Simple individual-based models effectively represent Afrotropical forest bird movement in complex landscapes

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Summary

1. Reliable estimates of dispersal rates between habitat patches (i.e. functional connectivity) are critical for predicting long-term effects of habitat fragmentation on population persistence. Connectivity measures are frequently derived from least cost path or graph-based approaches, despite the fact that these methods make biologically unrealistic assumptions. Individual-based models (IBMs) have been proposed as an alternative as they allow modelling movement behaviour in response to landscape resistance. However, IBMs typically require excessive data to be useful for management. Here, we test the extent to which an IBM requiring only an uncomplicated set of movement rules [the ‘stochastic movement simulator’ (SMS)] can predict animal movement behaviour in real-world landscapes.

2. Movement behaviour of two forest birds, the Cabanis’s greenbul Phyllastrephus cabanisi (a forest specialist) and the white-starred robin Pogonocichla stellata (a habitat generalist), across an Afrotropical matrix was simulated using SMS. Predictions from SMS were evaluated against a set of detailed movement paths collected by radiotracking homing individuals.

3. SMS was capable of generating credible predictions of bird movement, although simulations were sensitive to the cost values and the movement rules specified. Model performance was generally highest when movement was simulated across low-contrasting cost surfaces and when virtual individuals were assigned low directional persistence and limited perceptual range.

4. SMS better predicted movements of the habitat specialist than the habitat generalist, which highlights its potential to model functional connectivity when species movements are affected by the matrix.

5. Synthesis and applications. Modelling the dispersal process with greater biological realism is likely to be critical for improving our predictive capability regarding functional connectivity and population persistence. For more realistic models to be widely applied, it is vital that their application is not overly complicated or data demanding. Here, we show that given relatively basic understanding of a species’ dispersal ecology, the stochastic movement simulator represents a promising tool for estimating connectivity, which can help improve the design of functional ecological networks aimed at successful species conservation.

Key-words: dispersal, functional connectivity, habitat fragmentation, homing experiment, perceptual range, true skill statistic

Introduction

Habitat loss has been identified as one of the main factors driving the decline in biodiversity world-wide (Gibson et al. 2011). In the process, original habitat cover is frequently reduced to isolated remnants resulting in the spatial segregation of once continuous populations. If the size of these remnants falls below species-specific thresholds, populations are likely to go extinct due to the negative effects of declines in genetic diversity (Dixo et al. 2011).
et al. 2009; Agudo et al. 2012) and the occurrence of demographic and environmental stochastic events. An important additional factor in explaining elongation risk of populations in fragmented landscapes is the degree of landscape connectivity (i.e., the degree to which the landscape facilitates or impedes movement among habitat patches), as exchange of individuals among patches directly affects local population densities, gene flow and patch (re)colonization probabilities (Benton & Bowler 2012). Therefore, reliable connectivity estimates are central for a correct assessment of the dynamics and viability of fragmented populations and have practical applications in landscape planning and species conservation by allowing conservation managers to assess the effectiveness of management scenarios (Baguette et al. 2013). However, connectivity is frequently estimated using models which oversimplify the process actually driving the loss of connectivity (Moilanen 2011).

Connectivity is driven by spatial displacement of individuals. For most animals inhabiting terrestrial fragmented landscapes, spatial displacement involves active locomotion across land-cover types comprising the intervening landscape (hereafter ‘the matrix’). Empirical studies have demonstrated that movement patterns across landscapes are not random but rather reflect behavioural responses to environmental factors. Mainly using experimental release experiments, these studies have shown that individuals may alter their movement trajectories in response to boundaries between different matrix land-cover types (Haddad 1999; Gillies & St. Clair 2010; Aben et al. 2012) and that permeability of boundaries may be modulated by the width of gaps (Bakker & Van Vuren 2004; Ibarra-Macias, Robinson & Gaines 2011). These matrix effects on movement behaviour can affect the length of movement trajectories (Gillies & St. Clair 2008; Hadley & Betts 2009), time spent in the matrix (Belisle, Desrochers & Fortin 2001; Kennedy & Marra 2010) and return success to the patch of origin (Belisle, Desrochers & Fortin 2001; Gillies & St. Clair 2008). In line with these behavioural observations, the degree to which patches are functionally connected is strongly determined by properties of the matrix (Ferreras 2001; Revilla et al. 2004; Bender & Fahrig 2005). Because the rate of interpatch movement is a crucial parameter for the predictions of spatially explicit population models, connectivity measures that adequately describe landscape effects on the outcome of the dispersal process are needed to improve their predictive power (Revilla & Wiegal 2008).

However, despite the recognition that animal dispersal is driven by the complex interaction between movement and external environmental factors, in the context of landscape planning and species management, connectivity has hitherto almost exclusively been modelled using simple distance-based functions (Moilanen & Nieminen 2002), the least cost path (LCP, e.g. Cushman, McKelvey & Schwartz 2009) or graph-theoretic methodologies (e.g. Alagador et al. 2012) which themselves typically employ Euclidean or cost distances between patches. The assumption that displacement of individuals among sites is a deterministic function of Euclidean interpatch distance implies either that the interpatch matrix is homogeneous or that animal movement is unaffected by environmental heterogeneity; conversely, the assumption that animals move along optimal interpatch linkages (LCPs) implies that dispersers know the location of a target patch and are able to evaluate potential routes to it (Palmer, Coulon & Travis 2011). Although these measures can be informative for the purpose of corridor design on larger geographical scales (Alagador et al. 2012), their limitations in predicting interpatch movement rates across landscapes (i.e. functional connectivity sensu Taylor et al. 1993) severely limit their use to design landscapes aimed at maximizing the persistence of focal species (Baguette et al. 2013).

A potentially more realistic framework for estimating functional connectivity comprises individual-based models (IBMs), as these allow explicit simulation of animal movement across realistic landscapes (e.g. Zöllner & Lima 1999; Bartoň et al. 2012). By incorporating correlation between movement steps and bias towards or away from different environments, IBMs can be designed to reproduce interactions between individual movement behaviour and landscape properties, which are considered important drivers of functional connectivity. However, although IBMs have been proven useful for addressing theoretical questions regarding sensitivity of connectivity predictions to variation in movement parameters [perceptual range (e.g. Pe’er & Kramer-Schadt 2008), directionality (e.g. Zöllner & Lima 1999), properties of the matrix (e.g. Gustafson & Gardner 1996)], few attempts have been made to make IBMs accessible to landscape managers (but see Pe’er et al. 2011). A principal reason for this is the challenge of obtaining the detailed species-specific movement data typically required for parameterization of these models (Baguette et al. 2013). Hence, there is a need for IBMs that allow estimating functional connectivity in the face of generally poor (empirical) knowledge of species’ movement behaviour.

To address this, Palmer, Coulon and Travis (2011) recently developed a simple IBM, the ‘stochastic movement simulator’ (SMS). In SMS, mechanistic representation of animal movement is governed by two critical parameters controlling the degree of correlation between successive steps and the range over which landscape cost values affect movement behaviour, that is, the perceptual range. Another advantage of SMS is that landscape effects on functional connectivity are based on the same landscape information as used by LCP models (i.e. cost values for each of the matrix elements), which can be estimated without very extensive data on animal movement (Richard & Armstrong 2010). Despite its simplicity, by translating landscape effects on animal movement at the appropriate scale (i.e. the individuals’ perceptual range), SMS relaxes the unrealistic assumptions made by LCP methodologies and is therefore expected to generate more credible estimates of functional connectivity.
However, the key question remains whether such a simple model is capable of usefully describing animal movement across real-world landscapes. To test this, we validated SMS simulations with detailed movement paths collected using radiotelemetry on two forest bird species (Cabani's greenbul Phyllastrephus cabanisi and white-starred robin Pogonochila stellata) in an Afrotropical matrix. As these species have been shown to differ in overall mobility at the scale of interpatch movements (Lens et al. 2002; Callens et al. 2011) and also in their relative preference for matrix land-cover types at a finer scale (Aben et al. 2012), their movement paths are perfectly suited to test to what degree SMS can capture species-specific variation in movement behaviour. Because detailed movement data for spontaneously dispersing animals are generally difficult to obtain, we used experimentally induced movement data collected during a translocation experiment (Aben et al. 2012). Experimental releases are commonly used to study movement behaviour as a proxy for natural dispersal behaviour (e.g. Gillies & St. Clair 2010; Kennedy & Marra 2010). However, the tendency of animals to return to their territory means that movement paths were influenced by homing behaviour, and we accounted for this in our methods.

Materials and methods

THE STOCHASTIC MOVEMENT SIMULATOR

The SMS is a stochastic IBM in which virtual animals disperse from a pre-defined location and move independently across a grid-ded landscape according to simplified movement rules until they reach a habitat patch, emigrate from the landscape under study or die after a given number of steps (Palmer, Coulon & Travis 2011). Movement rules were specified using a combination of four parameters: the animal's perceptual range, its tendency to follow a correlated path (directional persistence (DP)), its tendency to move in the direction of its fragment of origin (goal bias) and the distance over which DP is maintained (memory size); the original version of SMS (Palmer, Coulon & Travis 2011) did not incorporate goal bias and memory size, which we added for reasons described below. The chosen direction at each step was based on these parameters in combination with the cost values of the cells surrounding the animals within the specified perceptual range. Code for the enhanced version of SMS is available on request.

For each empirical movement path collected in the field (see below), we simulated 1000 individuals from the corresponding release location. Movement decisions at each location (i.e. each 5 m × 5 m grid cell, see below) are driven by the distribution of selection probabilities for each of the eight surrounding cells. A cell's selection probability is proportional to the reciprocal of its 'effective cost', which in turn is the harmonic mean of the cost values of that particular cell and its neighbouring cells in an array extending to the edge of the animal's perceptual range (Palmer, Coulon & Travis 2011). We set the perceptual range at 5, 10 or 20 grid cells, where the maximum value for this parameter was based on the largest step lengths observed in the field (i.e. the largest distance at which individuals responded to visual cues of the landscape; J. Aben, unpublished data).

The tendency of animals to move in a straight line is controlled by modifying effective costs by a weighting factor, which is lowest for the neighbouring cell located in the same direction as taken in the previous step and highest for the cell in the opposite direction (i.e. a 180° turn). The weighting is controlled by the DP parameter; larger values reduce the tendency for the path to deviate from a straight line (Palmer, Coulon & Travis 2011). In this study, we used DP values 2, 3 and 4.

If DP only considers the direction of the previous step, a sharp turn corresponding to a single cell can completely change an animal's direction. Although dispersing animals typically have no pre-defined goals, and hence could be suspected to lack an intrinsic motivation to move along cardinal or ordinal axes, both theoretical studies (Zollner & Lima 1999; Bartoń et al. 2012) and empirical observations (Delgado et al. 2009) indicate that dispersing individuals follow correlated paths at scales exceeding those of individual steps. To account for this behaviour, the original model was extended by applying DP to the mean direction averaged over a number of preceding steps determined by an additional parameter (memory size; either 2, 4 or 6 steps in this study). Thus, individuals with a large memory size are more likely to resume their original movement direction after a temporary change in direction.

To control for the paths used to validate SMS simulations being influenced by homing behaviour of translocated birds, the goal bias parameter was introduced. This parameter controls the weighting of surrounding cells in relation to their deviation from the goal (i.e. the bird's capture location) in a similar way to DP. We used goal bias values of 1, 0.5, 1, 1, 1.2 and 1.3, where higher values indicate a stronger tendency of the simulated individuals to move towards their capture location.

STUDY AREA AND MOVEMENT PATHS

Movement paths were collected in a montane Afrotropical landscape (Taita Hills, south-east Kenya (03°20'S, 38°15'E); Aben et al. 2012), consisting of a fine-grained mosaic of human settlements, smallholder cultivation plots and indigenous forest remnants (Pellikka et al. 2009). Land-cover information for the study area was derived from airborne true-colour images converted to image mosaics at a spatial resolution of 0.5 m (Pellikka et al. 2009). The cost surface was derived from the land-cover model used by Aben et al. (2012); a grid of 5 × 5 m cell size and seven land-cover types: indigenous forest, exotic plantation, agro-forestry, bush, field, built-up area and road. The cell size was chosen corresponding to the accuracy of our bird observations obtained by radiotelemetry. For the purpose of this study, we created a landscape grid omitting road (replacing it by the bordering land-cover type) because it was difficult to assign a relevant cost value. This modification is unlikely to affect SMS performance in predicting actual movement paths, as Aben et al. (2012) showed that the amount of road intersected by actual movement steps was not different from the amount in 20 random alternative steps.

The movement data used for SMS validation were represented by detailed movement paths of two forest bird species [P. cabanisi (n = 27) and P. stellata (n = 21)]. Both species are representative of the forest bird community of the Taita Hills but they are not equally dependent on intact indigenous forest; P. cabanisi exclusively occurs in indigenous forest fragments (Callens et al. 2011), whereas P. stellata also inhabits disturbed and plantation
forests (Githiru, Lens & Bennun 2007). Additionally, movement of *P. cabanisi* was more affected by the matrix (Aben et al. 2012) and its populations showed higher genetic differentiation between three forest fragments in the Taita Hills (Callens et al. 2011), suggesting that higher forest dependency results in lower matrix permeability. Henceforth, based on this information, we will treat *P. cabanisi* as a forest specialist and *P. stellata* as a forest generalist.

Movement paths were generated from successive bird locations recorded during translocation experiments (see Aben et al. 2012 for methods and example paths). Four individuals (one *P. cabanisi* and three *P. stellata*) were discarded for the purpose of the present study, because large parts of their paths (>50% of their total length) could not be reliably documented.

**COST VALUES**

The SMS algorithm incorporates a cost surface similar to LCP (i.e. cost values are scaled relative to preferred habitat; see Adriaensen et al. 2003). In our study, cost values were assigned to the five matrix land-cover types to reflect their hypothesized resistance to movement relative to indigenous forest. We created seven cost surfaces with cost value of 10 for field, but different values for exotic plantation, agroforestry and bush (sets 1–7, Table 1). Also, to evaluate the sensitivity of SMS performance to differences in contrast between woody and non-woody matrix land-cover types, we created two alternative cost surfaces based on set 2, where field was assigned a cost value of 5 and 20 (set 8 and 9, respectively; Table 1). Built-up area was assigned a cost value 100 times higher than field in all cost surfaces, as this land-cover type was regarded to be invariably highly resistant to movement. Finally, we created a homogeneous cost surface where all land-cover types were assigned a cost value of 1 (set 0, Table 1).

**ASSESSING IBM PERFORMANCE**

Model performance was judged based on the frequency of visits to grid cells by simulated individuals (henceforth ‘cell selection probability’). For every grid cell in each simulation, we calculated this probability as the proportion of simulated individuals (out of 1000) that passed through this cell at least once. To evaluate the spatial fit between simulated movements and actual movement paths, we compared the cell selection probabilities to the actual movement paths of birds using the true skill statistic (TSS, Allouche, Tsoar & Kadmon 2006). The TSS ranges from –1 to 1, where evaluation values of TSS > 0.4 are considered to be indicative of good predictions (Eskildsen et al. 2013). The TSS is an often used evaluation statistic in species distribution modelling but has also been used to evaluate predictions based on dispersal simulations (La Morgia et al. 2011). It is based on the proportion of correctly predicted presences (sensitivity, cells visited by both actual birds and simulated individuals) and the proportion of correctly predicted absences (specificity, cells neither visited by actual birds nor by simulated individuals). Predicted absences were only considered if a particular cell could have been visited by a bird during the duration of the translocation experiment (i.e. a ‘true’ absence). This applied to all cells that were located within an ellipse with foci on the release and capture location of each bird and with an eccentricity of 0·68 (cf. Aben et al. 2012) and that were located within a distance of the release location equaling the maximum observed distance travelled during a 1-day experiment (i.e. 1013 m for *P. cabanisi* and 945 m for *P. stellata*). We classified each grid cell either as a predicted presence or a predicted absence according to the threshold that maximized the sum of sensitivity and specificity MaxSens + Spec criteria in package PresenceAbsence (Freeman 2007) and calculated the corresponding TSS (i.e. sensitivity + specificity –1; Fig. 1).

In order to assess the effects of movement parameters and cost sets on the simulations, a TSS value was obtained for each combination of settings (*n* = 108) for each cost set and averaged over all simulated paths per species. We then used an *ANOVA* with TSS as the dependent variable and examined the variance explained by five main effects (i.e. cost, perceptual range, goal bias, DP, memory size) and their higher-order interactions. As statistical significance in itself is relatively uninformative in the case of simulated data, we assessed the strength of the associations between TSS and the explanatory variables through the examination of partial eta-squared $\eta^2_p = \text{SSeffect}/(\text{SSeffect} + \text{SSerror})$; R package `heplots` (Fox et al. 2012). Like $R^2$, $\eta^2_p$ is a measure of effect size that is independent of the degrees of freedom used in the analyses. In addition, we assessed false-positive and false-negative error rates in models to interpret better the sources of prediction error.

Table 1. Cost sets used to evaluate sensitivity of SMS simulations to variation in landscape composition and contrast between land-cover types

<table>
<thead>
<tr>
<th>Relative cost values</th>
<th>Indigenous forest</th>
<th>Exotic plantation</th>
<th>Agroforestry</th>
<th>Bush</th>
<th>Field</th>
<th>Built-up area</th>
</tr>
</thead>
<tbody>
<tr>
<td>Set 0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Set 1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>10</td>
<td>1000</td>
</tr>
<tr>
<td>Set 2</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
<td>10</td>
<td>1000</td>
</tr>
<tr>
<td>Set 3</td>
<td>1</td>
<td>2</td>
<td>4</td>
<td>3</td>
<td>10</td>
<td>1000</td>
</tr>
<tr>
<td>Set 4</td>
<td>1</td>
<td>3</td>
<td>2</td>
<td>4</td>
<td>10</td>
<td>1000</td>
</tr>
<tr>
<td>Set 5</td>
<td>1</td>
<td>3</td>
<td>4</td>
<td>2</td>
<td>10</td>
<td>1000</td>
</tr>
<tr>
<td>Set 6</td>
<td>1</td>
<td>4</td>
<td>3</td>
<td>2</td>
<td>10</td>
<td>1000</td>
</tr>
<tr>
<td>Set 7</td>
<td>1</td>
<td>4</td>
<td>2</td>
<td>3</td>
<td>10</td>
<td>1000</td>
</tr>
<tr>
<td>Set 8</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
<td>5</td>
<td>500</td>
</tr>
<tr>
<td>Set 9</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
<td>20</td>
<td>1000</td>
</tr>
</tbody>
</table>

SMS, stochastic movement simulator.
Predicting animal movement using a simplified IBM

Stochastic movement simulator simulations were sensitive to the movement rules specified and the cost values assigned to the landscape which profoundly influenced their accuracy in predicting the movement paths of both forest bird species (range of TSS values obtained was 0.297–0.586 for P. cabanisi and 0.276–0.481 for P. stellata).

The five-factor ANOVA revealed four significant four-way interactions (Table 2). However, effect sizes indicated that only the interaction between goal bias, DP, memory size and the cost set used (\(\eta_p^2\) 0.46 and \(\eta_p^2\) 0.44 for P. cabanisi and P. stellata, respectively), and between goal bias, DP, perceptual range and the cost set used (\(\eta_p^2\) 0.42, P. cabanisi only) could be considered important.

For each species, the most important four-way interaction was examined visually by plotting the TSS for different cost sets and for each level of goal bias, memory size and DP (Fig. 2). The effect of goal bias on model performance differed strongly between species (Fig. 2). For P. cabanisi, model performance clearly peaked when simulations were only weakly biased towards the location of capture but decreased markedly when this bias increased, especially when DP was low and memory size small. For P. stellata, the effect of goal bias was only present when DP was low and memory size either low or moderate (Fig. 2Ba,b). For both species, the effect of memory size was relatively small at low levels of DP but had a strong negative effect on model performance when DP was high (Fig. 2g–i). The combination of strong DP and a large memory size resulted in the poorest SMS predictions for both species (Fig. 2i).

The second most important four-way interaction (Fig. 3) showed that model predictions were most accurate at the smallest perceptual range. At larger PRs model performance decreased. This negative relationship was most pronounced at low DP and for the cost set which represented the strongest contrast in cost values between

Table 2. ANOVA of the effects of goal bias (GB), directional persistence (DP), memory size (MS), perceptual range (PR) and cost set (Cost) on the spatial agreement (TSS) between SMS simulations and movement paths of two forest bird species

<table>
<thead>
<tr>
<th></th>
<th>Phyllastrephon cabanisi</th>
<th>Pogonocichla stellata</th>
</tr>
</thead>
<tbody>
<tr>
<td>d.f.</td>
<td>F-value</td>
<td>(\eta_p^2)</td>
</tr>
<tr>
<td>Cost</td>
<td>9</td>
<td>1836.7*** 0.987</td>
</tr>
<tr>
<td>GB</td>
<td>3</td>
<td>12444.5*** 0.994</td>
</tr>
<tr>
<td>DP</td>
<td>2</td>
<td>1001.6*** 0.903</td>
</tr>
<tr>
<td>MS</td>
<td>2</td>
<td>3668.5*** 0.971</td>
</tr>
<tr>
<td>PR</td>
<td>2</td>
<td>4673.6*** 0.977</td>
</tr>
<tr>
<td>Cost : GB</td>
<td>27</td>
<td>72.9*** 0.901</td>
</tr>
<tr>
<td>Cost : DP</td>
<td>18</td>
<td>29.8*** 0.713</td>
</tr>
<tr>
<td>GB : DP</td>
<td>6</td>
<td>428.5*** 0.923</td>
</tr>
<tr>
<td>Cost : MS</td>
<td>18</td>
<td>29.8*** 0.710</td>
</tr>
<tr>
<td>GB : MS</td>
<td>6</td>
<td>210.0*** 0.854</td>
</tr>
<tr>
<td>DP : MS</td>
<td>4</td>
<td>858.0*** 0.941</td>
</tr>
<tr>
<td>Cost : PR</td>
<td>18</td>
<td>223.1*** 0.949</td>
</tr>
<tr>
<td>GB : PR</td>
<td>6</td>
<td>66.5*** 0.649</td>
</tr>
<tr>
<td>DP : PR</td>
<td>4</td>
<td>50.1*** 0.481</td>
</tr>
<tr>
<td>MS : PR</td>
<td>4</td>
<td>14.1*** 0.207</td>
</tr>
<tr>
<td>Cost : GB : DP</td>
<td>54</td>
<td>5.0*** 0.554</td>
</tr>
<tr>
<td>Cost : GB : MS</td>
<td>54</td>
<td>3.4*** 0.460</td>
</tr>
<tr>
<td>Cost : DP : MS</td>
<td>36</td>
<td>12.2*** 0.670</td>
</tr>
<tr>
<td>GB : DP : MS</td>
<td>12</td>
<td>10.6*** 0.370</td>
</tr>
<tr>
<td>Cost : GB : PR</td>
<td>54</td>
<td>2.5*** 0.386</td>
</tr>
<tr>
<td>Cost : DP : PR</td>
<td>36</td>
<td>5.6*** 0.484</td>
</tr>
<tr>
<td>GB : DP : PR</td>
<td>12</td>
<td>2.7*** 0.130</td>
</tr>
<tr>
<td>Cost : MS : PR</td>
<td>36</td>
<td>2.5*** 0.296</td>
</tr>
<tr>
<td>GB : MS : PR</td>
<td>12</td>
<td>1.6</td>
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<tr>
<td>DP : MS : PR</td>
<td>8</td>
<td>3.4*** 0.112</td>
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<tr>
<td>Cost : GB : MS</td>
<td>108</td>
<td>1.7*** 0.461</td>
</tr>
<tr>
<td>DP : MS</td>
<td>Cost : GB : DP</td>
<td>108</td>
</tr>
<tr>
<td>Cost : GB : PR</td>
<td>108</td>
<td>1.0</td>
</tr>
<tr>
<td>Cost : MS : PR</td>
<td>72</td>
<td>0.6</td>
</tr>
<tr>
<td>GB : MS : PR</td>
<td>24</td>
<td>1.3</td>
</tr>
<tr>
<td>Residuals</td>
<td>216</td>
<td></td>
</tr>
</tbody>
</table>

SMS, stochastic movement simulator; TSS, true skill statistic. Significance level of F-tests: *P < 0.05, **P < 0.01, ***P < 0.001; effect sizes measured as partial eta-squared (\(\eta_p^2\)).
the woody matrix and field (i.e. set 1, Fig. 3). In contrast, model performance was not sensitive to variation in perceptual range when contrast between land-cover types was low (i.e. set 8, Fig. 3).

COST SETS

Model performance was sensitive to the cost values assigned to the different matrix land-cover types. In particular,
performance peaked when there was a relatively low contrast between woody matrix land-cover types and field (i.e. set 8) and was poorest when this contrast was strong (i.e. set 1). Inspection of the mean error rates in predictions showed that this was primarily attributable to differences in the proportion of false negatives (i.e. actual occurrence at predicted absence) between cost sets, which were lowest when contrasts were low and vice versa (Fig. 4).

Based on the $F$-values, results of the original ANOVA indicated that properties of the landscape had a larger effect on model performance for *P. cabanisi* compared to *P. stellata* (Table 2). However, differences between species in the effect size for the cost set as explanatory variable were small. To confirm this trend, we repeated the ANOVA for the cost sets which differed only in the ranking of the woody matrix land-cover types (i.e. sets 2–7). Now, the effect size for the cost set remained high for *P. cabanisi* ($\eta^2_p = 0.964$) but dropped considerably for *P. stellata* ($\eta^2_p = 0.696$). Within these costs sets, best predictions were obtained for set 2 and worst predictions for set 7 (based upon visual inspection of Fig. 2).

Finally, overall performance of the homogeneous cost set was relatively poor for *P. cabanisi* but relatively good for *P. stellata* (Fig. 2). This difference in performance between species was mainly attributable to the proportion of false positives (i.e. predicted presence but no actual occurrence) which was, compared to the other cost sets, highest for *P. cabanisi* and lowest for *P. stellata* (Fig. 4).

**Discussion**

Our results show that a simple IBM coupled to a cost surface is capable of predicting animal movement across heterogeneous landscapes. SMS thus represents a promising tool for translating animal–landscape interactions at the individual and local scales into higher-scale ecological and spatial patterns (e.g. estimating functional connectivity). Given the fact that accurate information on the landscape and cost surfaces are a core component of modern-day landscape and species management, SMS represents an attractive alternative to existing methods that typically rely upon Euclidean or least cost distances, often coupled with graph-theoretic methods. Moreover, IBMs such as SMS can increase (cost-)efficiency in planning conservation strategies, as they facilitate direct assessment of the functionality of structural linkages between habitat patches (e.g. the design of optimal corridors or stepping stones). For example, SMS could readily be used to determine both how frequently potential new stepping stones would likely to be used by dispersing individuals and how the addition of new stepping stones would likely impact interpatch transfer of individuals. In this respect, SMS can effectively be used as a stand-alone application to allow ranking of different management scenarios according to their corresponding contribution to functional connectivity between habitat patches, but it also has considerable potential to be used as a dispersal submodel implemented in spatially explicit population models to assess the effectiveness of alternative management interventions at the (meta)population level.

Our validation of SMS by means of detailed movement paths of two forest bird species showed that simulations were capable of usefully predicting such paths across a
relatively complex matrix landscape. We previously showed (Aben et al. 2012) that actual bird movements were particularly sensitive to boundaries between woody matrix land-cover types and fields, resulting in stronger deviation of movement trajectories. However, given the fact that the Taita matrix is very fine-grained, birds frequently had to cross open agricultural fields in order to return to their fragment of origin. In line with these observations, the ability of SMS to describe these movements depended strongly on the way this landscape effect was incorporated in the model. In general, SMS performance was optimal when the degree of contrast between the woody matrix land-cover types and field was relatively low. Inspection of error rates in predictions between the different cost sets suggests that this relationship was predominantly driven by the ability of SMS to predict actual movements across fields; simulated birds were able to move across fields at low contrast, whereas higher contrasts prevented these particular movements. The fact that the negative effect of highly contrasting fields on model performance was largest for the generalist P. cabanisi confirms this explanation, as this species is expected to cross this land-cover type more frequently than P. cabanisi. In contrast to the strong effect of fields on step selection of homing birds, boundaries between the woody matrix land-cover types invoked less pronounced and consistent behavioural responses (Aben et al. 2012). The fact that performance of SMS was not very sensitive to the ranking of these land-cover types therefore is in line with our expectation. However, besides avoidance of fields, route decisions of P. cabanisi were also driven by composition of the woody matrix as it moved in decreasing order of preference through indigenous forest, agroforestry and exotic plantation/bush, whereas P. stellata exhibited no such behaviour (Aben et al. 2012). The result that sensitivity of model performance to variation in the ranking of woody land-cover types was larger for P. cabanisi indicates that SMS simulations were able to capture differences in movement behaviour of a habitat specialist (whose movements are influenced by avoidance of fields and by the composition of the woody matrix) and a generalist (whose movements are mainly influenced by an avoidance of fields only).

Apart from the distribution of cost values, movements of virtual dispersers are affected by the movement parameters of SMS. Because movements are simulated on a cell-by-cell basis, SMS does not provide a perfect mechanistic description of field-derived movement rules (e.g. step lengths, turn angles, c.f. Revilla et al. 2004). Instead, each move results in a spatial displacement determined by the cell size of the landscape grid and an angle relative to the preceding step influenced by the degree of correlation specified. Hence, the ability of SMS to model species-specific movement patterns across landscapes is strongly dependent on the quality of information in the cost surface. Our results strongly emphasize this, not only because model fit differed markedly between cost sets (see above) but also because predictive accuracy of SMS peaked when the influence of the parameters governing the movement rules was minimized. As cell selection probabilities are determined by their effective cost value weighted by the parameters controlling degree of DP and goal bias, increasing the weighting factors of these parameters overrules landscape effects on simulated movements in favour of increased directionality or goal attraction. Illustrative of this effect is the clear difference in sensitivity of model performance to variation in the goal bias parameter between the two species; increasing the effect of homing behaviour on simulations strongly decreased the ability of SMS to predict movements of the forest specialist P. cabanisi (for which movements were strongly influenced by the matrix), while no such effect was apparent for the generalist P. stellata (for which movements were less consistently affected by the matrix). Another example is the strong negative effect of the interaction between DP and memory size on model performance for both species.

A strong DP in combination with a large memory size resulted in a higher proportion of false positives (data not shown) which indicate that at this combination of parameter settings, simulated individuals lose their flexibility to react to borders between land-cover types, resulting in an increase in suboptimal movements as individuals are being ‘pushed’ into high-cost land-cover types.

In contrast to the SMS parameters discussed above, the perceptual range does not directly control movement, but modifies the scale over which cost values are assessed. Because cell selection probabilities were based on the harmonic mean of the cost values within the perceptual range, they were particularly sensitive to prevalence of low costs. For instance, Palmer, Coulon and Travis (2011) showed that an increased perceptual range resulted in a greater number of virtual dispersers reaching a target patch, primarily because they were better at locating low-cost stepping stones embedded in a high-cost matrix. We found that perceptual range had little effect on predictive accuracy when matrix contrast was low, whereas model performance strongly decreased with perceptual range when contrast was strong. This negative relationship was mainly driven by an increase in the proportion of false negatives (data not shown). Our interpretation is that the enhanced detection of low-cost land-cover types by virtual dispersers reduced their use of fields in comparison with the empirical data, leading to a less accurate fit with actual movement across this land-cover type. This means that when more information is available for virtual dispersers they are increasingly capable of finding the least costly option through the matrix. The fact that this negatively affected model predictions may imply that movement decisions of actual birds were mainly driven by landscape cues perceived at relatively short distances.

**SYNTHESIS AND RECOMMENDATIONS FOR APPLICATION**

There is considerable current interest in the degree of complexity that should be incorporated in ecological models,
both in terms of models used for developing general insight and for models focussed on application (Evans et al. 2013a, b). Here, we argue that intermediate complexity, represented in this case by a relatively simple IBM of animal movement, can represent an extremely promising approach for developing more effective in silico testing of alternative landscape management scenarios. We have provided a demonstration of how such a movement model can be parameterized using relatively straightforward data on bird movement. We have deliberately employed a simple model that has as few parameters as possible, yet overcomes key limiting assumptions (i.e. omniscience and foreknowledge of a destination) that are inherent within the methods that remain most used, but are likely to be poor representations of how dispersing individuals behave (Palmer, Coulon & Travis 2011). Additionally, we have chosen to take a relatively simple approach to model validation, and we believe this is important in terms of encouraging wider application of IBMs.

Increasingly sophisticated approaches are currently being developed for the validation and inverse fitting of IBMs, including pattern-oriented modelling (POM; e.g. Grimm et al. 2005) and approximate Bayesian computation (ABC; e.g. Beaumont 2010). These approaches have the worthy goal of seeking to make the optimum use of all available data for improving a model for a particular species. However, there is a clear tension between the use of validation and fitting methodologies requiring high technical expertise and the desire for ease of application to a broad number of species and landscapes. Our view is that, for IBMs to be broadly applied in management, we currently need to be pragmatic. We emphasize the need for some form of ‘sanity check’ of model output, and a single-criterion validation such as that used in this study is straightforward to perform. It lacks the rigour and elegance of POM, or especially a method such as ABC, but it provides a rapid and effective insurance that the model specified by the user is not very wrong. Here, we chose to use the TSS for validation of model output against observed data. This is only one of many possible approaches. Another, which should not be underestimated, is straightforward visual inspection of animal movement trajectories and of simple summary data such as a distribution of dispersal distances. This can be particularly valuable when engaging with stakeholders both in terms of making best use of their knowledge and having them buy into the modelling process. For example, expert knowledge on occasional long-distance dispersal events might represent useful information to validate the model. If we are working with a species that is known to sometimes exhibit dispersal of >5 km and we never in 1000 replicates see simulated individuals disperse >2 km, we might want to consider which parameters can yield at least occasional longer-distance dispersal. Another stakeholder might have observed a species regularly moving along a habitat edge (e.g. woodland bordering field) yet very rarely recall having seen the species crossing an open field. This type of information can be used to help adjust parameters such that stakeholders see simulated individuals behaving in a way that they recognize. This is not formal statistical fitting, but the process can be an important way of soliciting valuable information from those who know a focal species and can also help in increasing confidence in the modelling approach of those who need to have trust in the recommendations arising from the outputs. We believe that such stakeholder-driven model fitting will often be at least as important as formal statistical validation, both because it uses a different form of valuable information and because it engages with those who will potentially benefit from the modelling in a manner much easier for them to understand than formal statistics.

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