Computers, Environment and Urban Systems 61 (2017) 49–55

Contents lists available at ScienceDirect

Computers, Environment and Urban Systems

journal homepage: www.elsevier.com/locate/ceus

Agent-based simulation of Muscovy duck movements using observed habitat transition and distance frequencies

James H. Anderson [a,*], Joni A. Downs [b], Rebecca Loraamm [c], Steven Reader [b]

[a] Department of Industrial and Systems Engineering, University of Oklahoma, United States
[b] School of Geosciences, University of South Florida, United States
[c] Department of Geography and Environmental Sustainability, University of Oklahoma, United States

ARTICLE INFO

Article history:
Received 19 January 2016
Received in revised form 16 September 2016
Accepted 17 September 2016
Available online 15 October 2016

Keywords:
Agent based model
Animal movement
Home range analysis
Muscovy duck

ABSTRACT

This paper presents an agent based model simulating animal tracking datasets for individual animals based on observed habitat use characteristics, movement behaviours and environmental context. The model is presented as an alternative simulation methodology for movement trajectories for animal agents, useful in home range, habitat use and animal interaction studies. The model was implemented in NetLogo 5.1.0 using observed behavioural data for the Muscovy duck, obtained in a previous study. Four test scenarios were completed to evaluate the fidelity of model results to behavioural patterns observed in the field. Results suggest the model framework illustrated in this paper provides an effective alternative to traditional animal movement simulation methods such as correlated random walks.

1. Introduction

Researchers simulate tracking data for individual animals for a number of purposes relevant to both GIScience and ecology. A popular reason is to generate a complete baseline dataset of known tracking data to test methods that are useful for analysing samples of VHF, GPS, or satellite data collected in the field. For example, simulated tracking data are routinely used to test methods of home range analysis, where the performance of different techniques is evaluated for samples of different sizes, tracking intervals, or other qualities (Downs & Horner, 2009, 2012; Getz et al., 2007; Girard, Ouellet, Courtois, Dussault, & Breton, 2002; Laver & Kelly, 2008). Simulated animal tracking data are also widely used as reference datasets for the purposes of quantifying animal interactions. Here, observed data are compared to simulated data to determine if animals come into contact more or less frequently than expected at random (Long, Nelson, Webb, & Gee, 2014; Miller, 2012, 2015; Richard, Calenge, Said, Hamann, & Gaillard, 2013). Similarly, simulated animal movement data are used to study habitat preferences of animals through the use of step selection functions, which compare observed tracking data to simulated random movement data to infer resource selection (Duchesne, Fortin, & Rivest, 2015; Forester, Im, & Rathouz, 2009).

There are several ways that animal tracking data for individuals have been simulated in practice. The first approach is to generate point patterns of data that conform to particular statistical distributions, such as Poisson clusters or bivariate normal mixtures (Gitzen & Millspaugh, 2003; Gitzen, Millspaugh, & Kernohan, 2006). Sometimes the geometries of these patterns are modified to create locational data that conform to particular shapes (Downs & Horner, 2008). Alternatively, the density of points in a core location are artificially increased for the purpose of creating data with non-stationary spatial properties consistent with repeated use of a nest or den site (Downs et al., 2012). Often times, the generated point data represent an animal's known locations, and simulated tracking data are created by randomly sampling specified numbers of points from the distribution. The downside of point pattern approaches is that the locational data are not generated with explicit time stamps. This means that consecutive points in the dataset are not modelled as components of a continuous movement trajectory, which makes the data less representative of animal movements (Downs, 2010).

Tracking data have been more realistically modelled using random walk models, such as correlated random walks, Lévy walks and step selection functions which simulate an ordered set of spatial locations that constitute a movement trajectory (Bartumeus, Da Luz, Viswanathan, & Catalan, 2005; Bergman, Schaefer, & Luttich, 2000; Byers, 2001; Codling, Plank, & Benhamou, 2008; James, Plank, & Edwards, 2011; Thurfjell, Ciuti, & Boyce, 2014). Random walk models generally use two main parameters to model movement: turn angle and step length. In practice, these two parameters have specified frequency distributions that are used to control the properties of the modelled trajectory, such as whether sharp turns or long steps are more or less likely. Tracking data is simulated in this way by randomly generating values from those distributions and plotting the resulting spatial coordinates over

* Corresponding author.
E-mail address: jhowardanderson@ou.edu (J.H. Anderson).

http://dx.doi.org/10.1016/j.compenvurbsys.2016.09.002

time. Extensions to random walk models use maximum likelihood approaches to model and incorporate the effects of resource availability and habitat configuration from observed animal paths into simulated trajectories (Moorcroft, Lewis, & Crabtree, 2006). Additionally, the simulated data can be constrained to specific spatial areas, such as known home ranges, so that they better correspond to observed data or conform to particular sizes or shapes (Jeanson et al., 2003; Miller, Christman, & Estevez, 2011; Miller, 2012). A limitation of this approach is that turn angles are not always good predictors of animal movements (Holloway & Miller, 2014; Nams, 2013; Wilson et al., 2013). It is possible that some species do not have preferences for turning at particular angles, or that other contextual factors such as habitat preferences play larger roles in determining how animals move about space.

A somewhat less explored but promising approach to simulating animal tracking data for individuals involves using an agent-based model (ABM). Spatially-explicit ABMs are routinely used to model movement in complex geographical systems for a wide range of applications, such as modelling disaster response (Widener, Horner, & Ma, 2015), pedestrian behaviour (Torrens et al., 2012), traffic (Manley, Cheng, Penn, & Emmonds, 2014), crime (Malleson & Birkin, 2012), urban processes (Ettema, 2011), and humanitarian relief (Crooks & Wise, 2013). ABMs have been used to model animal movements, though generally the purpose is to model how animals interact with one another and the environment across space and time in order to understand dynamic population and landscape processes, rather than to explicitly simulate tracking data per se (McLane, Semeniuk, McDermid, & Marceau, 2011). Tang and Bennett (2010) provide an excellent review of ABMs for animals, some examples include those developed to model migration (Bennett & Tang, 2006), population dynamics (Carter, Levin, Barlow, & Grimm, 2015), predator-prey interactions (Ringelman, 2014), and group behaviour (Bonnell et al., 2013; Strombom et al., 2014).

Though random walk models may appear similar in function to simple ABMs, more complex ABMs could potentially be used to simulate more realistic tracking data for individual animals for testing home range estimation methods, studying interactions, and related purposes. The ABM approach differs from random walk models and their derivatives as ABMs generate movement trajectories based on context-aware decision-making logic defined for each fundamental actor in the ABM model environment. The resulting ABM-generated movement trajectories represent the aggregate of actor decisions. Consequently, the ABM approach offers an alternative to empirical reduction or model fitting on a priori animal trajectory datasets, as used in random walk implementations or step selection functions (Epstein, 1999). This paper presents an ABM that simulates animal tracking data for individual animals based on observed movement behaviour and environmental context. The model uses three main behavioural variables—habitat transition, step length, and return time—that operate within the context of an environment of habitat types. The goal is to develop an alternative platform for simulating animal locational data for future studies, though the model is created specifically for Muscovy ducks (*Cairina moschata*) in a study area where one year of field data on their habitats and movements were collected. The paper is organised as follows. Section 2 describes the modelling framework. Section 3 provides an overview of the field observations, model simulations, and methods of analysis. The corresponding modelling and analysis results are detailed in Section 4. Finally, discussions and conclusions are presented in Section 5.

2. Model framework

2.1. Overview

Tang and Bennett (2010) provide a detailed review of spatially-explicit ABMs and their features. Minimally, an ABM requires three basic components: agents, environment, and behaviour. Agents are the fundamental actors in an ABM; they move about and interact with the model environment according to sets of behavioural rules. The model environment provides the context for agent movement and interaction. For animals, the environment is generally modelled as a set of discrete patches of habitat that may or may not have other attributes. Behavioural rules control how the agents move within the environment, for instance by specifying possible step lengths or types of habitats that can be occupied. Movements and actions carried out by agents occur at discrete time steps, or ticks. At each tick, random behaviours are selected by the model and enacted by agents. In more complex models, agents have internal states that influence their behaviour, enabling agents to interact; influencing one another and the environment (Ahern, Smith, Joshi, & Ding, 2001).

In our model for simulating the movements of a single animal, though, we specify a single agent—an individual Muscovy duck. The model environment is composed of a grid of cells, or patches, classified by habitat types relevant to the species of interest. The duck agent starts the day at a designated known shoreline roosting location. After that, the duck's movement is controlled by three sets of behavioural rules that are explicitly linked to one another: habitat transition, step length, and return time. The model simulates the duck's movement every 15 s within and between habitats in the environment over 28 15-hour diurnal periods from 06:00:00 to 21:00:00. The 9-hour night time period, when the duck is expected to roost in the same location on the shoreline, is not modelled. The model output includes the duck's position and habitat at each time step. The model is implemented in NetLogo version 5.1.0, as described below (Fig. 1).

2.2. Agents

The animal species selected for this model is the Muscovy duck. The Muscovy duck is a species of waterfowl native to South and Central America, though populations have been introduced nearly worldwide and are considered invasive in some locales. Though there is little published literature on introduced Muscovy ducks, a population of about 120 individuals at the University of South Florida campus in Tampa, FL, is relatively well studied (Anderson, 2012). A previous study by Downs et al. (under review) documented habitat use and behavioural patterns of this population. There, Muscovy ducks occupied urban environments where open water was present. They utilized five main habitat types during the daytime: water (pond, lake, or wetland), shoreline (edge of pond, lake, or wetland), grass (open lawn), tree and shrub cover, and urban (roads, buildings, parking lots, sidewalks, etc.). They roosted on shoreline overnight, typically returning several times per day. Additionally, Muscovy ducks are capable of flight, however they fly relatively infrequently, locomoting mostly by walking and swimming. Movement data collected at the same time but not published with those observations are reported here and used to inform the agent's behavioural rules (see Section 2.4).

2.3. Model environment

The model environments consisted of rectangular grids of cells classified by habitat type. For this study, two model environments, or habitat maps, were used for comparison: an observed study area and a random habitat map (Fig. 2). The study area consisted of a 0.28 km^2 area that included a pond where a portion of the behavioural data were collected. The study area was divided into square grid cells at a 5 m resolution. The choice of a 5 m cell resolution was motivated by the distribution of distances in observed duck movements, the size and habitat gradient in the study area, and the need for abstraction in terms of the model implementation. The 5 m resolution represents a compromise level of abstraction where both habitat type gradient could be effectively captured and animal movements effectively simulated. Duck agent location is understood by the model in terms of continuous X/Y coordinates, an agent can be located at any location within any habitable environment cell. The study area comprised 86 rows and 132 columns of cells. Each cell

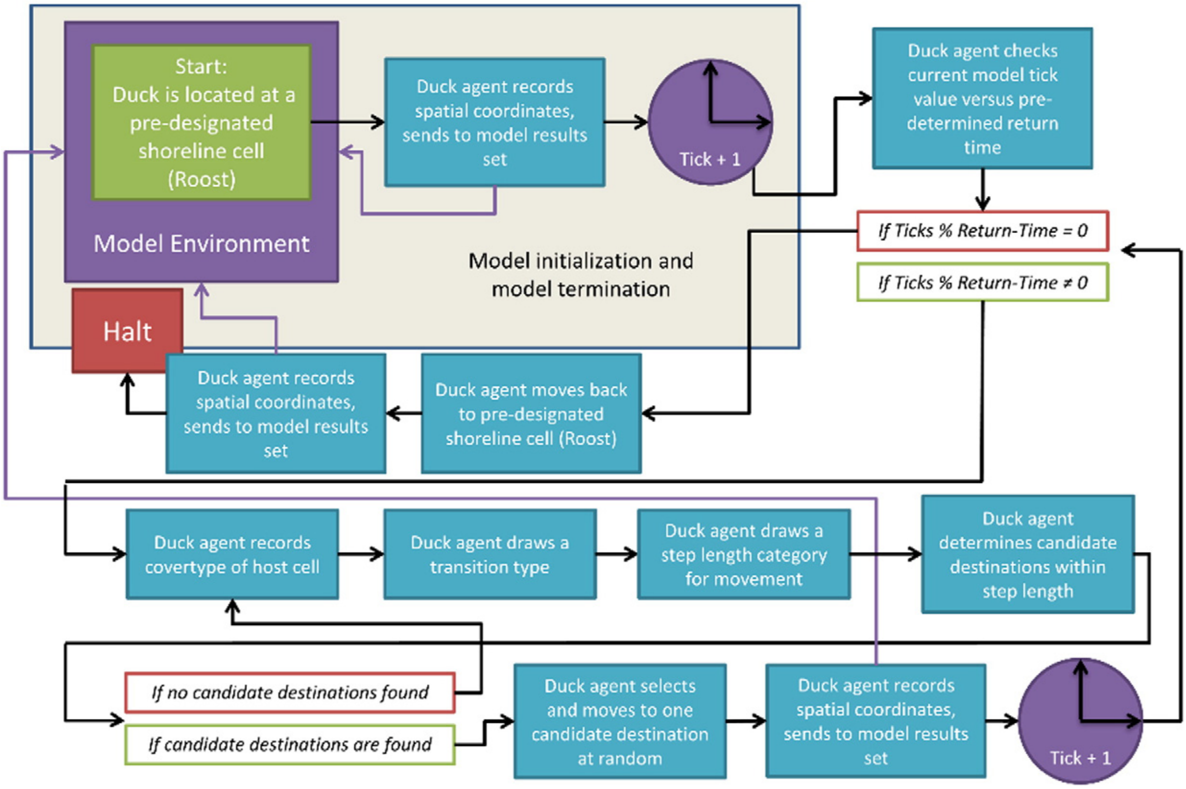

Fig. 1. Muscovy duck agent-based model diagram.

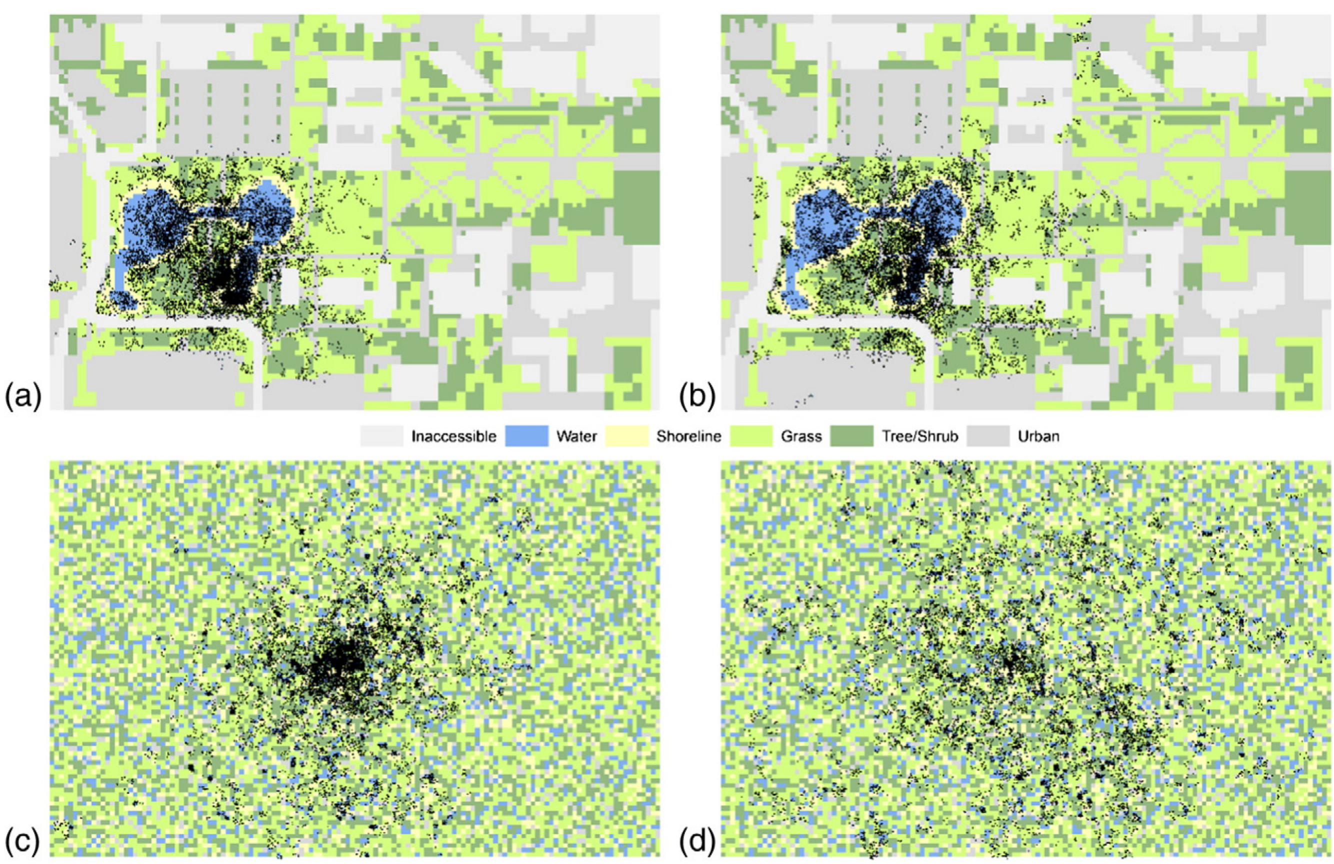

Fig. 2. Sample simulated Muscovy duck tracking data for four scenarios: study area with a 720 tick return time (a), study area with a 3600 tick return time (b), random landscape with a 720 tick return time (c), and random landscape with a 3600 tick return time (d).

was manually assigned one of five habitat classes corresponding to previous studies: water, shoreline, grass, tree-shrub, and urban. An inaccessible class is also included to exclude buildings and major roadways where ducks were not expected to visit. For comparison, a random model environment was also created by randomly assigning cells in the original study area to one of the five habitat classes. Habitats were randomly assigned in proportion to how often ducks were observed to spend time in them (12% water, 13% shoreline, 42% grass, 26% tree and shrub, and 7% urban). Both habitat maps were created using GIS (ArcMap v 10.1, ESRI Inc.) and saved as polygon shapefiles in a UTM projection. For these shapefiles, each habitat cell consisted of a single, square-shaped polygon feature, with cells arranged in a regular grid or "fishnet" configuration. The vector shapefile maps were later imported into the NetLogo software to serve as the model environments. The import routine implemented by the NetLogo software package enables a one-to-one mapping of vector grid cells into model environment patches carrying corresponding habitat type information.

2.4. Agent behaviours

The model of Muscovy duck movements utilizes three behavioural rules: habitat transition, step length, and return time. Habitat transition refers to the duck's decision at each time step to either remain in the same habitat or move to another. There were 25 possible transitions observed for the study area environment, which involved 5 habitat classes. The step length specifies the distance the duck desires to move within or between habitats. In this case, observed step lengths were categorized into five ranges of distances relevant to the species of interest: 0 m, 1–5 m, 6–20 m, 21–40 m, and 41–100 m. The first category represents a lack of animal movement coinciding with resting or loafing behaviour. The second corresponds to movement by walking or swimming within a single cell in the model environment, depending on the habitat type. The third encompasses movements into nearby cells by walking, swimming, or flying. The fourth and fifth categories represent longer movements that occur at higher speeds and correspond exclusively to flight behaviour. The return time specifies the frequency at which the duck returns to the roost (i.e. homing behaviour directs the animal to its starting location), measured as the number of model ticks passing before it returns. For example, a return time of 3600 forces the duck to return to the roost at the start of every diurnal period. A return time of 720 requires the duck to return to the roost every three hours, or at 06:00:00, 09:00:00, 12:00:00, 15:00:00, and 18:00:00. The decision to set the temporal resolution of the model to 15 s per tick was motivated by the resolution at which field observations were collected, in the context of consideration surrounding observed movement distances and the overall extent of the study area environment. Given the extent of the study area and the capabilities for animal movement observed, a temporal resolution of 15 s was deemed appropriate to model both short and long distance transitions for duck agents.

Frequency distributions constructed from habitat transition and associated step length observations were used to inform agent decision-making in the model. During a given model tick where a return-to-roost is not required, the duck agent will randomly draw an element from the transition frequency distribution corresponding to its current habitat situation. For example, if a duck agent is currently situated in shoreline cover, a transition type of "to-water" might be drawn. Based on the result of the initial transition draw, the duck agent proceeds to draw a step length from a step length distribution associated with the chosen transition type. In the case of a shoreline-to-water transition, step length draws of 1-5 m and 6-20 m are possible.

2.5. Model steps

The ABM models duck movement based on the observed habitat transition, step length, and return frequencies within the habitat map using the following procedure:

Step 1: Initialization.

a. A single duck is located at a pre-designated shoreline cell at tick 0 (i.e. 06:00:00).
b. The duck's spatial coordinates are recorded.
c. 1 tick (15 s) is added to the model clock.
d. Duck proceeds to Step 2.

Step 2: Duck movement.

a. The duck counts the number of ticks that have passed.

1. If the number of ticks is equally divisible by the specified return time:
   a. The duck returns to the roost.
   b. The duck records its spatial position.
   c. 1 tick (15 s) is added to the model clock.
   d. The duck proceeds to Step 3.

2. If the number of ticks is not equally divisible by the specified return time:
   a. The duck identifies the habitat type of its current position.
   b. The duck randomly draws a habitat transition type from a habitat transitions distribution corresponding to its current habitat situation.
   c. The duck randomly draws from a step length distribution for the selected habitat transition.
   d. The duck determines possible target cells given its current position, selected habitat transition, and selected range of movement/step length.
      i. If possible target cells are identified within range of the chosen step length:

1. The duck randomly selects one of the potential cells.
2. The duck moves to a random location within that selected cell.
3. The duck records its spatial position.
4. 1 tick (15 s) is added to the clock.
5. The duck proceeds to Step 3.

      ii. If possible target cells are not identified, for example, no cells of the drawn transition type are available within the drawn step length:

1. The duck returns to Step 2.a.

3. If the number of ticks is equally divisible by the specified return time:
   a. The duck immediately returns to the original roost location via a direct-flight.

Step 3. Model continuation or end.

b. If the final number of ticks (100800) has not been reached, the duck returns to Step 2.
c. If the final number of ticks (100800) has been reached, the model ends.

3. Methods

3.1. Field observations

Habitat transition and movement data were collected alongside other behavioural data at the University of South Florida Tampa campus (paper under review). Field observations were conducted from January 2012 to January 2013 during daylight hours. The protocol began with the researcher visiting a designated part of the campus and randomly selecting a duck to observe. Observations of individual ducks were

Table 1
Observed transition frequencies from one habitat (row) to another (column) for Muscovy ducks.

Habitat	Water	Shoreline	Grass	Tree-shrub	Urban
Water	2796	113	4	0	0
Shoreline	80	2705	78	2	2
Grass	21	76	8807	101	124
Tree-shrub	8	3	75	5794	30
Urban	0	0	133	38	1393

Table 2
Observed movement distances associated with habitat transitions for Muscovy ducks.

From	To	Distance (m)				
Habitat	Habitat	0	1–5	6–20	21 to 40	41 to 100
Water	Water	2276	504	14	0	2
Water	Shoreline	0	77	36	0	0
Water	Grass	0	0	3	1	0
Water	Tree-shrub	0	0	0	0	0
Water	Urban	0	0	0	0	0
Shoreline	Water	0	56	24	0	0
Shoreline	Shoreline	2682	22	0	0	1
Shoreline	Grass	0	45	31	1	1
Shoreline	Tree-shrub	0	2	0	0	0
Shoreline	Urban	0	0	2	0	0
Grass	Water	0	7	2	5	7
Grass	Shoreline	0	38	22	5	11
Grass	Grass	8470	315	8	5	9
Grass	Tree-shrub	0	62	37	2	0
Grass	Urban	0	88	35	0	1
Tree-shrub	Water	0	6	1	1	0
Tree-shrub	Shoreline	0	1	1	1	0
Tree-shrub	Grass	0	44	31	0	0
Tree-shrub	Tree-shrub	5761	32	0	0	1
Tree-shrub	Urban	0	21	9	0	0
Urban	Water	0	0	0	0	0
Urban	Shoreline	0	0	0	0	0
Urban	Grass	0	92	25	10	6
Urban	Tree-shrub	0	28	9	1	0
Urban	Urban	1364	28	1	0	0

conducted for 10-min time periods. Relevant to this study, the habitat in which the duck was located was recorded every 15 s, along with the approximate distance it travelled between each 15 s interval. The final dataset included >22,000 observed habitat transitions and their associated distances, as summarized in Tables 1 and 2. Table 1 shows how Muscovy ducks tended to stay within the same habitat during most observed transitions. Some transitions between habitats were fairly common, such as those between water and shoreline and those between shoreline and grass. Ducks were never observed moving directly from water to urban habitat, or vice versa. The second table summarizes the distances associated with each of the transition types. Note, the values are directly linked. For example, of 102 transitions from water to shoreline 77 were associated distances <1–5 m, and 25 were associated with distances of 6–20 m. Overall, it is clear from the tables that the ducks overwhelmingly moved rather small distances during 15 s intervals, though these are punctuated by less frequent, relatively long flights. The longer flights mostly occurred between grass and other habitats.

3.2. Model specification and simulations

The Muscovy duck agent-based model was run under four scenarios. All scenarios utilized the observed habitat transition and step length distributions. Upon any random draw, the duck agent has access to habitat transition and step length distributions corresponding to the habitat type currently occupied and has access to a step length distribution corresponding to its chosen destination. Once a destination is selected, the duck agent proceeds to the destination without further consideration of possible, intermediate habitat changes occurring along its path of movement between the origin and destination habitat cell. Environment cells of inaccessible type are omitted from agent consideration for movement. No duck agent can move to an inaccessible cell, as no transitions to inaccessible habitat were observed or included in transition distributions. In terms of the model time elapsed during movement, the duck agent executes its chosen transition within the span of a single tick once habitat transition type and distance have been drawn. In this sense, the model generates animal movements which are possible in the span of 15 s, consistent with the 15 s long field observations collected. Upon reaching a return-to-roost tick, movement is also instantaneous, representing a return to the roost via direct flight of the duck. For model runs conducted as part of this research, four scenarios were evaluated by using all combinations of the two landscapes (study area and random) and two return times (3600 and 720 ticks), as described in Section 2. The models for the study area were initialized using a predetermined list of observed duck shoreline roosting locations for consistency between the two different return time scenarios for that model environment. Similarly, sets of shoreline roosts were specified for the random landscape toward the centre of the map. The model was run 60 times for each scenario, producing a total of 240 individual movement trajectories (Fig. 3). The generated tracking point datasets for each model run were exported as shapefiles for further analysis in a GIS.

3.3. Analysis

Two measurements were calculated for each individual tracking dataset for comparison among scenarios, as well as for comparison to

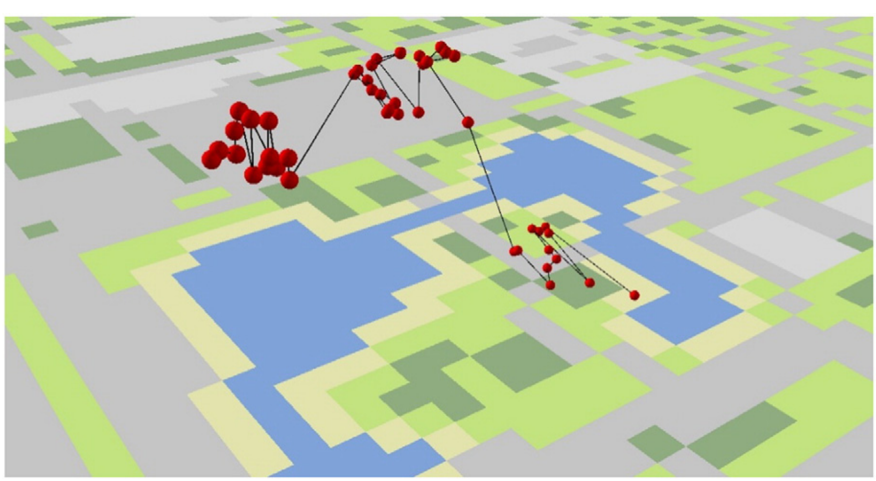

Fig. 3. Subset of a single simulated Muscovy duck trajectory (origin at shoreline, symbol height (z-axis) indicates model ticks elapsed).

Table 3
Mean percent and standard deviation of points located in each habitat type for four model scenarios of 60 runs each.

Scenario		Water		Shoreline		Grass		Tree/shrub		Urban	
Landscape	Return time	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.
Study area	720	12.8	2.1	12.0	1.5	47.9	2.3	23.5	1.9	4.0	0.9
Study area	3600	10.7	1.3	8.7	0.9	49.9	1.8	25.6	3.1	4.7	0.5
Random	720	10.1	1.1	11.4	0.9	44.8	1.5	29.7	1.2	4.0	0.4
Random	3600	9.0	0.8	9.3	0.6	45.0	5.4	32.0	1.3	4.1	0.3

existing studies of Muscovy ducks. First, percentages of points located in each habitat type were calculated as a measure of habitat usage. This was calculated in order to compare habitat use simulated by the model to that observed in the original field study. Second, the number of occupied cells (i.e. grid cells containing a tracking point) were counted as a simple measure of the spatial extent of the duck's movements. This can loosely be considered as a measure of the duck's home range. For both measures of model output, basic summary statistics were compiled for each of the four scenarios. Analysis of variance (ANOVA) using Tukey's HSD test was used to determine if these measures differed between scenarios.

4. Results

Model runs produced habitat percentages that were very similar to those observed in the field (12% water, 13% shoreline, 42% grass, 27% tree and shrub, and 7% urban), though there were differences between scenarios (Table 3). While the mean percentages only differed by a few percentage points between scenarios, the differences were significant ($p < 0.05$) as the variance within scenarios was low. Tukey's HSD test indicated that percentages differed between all scenarios for water, shoreline, grass, and tree-shrub. Urban percentages were only different for the second scenario. The first scenario (study area map with a return time of 720) produced percentages most similar to those observed in the field for water and shoreline, the most critical duck habitats. Usage was lower for all other scenarios. The second scenario (study area map with a return time of 720) generated the most accurate tree-shrub percentages, though all scenarios produced results that were slightly higher than observed. The random habitat map scenarios best simulated grass usage, although all models predicted slightly higher usage than observed in the field. All scenarios produced urban percentages that were slightly lower than observed.

Sample Muscovy duck tracking data sets for each of the four model scenarios are illustrated in Fig. 2. The different scenarios produced tracking data sets with different spatial characteristics. The first scenario produced the smallest occupied areas, on average 1616 cells or 0.040 km^2 (Table 4). When only a single return to the roost at the start of each day was modelled in the same landscape, the size increased to an average of 2140 cells or 0.054 km^2. Compared to the study area environment, the simulated duck tracking for the random scenarios data covered larger spatial areas, an average of 1967 cells or 0.050 km^2 under 720-tick return times and an average of 3023 cells or 0.076 km^2 for 3600-tick return times. Although there were 11,352 grid cells in each model environment, numbers of occupied cells did not vary greatly within each scenario, with a difference of at most 665 cells between the minimum and maximum values within any one scenario (Table 4). ANOVA and Tukey's HSD test indicated that the numbers of occupied cells differed among all scenarios.

Table 4
Mean, standard deviation, minimum, and maximum numbers of occupied cells for four landscape and return time scenarios of Muscovy duck agent-based model runs.

Landscape	Return time	Mean	s.d.	Minimum	Maximum
Study area	720	1616	94	1377	1785
Study area	3600	2140	145	1856	2488
Random	720	1967	85	1786	2169
Random	3600	3023	123	2606	3271

5. Discussion

The agent-based model of Muscovy duck movements produced simulated tracking data with habitat use characteristics similar to the percentages reported in a previous study. The best performing model—the first scenario with frequent return times in the study area map—produced habitat percentages most similar to those observed in the field. This scenario produced tracking data with the smallest spatial extents, which is not surprising as each duck was required to return to the shoreline at regular intervals. A once daily return time caused relative decreases in water and shoreline usage—compared to both the first scenario and the observed field data—because whenever the duck was located >100 m from the pond, it could not return there even when transitions to water or shoreline were drawn. As ducks in the study area were observed returning to the water several times each day, incorporating a shorter return time into the model improved the results. Alterations in return time for either landscape composition may significantly affect associated home range estimates in situations where convex hulls are constructed from multiple simulated trajectories.

The model's performance in random habitats illustrated how the model output differed with changes landscape composition and configuration. Despite water and shoreline being distributed throughout the random landscape, usage of these habitats was slightly less than that generated by the study area models. This is because those habitats were distributed mostly as isolated cells, so habitat transitions between water and shoreline often could not be completed if the cells were not adjacent to one another. The declines in water and shoreline were associated with increased in grass and tree-shrub usage. Despite approximating habitat usage fairly accurately, the models for the random environment produced tracking data with different spatial features than produced for the study area scenarios. First, the random models produced tracking data that covered larger spatial extents. This is because inaccessible cover types were included in the map while preferred habitats were more continuously available throughout the landscape, which imposed less restrictions on movement. Second, the shapes of the point clouds of tracking data tended to be more circular or radial, particularly for the frequent return time scenario. In comparison, those for the study area map tended to follow the configuration of suitable habitat features.

In summary, the agent-based modelling approach described in this paper provides a useful method for simulating tracking data. Such data could be used in future studies that test methods of home range analysis or quantify animal interactions. Rather than using turn angles in conjunction with step length frequencies, habitat transition frequencies and return times were used to model animal tracking data in different landscape contexts. This approach contributes a novel extension to the process of simulating animal movements, as habitat preferences and landscape features are directly incorporated into the model. Additionally, the use of the return time feature allows intensive use of core areas to be modelled, which could be useful for species that repetitively visit particular locations, such as roosts, nests, or dens.

Concerning limitations of the current model implementation, future development could address logical issues surrounding the sensitivity of the model components to the structure and size of the study area and observed movement datasets. For example, in the case of this study, a small study area combined with the available range of distance choices for animal locomotion during transitions rendered the majority of model environment readily accessible (except for inaccessible cells) to agents in situations such as direct and long flight movements. If this model were specified for a larger study area, the movement dynamics analysed and reported in this research could change. Additional agent decision-making logic or the incorporation of agent state information capturing a time-budget for return-to-roost state in agents could resolve complications brought about by larger model environments (agents becoming too far from roost to effectively return during a single tick). Further, the approach detailed in this study has the goal of generating movement trajectories which are representative of a population resident to a study area, using observations taken from individuals. Due to the nature of this approach, the model does not simulate any behaviours unique to one individual animal, for example simulation of an individual where specific biases in habitat preferences have been observed. This is lost upon aggregation of the observed data informing the model. Ultimately, this renders simulation problematic where uniqueness in behaviour between animal agents is a research requirement. Alteration of the data aggregation methods and collection of additional observational datasets which focus on individuals across a series of repeat observation efforts could be used to relax this limitation in the future.

Though the approach was employed for Muscovy ducks, the general approach is flexible enough to simulate tracking data for other species if habitat transition and step length frequency data can be collected or estimated. In this study relevant data were collected via visual observations, but deriving this information from high temporal frequency GPS or satellite tracking data also should be possible. Additionally, other types of agent behaviours could be incorporated into the model to generate tracking data with other types of characteristics. For example, if particular animals move in groups, then spatial dependency among agents could be explicitly modelled. It would also be straight forward to model constrained movements within predefined home ranges, such as is commonly done to model animal interactions. This could be accomplished by altering the model environment to exclude additional inaccessible areas outside a designated home range area. Another interesting addition might be to include dynamic changes in the model environment, such as resource availability, or behavioural states of the agents, such as hunger, which are commonly modelled for other purposes.

References

Ahern, S. C., Smith, J. L. D., Joshi, A. R., & Ding, J. (2001). TIGMOD: An individual-based spatially explicit model for simulating tiger/human interaction in multiple use forests. *Ecological Modelling*, *140*, 81–97.

Anderson, J. H. (2012). A spatially explicit agent based model of Muscovy duck home range behavior. *Graduate theses and dissertations* http://scholarcommons.usf.edu/etd/3950.

Bartumeus, F., Da Luz, M. G. E., Viswanathan, G. M., & Catalan, J. (2005). Animal search strategies: A quantitative random-walk analysis. *Ecology*, *86*, 3078–3087.

Bennett, D. A., & Tang, W. (2006). Modelling adaptive, spatially aware, and mobile agents: Elk migration in Yellowstone. *International Journal of Geographical Information Science*, *20*, 1039–1066.

Bergman, C. M., Schaefer, J. A., & Luttich, S. N. (2000). Caribou movement as a correlated random walk. *Oecologia*, *123*, 364–374.

Bonnell, T. R., Campenni, M., Chapman, C. A., Gogarten, J. F., Reyna-Hurtado, R. A., Teichroeb, J. A., ... Sengupta, R. (2013). Emergent group level navigation: An agent-based evaluation of movement patterns in a folivorous primate. *PloS One*, *8*.

Byers, J. A. (2001). Correlated random walk equations of animal dispersal resolved by simulation. *Ecology*, *82*, 1680–1690.

Carter, N., Levin, S., Barlow, A., & Grimm, V. (2015). Modeling tiger population and territory dynamics using an agent-based approach. *Ecological Modelling*, *312*, 347–362.

Codling, E. A., Plank, M. J., & Benhamou, S. (2008). Random walk models in biology. *Journal of the Royal Society Interface*, *5*, 813–834.

Crooks, A. T., & Wise, S. (2013). GIS and agent-based models for humanitarian assistance. *Computers, Environment and Urban Systems*, *41*, 100–111.

Downs, J. A. (2010). Time-geographic density estimation for analysing moving point objects. *Lecture Notes in Computer Science*, *6292*, 16–26.

Downs, J. A., & Horner, M. W. (2008). Effects of point pattern shape on home range estimates. *Journal of Wildlife Management* (article in press).

Downs, J. A., & Horner, M. W. (2009). A characteristic-hull based method for home range estimation. *Transactions in GIS*, *13*, 527–537.

Downs, J. A., & Horner, M. W. (2012). Analysing infrequently sampled animal tracking data by incorporating generalized movement trajectories with kernel density estimation. *Computers, Environment and Urban Systems*, *36*, 302–310.

Downs, J. A., Heller, J. H., Loraamm, R., Stein, D. O., McDaniel, C., & Onorato, D. (2012). Accuracy of home range estimators for homogeneous and inhomogeneous point patterns. *Ecological Modelling*, *225*, 66–73.

Duchesne, T., Fortin, D., & Rivest, L. P. (2015). Equivalence between step selection functions and biased correlated random walks for statistical inference on animal movement. *PloS One*, 10.

Epstein, J. M. (1999). Agent-based computational models and generative social science. *Complexity*, *4*(5), 41–60.

Ettema, D. (2011). A multi-agent model of urban processes: Modelling relocation processes and price setting in housing markets. *Computers, Environment and Urban Systems*, *35*, 1–11.

Forester, J. D., Im, H. K., & Rathouz, P. J. (2009). Accounting for animal movement in estimation of resource selection functions: Sampling and data analysis. *Ecology*, *90*, 3554–3565.

Getz, W. M., Fortmann-Roe, S., Cross, P. C., Lyons, A. J., Ryan, S. J., & Wilmers, C. C. (2007). LoCoH: Nonparameteric kernel methods for constructing home ranges and utilization distributions. *PloS One*, *2*.

Girard, I., Ouellet, J. P., Courtois, R., Dussault, C., & Breton, L. (2002). Effects of sampling effort based on GPS telemetry on home-range size estimations. *Journal of Wildlife Management*, *66*, 1290–1300.

Gitzen, R. A., & Millspaugh, J. J. (2003). Comparison of least-squares cross-validation bandwidth options for kernel home-range estimation. *Wildlife Society Bulletin*, *31*, 823–831.

Gitzen, R. A., Millspaugh, J. J., & Kernohan, B. J. (2006). Bandwidth selection for fixed-kernel analysis of animal utilization distributions. *Journal of Wildlife Management*, *70*, 1334–1344.

Holloway, P., & Miller, J. (2014). Uncertainty analysis of step-selection functions: The effect of model parameters on inferences about the relationship between animal movement and the environment. In M. Duckham, E. Pebesma, K. Stewart, & A. Frank (Eds.), *Geographic Information Science. 48–63*, . Springer International Publishing.

James, A., Plank, M. J., & Edwards, A. M. (2011). Assessing Levy walks as models of animal foraging. *Journal of the Royal Society Interface*, *8*, 1233–1247.

Jeanson, R., Blanco, S., Fournier, R., Deneubourg, J. L., Fourcassie, V., & Theraulaz, G. (2003). A model of animal movements in a bounded space. *Journal of Theoretical Biology*, *225*, 443–451.

Laver, P. N., & Kelly, M. J. (2008). A critical review of home range studies. *Journal of Wildlife Management*, *72*, 290–298.

Long, J. A., Nelson, T. A., Webb, S. L., & Gee, K. L. (2014). A critical examination of indices of dynamic interaction for wildlife telemetry studies. *Journal of Animal Ecology*, *83*, 1216–1233.

Malleson, N., & Birkin, M. (2012). Analysis of crime patterns through the integration of an agent-based model and a population microsimulation. *Computers, Environment and Urban Systems*, *36*, 551–561.

Manley, E., Cheng, T., Penn, A., & Emmonds, A. (2014). A framework for simulating large-scale complex urban traffic dynamics through hybrid agent-based modelling. *Computers, Environment and Urban Systems*, *44*, 27–36.

McLane, A. J., Semeniuk, C., McDermid, G. J., & Marceau, D. J. (2011). The role of agent-based models in wildlife ecology and management. *Ecological Modelling*, *222*, 1544–1556.

Miller, J. A. (2012). Using spatially explicit simulated data to analyze animal interactions: A case study with brown hyenas in Northern Botswana. *Transactions in GIS*, *16*, 271–291.

Miller, J. A. (2015). Towards a better understanding of dynamic interaction metrics for wildlife: A null model approach. *Transactions in GIS*, *19*, 342–361.

Miller, C., Christman, M. C., & Estevez, I. (2011). Movement in a confined space: Estimating path tortuosity. *Applied Animal Behaviour Science*, *135*, 13–23.

Moorcroft, P. R., Lewis, M. A., & Crabtree, R. L. (2006). Mechanistic home range models capture spatial patterns and dynamics of coyote territories in Yellowstone. *Proceedings of the Royal Society B*, *273*, 1651–1659.

Nams, V. O. (2013). Sampling animal movement paths causes turn autocorrelation. *Acta Biotheoretica*, *61*, 269–284.

Richard, E., Calenge, C., Said, S., Hamann, J. L., & Gaillard, J. M. (2013). Studying spatial interactions between sympatric populations of large herbivores: A null model approach. *Ecography*, *36*, 157–165.

Ringelman, K. M. (2014). Predator foraging behavior and patterns of avian nest success: What can we learn from an agent-based model? *Ecological Modelling*, *272*, 141–149.

Strombom, D., Mann, R. P., Wilson, A. M., Hailes, S., Morton, A. J., Sumpter, D. J. T., & King, A. J. (2014). Solving the shepherding problem: Heuristics for herding autonomous, interacting agents. *Journal of the Royal Society Interface*, *11*, 9.

Tang, W., & Bennett, D. A. (2010). Agent-based modeling of animal movement: A review. *Geography Compass*, *4*, 682–700.

Thurfjell, H., Ciuti, S., & Boyce, M. S. (2014). Applications of step-selection functions in ecology and conservation. *Movement Ecology*, *2*, 4.

Torrens, P. M., Nara, A., Li, X., Zhu, H., Griffin, W. A., & Brown, S. B. (2012). An extensible simulation environment and movement metrics for testing walking behavior in agent-based models. *Computers, Environment and Urban Systems*, *36*, 1–17.

Widener, M. J., Horner, M. W., & Ma, K. (2015). Positioning disaster relief teams given dynamic service demand: A hybrid agent-based and spatial optimization approach. *Transactions in GIS*, *19*, 279–295.

Wilson, R. P., Griffiths, I. W., Legg, P. A., Friswell, M. I., Bidder, O. R., Halsey, L. G., ... Shepard, E. L. C. (2013). Turn costs change the value of animal search paths. *Ecology Letters*, *16*, 1145–1150.