only (dashed line) or males only (dotted line).

biological considerations such as whether the absolute or relative distances are likely to be relevant (whether to log-transform or not), and on statistical considerations, that is, what kind of distributions of the explanatory and/or response variables arise when a given kind of index is applied to the data in hand.

We define the sociability measure S as the difference between the observed and null proximity measures: $S = P^{obs} - E[P^{null}]$. Here, P^{obs} is the observed proximity of the focal individual to the other individuals after it has taken a movement step, and $E[P^{null}]$ is the expected proximity over the distribution of null locations. Assuming that the individuals make their movement decisions based on the locations of the other individuals at time t_1 , the proximity of the location $\mathbf{z}(t_2)$ should be measured against the locations of conspecifics at time t_1 . We denote the sociability measure corresponding to this choice by S^{t_1} . If the individual continuously tracks the other individuals (as may often be the case for real individual movements), the sociability measure should be evaluated by the locations of conspecifics at time t_2 ; we denote this sociability measure as S^{t_2} . The inferential difference between S^{t_1} and S^{t_2} depends on how much the other individuals move during one time step and hence on the product between the time interval and the movement speed. The measures S^{t_1} and S^{t_2} quantify whether the focal individual at $\mathbf{z}(t_2)$ is closer or further away than expected by the null model from where its conspecifics were at times t_1 and t_2 , respectively. A value of $S > 0$ can be interpreted so that the focal individual was attracted by conspecifics, whereas $S < 0$ indicates that the focal individual avoided conspecifics.

STATISTICAL MODELS

The response variable in our model is S_{it} , that is, the observed sociability of individual i based on the movement step that started at time t . The main covariate is P_{it} , the proximity of the individual to conspecifics at time t . We normalized P_{it} to zero mean and unit variance, and S_{it} to unit variance, but did not normalize the mean of S_{it} to zero as it is of interest to ask whether the individuals are on average attracted to or repulsed from conspecifics. For simplicity, we assume the linear regression model.

$$S_{it} = \mu + \mu_i^H + \mu_i^T + (\beta + \beta_i^H + \beta_i^T)P_{it} + \varepsilon_{it},$$

where the intercept μ estimates the population mean level of sociability and the slope β the effect of the proximity of conspecifics on sociability. The model has two random components that relate to population heterogeneity (superscript H for random variation among individuals) and to temporal heterogeneity (superscript T for random variation within individuals over time). Both of these random components are assumed to follow bivariate normal distributions with covariance structures $Cov(a_i^H, b_i^H) = \delta_{ii} \Sigma_{ab}^H$ and $Cov(a_{it}^T, b_{it}^T) = \delta_{ii} \Sigma_{ab}^T f(t, t', T)$, where $a, b \in \{\mu, \beta\}$. Here, Σ^H and Σ^T are 2×2 variance-covariance matrices, and δ_{ii} is Kronecker's delta specifying that the effects are independent among the individuals. We model temporal autocorrelation assuming exponential decay at temporal scale T , $f(t, t', T) = \exp(-|t - t'|/T)$ and assume that the residual variation ε_{it} follows normal distribution with zero mean and variance σ^2 .

We used Bayesian inference to estimate model parameters. The choices of priors for model parameters ($\mu, \beta, \Sigma^H, \Sigma^T, T$ and σ^2), as well as a description of the Markov chain Monte Carlo (MCMC) algorithm used to sample the posterior distribution are described in Appendix S1. We examined how the squared response in the fitted model $V = E[S^2]$ is split up into the four components of the model (1): variation V_P related to population mean, variation V_H related to population heterogeneity, variation V_T related to temporal heterogeneity and residual

variation V_R . Expanding S^2 and noting that the covariate P is normalized to zero mean and unit variance, these can be written as $V_P = \mu^2 + \beta^2, V_H = \Sigma_{\mu\mu}^H \Sigma_{\beta\beta}^H, V_T = \Sigma_{\mu\mu}^T + \Sigma_{\beta\beta}^T$ and $V_R = \sigma^2$.

GENERATION OF SIMULATED DATA

The simulations were conducted in a square with area 10×10 km. We assumed the average density to be one individual per km^2 , and the simulation was initialized by randomizing the 100 individuals according to complete spatial randomness (CSR). With CSR and density $1/\text{km}^2$, the mean distance to the nearest neighbour is 500 m, with 95% quantile ranging from 90 m to 1.1 km (Kingman 1993). To mimic infinite space, we assumed toroidal boundary conditions. We simulated the chosen process with day as a time step, first removing a transient of 100 days and then collecting data for $T = 100$ days. In all models, individuals moved with constant steps of 100 m each day. The decision of where to move next (day $t + 1$) was based on information about the current location of the other individuals (day t).

Data were simulated according to the following six scenarios. In Scenario 0 (independent movements), the direction of the next step is random. In Scenario 1 (preferred distance to the nearest conspecific), the focal individual prefers to have a distance of 250 m to the nearest conspecific, thus creating a tendency to form aggregations with circa fourfold density relative to the case of CSR. The individual samples $k = 5$ potential locations at random directions from the present location and chooses the one which is closest to its preference. Note that higher values of k would lead to more deterministic movements towards the preferred state, whereas $k = 1$ would result in a simple random walk; k therefore captures the completeness of the individuals knowledge of its surroundings. In Scenario 2 (preferred local density of conspecifics), the individual prefers to have 12 other individuals in a circle of 1 km radius from its location, corresponding again to ca. fourfold density compared with the mean density. As in Scenario 1, the next location is selected as the most preferred one among $k = 5$ randomly selected locations. In Scenario 3 (heterogeneous population), half of the individuals are socially independent and half socially dependent, the rules being like in Scenarios 0 and 1, respectively. In Scenario 4 (behavioural switching), we consider that individual decisions regarding conspecifics might change over time depending on different ecological circumstances (e.g. predation risk, resource depletion), and thus, each individual has two possible behavioural modes, socially independent and socially dependent, the rules being as in Scenarios 0 and 1, respectively. The initial condition is as in Scenario 3, after which at each time step, each individual switches its mode with probability $p = 0.1$. In Scenario 5 (confounding factors), we simulated an underlying resource distribution that changes in time and space. Resources are modelled as points, which are initially randomly distributed over the domain with density $\rho = 0.1$ per unit area. At each time step, each resource point is displaced (i.e. disappears and appears in a new random location) with probability $q = 0.1$. Each individual samples $k = 5$ locations and selects the one that is closest to the nearest resource point, independent of the presence of conspecifics. Under this scenario, individual movements may appear to be dependent on the behaviour of conspecifics, though there are no direct social interactions.

We first asked whether the statistical models described in the previous section are structurally adequate for capturing the mechanisms behind the individual-based simulation models described in this section. Here, we assumed the availability of much data (100 steps observed for 100 individuals) and applied the proximity measure that

corresponded to each of the scenarios (density at spatial scale of 1 km for Scenario 2, nearest neighbour measure for the other scenarios). Secondly, to ask whether the model could correctly identify the spatial scale at which the decisions were made in the simulations, we fitted the data on Scenarios 1 and 2 with both proximity measures (for density with spatial scales $d = 0.25, 0.5, 1.0, 2.0, 4.0$ km). Finally, we assessed the performance of the statistical models to work with incomplete data by modifying the Scenarios 3 and Scenario 4 as follows. To examine the effect of missing individuals, we assumed that we had data only on 25 or 50 of the 100 individuals. To examine the effect of the sampling interval, we subsampled the data twofold or fourfold, resulting into 50 or 25 observed movement steps during the study period of $T = 100$ days.

EMPIRICAL DATA ON EAGLE OWLS

We focus here on the wandering phase of dispersal, that is, when individuals explore different areas for a variable time period before settling in a new area (Delgado *et al.* 2010), of 55 juvenile eagle owls (36 males and 19 females) radiotagged in south-western Spain during the years 2003–2007. Owls were located at their diurnal roosts ($n = 766$; 538 locations for males and 228 locations for females), the data including on average 12.8 (SD = 7.1) observations for each individual, sampled on average at 10.5 day (SD = 11.6) intervals. Locations were obtained using triangulation with a three-element handheld Yagi-antenna connected to ICOM portable receivers. We used a slightly modified version of the statistical modelling framework described above to ask whether and how owls responded to conspecifics during dispersal. First, when computing P^{null} , we accounted for variation in step lengths by fitting a linear model $\log(\text{step length}) \sim \log(\text{duration of sampling interval})$ separately for each owl (average R^2 value of the linear models = 0.20, ranging from 0.00001 to 0.92) and then used these models to sample step lengths in the null model. Thus, the response variable S_{it} here reflects not only whether the owl avoided or was attracted to other owls in terms of the direction, but also in terms of the distance it moved. By randomizing the distance for each step rather than using a fixed step length makes the null model more realistic. Even though the data behind the null model (i.e. the actual movement data) are necessarily influenced by conspecifics, the null model averages over all kinds of conditions that the individual has encountered during the data collection period. Secondly, we accounted for a possible preference for habitat by accepting in the null set only locations which consisted of the same habitat as the location the individual moved to in reality (see Delgado *et al.* 2010 for habitat classification). The error in radiotracking localization (accuracy of mean \pm SE = 83.5 \pm 49.5 m; Delgado *et al.* 2010) was small compared with the sizes of habitat patches on the landscape (mean patch size \pm SD = 4.8 \pm 133.9 km²). Thus, the possibility of erroneously classifying the habitat association of each location was negligible in this study. As location data for all individuals were not obtained simultaneously, the locations of the other owls were typically not known exactly at the time when the observation of the focal owl was made. As a simple solution to this problem, we used linear interpolation between observed locations to estimate the location of each owl at any time. Interpolated locations landed in almost all cases in habitats used by owls during dispersal (see Appendix S4).

We assumed that individual movement response to the social environment may depend on the state of the individual, for which we considered the three variables of (1) sex, (2) body condition index (BCI) and (3) haematocrit index. Higher values of parameters 2 and 3 correspond to better individual condition (for more details on the empirical

study and the measurement of these two indices, as well for earlier results, see Delgado *et al.* 2010). We modelled the effect of the individual as $\mu_i^H = \sum_k x_{ki} \gamma_k + \mu_i^{RH}$, $\beta_i^H = \sum_k x_{ki} \vartheta_k + \beta_i^{RH}$, where x_{ki} is the covariate of type $k = 1, 2, 3$ measured for individual i , and parameters γ_k and ϑ_k measure the effect of covariates on the behavioural rule, that is, to the overall level of sociability and its dependence on conspecifics. The residual components of variation μ_i^{RH} and β_i^{RH} were modelled as μ_i^H and β_i^H in the original model. To explore whether individuals were responding to overall conspecific density or specifically to the density of the same or opposite sex, we fitted the models so that proximity (and thus also sociability) was based solely on females or males. The statistical models were implemented in Mathematica (source code and binaries can be found in supplements).

Results

In general, the partitioning of variance in the fitted statistical models was consistent with the simulated behaviour of the individual-based models. When movements were not affected by conspecifics (Scenario 0; Fig. 2a), almost all model variance was assigned to the residual. For Scenarios 1 and 2 (Fig. 2b,c, respectively), almost all of the non-residual variance was assigned to component V_P , indicating that the individuals were similarly affected by their social environment. For the case of a heterogeneous population (Scenario 3; Fig. 2d), a substantial amount of variation was assigned to component V_H measuring variation among individuals. For the case of behavioural switching (Scenario 4; Fig. 2e), a considerable proportion of variation was assigned to component V_T , which measures temporal heterogeneity within the individuals. In this scenario, the temporal scale of the autocorrelation reflected the frequency with which the individuals switched their behaviour. In the case where the individuals tracked the changing distribution of resource points (Scenario 5; Fig. 2f), the fitted statistical model resembled that of behavioural switching, though with a low scale of temporal autocorrelation. Figure 2 shows that for both Scenarios 1 and 2, the best model fit in terms of lowest residual variance was obtained for the statistical model with nearest neighbour proximity. We note that for Scenario 2, a large amount of variation in this model was assigned to temporal heterogeneity V_T with temporal scale T very close to zero; in this case, the variance component V_T is equivalent to residual variation (see Appendix S1). Therefore, for Scenario 2 the best fitting statistical model was the one where proximity is based on individual density within 1 km around the focal individual, that is, the model that corresponds with the simulated scenario.

These results indicate that the statistical models can correctly describe the underlying movement behaviour when abundant and high-quality data are available. As expected, the ability of these models to disentangle the variance components decreases both with the number of missing individuals and with the length of the sampling interval (Fig. 2d,e). The identification of population heterogeneity is more sensitive to the number of sampled individuals than to the sampling interval, whereas data for many steps per individual are required to identify behavioural switching. Repeating the analyses with

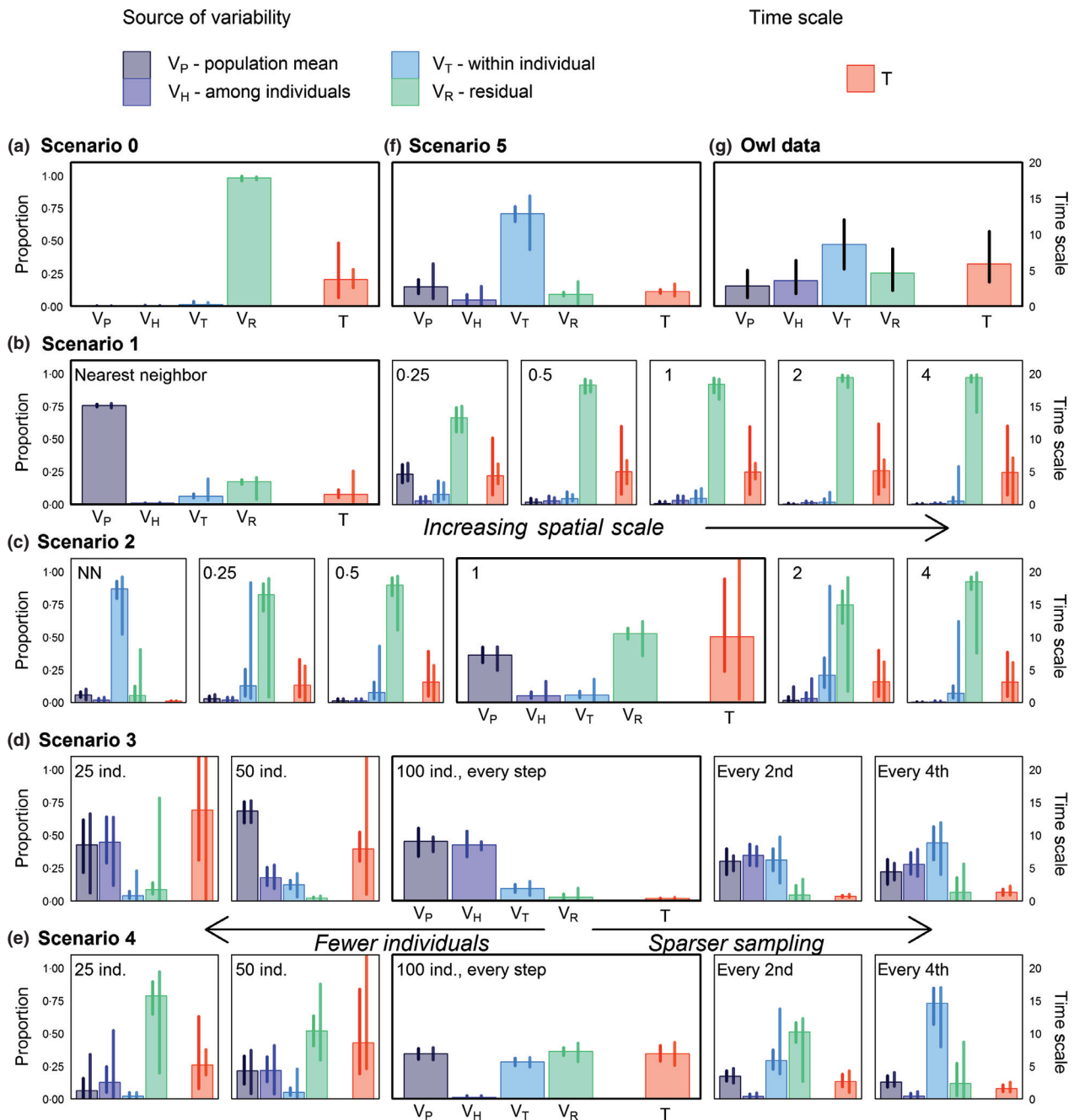


Fig. 2. Performance of the statistical framework for inferring movement behaviour from simulated (a–f) and eagle owl (g) data, including the ability of the models to pinpoint the spatial scale at which the individuals assess proximity (for Scenarios 1 and 2), and the effect of sample size in terms of number of tracked individuals and the sampling interval (for Scenarios 3 and 4). In all panels, bars show averages (over replicates and posteriors) of the four variance components. The smaller (bold) error bars show parameter uncertainty measured as 95% quantile in the posterior distribution (averaged over replicates). The larger (light) error bars show additionally variation among replicates (minimal and maximal values among the 10 replicates). NN: nearest neighbour proximity measure. The time-scale (T) is the time-scale of temporal autocorrelation. For parameter values, see main text.

measure, S^{I2} lead to similar results though with a slightly worse model fit than with measure S^{I1} (Appendix S2).

EMPIRICAL DATA ON EAGLE OWLS

In the case of eagle owls, the proximity measure leading to the smallest residual variation was the nearest neighbour measure (Fig. 2g, Appendix S3). In this model, the variance was

partitioned as $V_P = 0.14$ (95% highest posterior density interval 0.06–0.25), $V_H = 0.18$ (0.09–0.32), $V_T = 0.43$ (0.26–0.60) and $V_R = 0.23$ (0.11–0.40), indicating a substantial amount of variability both among individuals and within individuals, the latter with temporal scale $T = 5.9$ (3.4–10.5) days. Owls were generally attracted to conspecifics, the strength of the attraction decreasing with increasing proximity (Fig. 1c). Females were more attracted to conspecifics than males, and both males

and females were more attracted towards females than males (Fig. 1c). Owls in good condition were generally less attracted to conspecifics than owls in poor condition, but this statement obtained only limited statistical support (Appendix S3).

Discussion

We have presented a statistical framework for inferring the influence of conspecifics on movement behaviour and illustrated its use both with simulated data and with a case study on eagle owl dispersal. Unlike much of the earlier work on collective movement behaviour (e.g. Couzin *et al.* 2002; Guttal & Couzin 2010), our approach is not based on specific assumptions about the underlying mechanisms, but is purely statistical. Our framework is related to previous approaches developed to infer drivers of animal space use patterns such as step selection functions (SSF; Fortin *et al.* 2005) in the sense that the locations of other individuals can be considered as a spatial factor that influences the individual movement decisions. In our framework, we have included all other aspects normally included in SSF (i.e. those related to habitats, movement modes etc.) in the null model and thus separated them from the influence of conspecifics. The first reason for doing so is that this allows making the conceptual framework related to proximity and sociability (Fig. 1) explicit. The second and somewhat related reason is that this allows for a more straightforward interpretation of the statistical model. The advantage of the present approach is in its generality: it can be applied to almost any movement data on interacting entities. However, a more mechanistic approach tailored to the specifics of a given case study is likely to yield more detailed information. Thus, we see our approach as a first step in the analysis of movement data potentially influenced by conspecific behaviour.

We have developed our approach in the context of hierarchical Bayesian models, which are becoming increasingly popular in many studies of ecological and evolutionary processes (Cressie *et al.* 2009), largely due to their flexibility in the accommodation of multiple levels of dependency, modelled through the effects of covariates and correlation structures (Gillies *et al.* 2006). We have selected the use of Bayesian statistics mainly for the reasons of computational feasibility. However, as our model is simply a regression model with fixed and random effects (Dingemans *et al.* 2012), it could also be fitted to the data using frequentist techniques. In either case, the practitioner needs to carefully check (as in any modelling exercise) that the assumptions of the model (such as normality and homoscedasticity of residual variance) are met, though our results based on simulated data turned out to be robust even though these assumptions were not necessarily always met.

As demonstrated by the application of the model to data generated through the simulation of different scenarios, the estimated variance components can be related in a biologically meaningful way to the actual mechanisms behind socially informed movement decisions. The main reason for focusing here on variance partitioning is that we found it to be the simplest and most robust way to quantify the importance of each behavioural component. In practice, if a practitioner fits

our statistical model to their data, then the question of ‘are the individuals responding to each other and in which way?’ can be addressed by looking at how much of the total variation is assigned to each component of the statistical model. In the eagle owl example, we found that dispersing individuals were attracted to others and that their movement rules varied not only among individuals, partly explained by measured variation in their internal states, but also within individuals.

There are two important considerations to be made when applying the framework developed here. First, the temporal resolution at which individuals make their movement decisions is usually unknown *a priori*. If individuals are sampled at very coarse temporal resolution, the statistical power for detecting interaction effects may be limited (Dingemans *et al.* 2012), as we illustrated by subsampling the simulated data. On the other hand, if individuals are sampled at a temporal resolution much higher than the interval at which movement decisions are made, then consecutive data points become statistically dependent on each other, potentially leading to a false impression of behavioural switching. This may be partially mitigated by having a more sophisticated null model, which includes autocorrelation in the movement.

Secondly, the fact that individuals live or move in a group does not necessarily imply that they interact socially (Bode *et al.* 2012). As demonstrated by the simulated Scenario 5, if individuals are attracted to the same resources (e.g. food or shelter), their movements may appear to be socially dependent even if this is not the case. It is worth noting the fact that, in this scenario, the scale of the behavioural responses of individuals is likely to be affected by the spatial aggregation and the temporal predictability of resources that we considered (e.g. Fauchald & Tveraa 2006). Again, in theory, this problem can be mitigated using a more sophisticated null model, in which all the non-social factors influencing movements are accounted for. This is by no means a trivial task, as many of these factors are likely to be unknown, and even the influences of the known factors can be hard to quantify reliably. Therefore, when applying our method to any real movement data, the practitioner needs to carefully think about the selection and parameterization of the null model, as in theory, the null model should incorporate all other factors influencing movement decision excepting the influence of conspecifics. While it is clear that the construction of a perfect null model is difficult if not possible, any other approach attempting to pinpoint the influence of conspecifics on movement decisions from non-manipulative observational data necessarily has the same shortcoming of the results being sensitive to the assumptions made on other factors influencing movement behaviour. Whatever the object of analysis, the choice of the temporal scale at which individuals are to be sampled, the construction of the appropriate null model and the interpretation of the statistical results all require a good understanding of the ecology and life history of the study species.

Our simulation experiments illustrate the ability of the proposed statistical framework in pinpointing different kinds of underlying mechanisms behind movement behaviour, as well as how its statistical power may depend on some issues

common in real data (such as missing individuals). However, it was not feasible in this study to exhaustively address all possible ways in which different confounding factors (e.g. spatial and temporal changes of habitat quality across the landscape) may lead to similar movement patterns than those generated by interaction individuals. When applying the method presented here, we encourage the practitioner to perform simulations that emulate the potential confounding factors of the system under study.

As was the case with the owl study, spatial positions are often not taken simultaneously for all individuals. Linear interpolation, or any other method to estimate the missing locations, will add noise to the measures of proximity and sociability, and thus, it is likely to reduce the ability of the statistical framework to detect non-random behaviour, making the results conservative.

Our study illustrates the general applicability of hierarchical Bayesian models in ecology (Clark 2005). The framework we have developed applies in principle to movement data on any kinds or particles, from organelles within cells to GPS tracking data on large animals. In particular, reintroduction projects in which animals are released into areas where conspecifics were absent are among the kind of studies for which this method might be most appropriate. The main limitation of the application of the methods is the need of high resolution movement data acquired simultaneously for a sufficiently large number of individuals. While such data are currently still rare, we expect that the ongoing revolution in tracking technology (Cagnacci *et al.* 2010) will result in a high flow of such data in future.

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Supporting Information

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

Appendix S1. Formal description of the hierarchical Bayesian model.

Appendix S2. Performance of the statistical framework with measure S^2 .

Appendix S3. Parameter estimates for the eagle owl case study.

Appendix S4. Habitat types associated with observed and interpolated owl locations.

Data S1. Mathematica codes and eagle owl data for fitting the hierarchical Bayesian model.