



Analysing small-scale aggregation in animal visits in space and time: the ST-BBD method

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Movement behaviour plays an important role in many ecological interactions. As animals move through the environment, they generate movement patterns, which are a combined result of landscape characteristics and species-specific behaviour. Measuring these ranging patterns is being facilitated by technological advances in collection methods, such as GPS collars, that are capturing movement on finer spatial and temporal scales. We propose the use of a novel spatiotemporal analytical framework (ST-BBD), based on the beta-binomial distribution (BBD) model, to measure small-scale aggregation in animal movement data sets, including two simulated and three collected primate data sets. We use this approach to distinguish different habitat uses of three primate species (red colobus, *Procolobus rufomitratus*, black howler, *Alouatta pigra*, and spider monkey, *Ateles geoffroyi*) and quantify their specific use of the landscape in space and in time, using a parameter of the BBD that measures the variation in sites visited on a landscape. We found that estimates of aggregation in habitat use were higher in the frugivorous spider monkey, compared to the more folivorous howler monkey, and that in the red colobus, aggregation in site visits was dependent on group size and food availability. Applications of this framework to animal movement data could be useful in understanding ecological systems where habitat use is an important factor, such as the relationships between hosts and parasites, or parent plants and seed dispersers.

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Movement is a vital process for many animals, affecting a broad spectrum of ecological processes and patterns observed in nature (Nathan et al. 2008). The study of animal movement behaviour has led to much insight into such fields as foraging ecology (Orians & Pearson 1979; Humphries et al. 2010), wildlife management (Chetkiewicz et al. 2006), plant seed dispersal (Vellend et al. 2003) and disease dynamics (Bartel et al. 2011).

With technological advances providing the increasing availability of high-resolution animal movement data, both in time and in space, there is a need to advance methodologies for analysing movement data. Movement is a spatiotemporal process in which an animal moves over a heterogeneous landscape through time. Thus, states and

conditions of both the animal in question and the landscape are continuously changing. Different methods have been developed to measure movement characteristics, each capturing some aspect of movement. These different measurements can be separated depending on whether the focus is on space, time, or space and time.

One main branch of spatial approaches focuses on point pattern analysis, where movement data are treated as (x, y) locations measured in a two-dimensional space (e.g. home range; Millsaugh et al. 2004). These methods search for patterns, or structure, in the distribution of points, which can provide insight into the behavioural ecology of the study species. Another, more complete approach is followed when a temporal component is added to points, tying them together by the sequence in which they were measured. This approach is characterized by the measurement of 'between-step characteristics' (e.g. step length or angle) at similar time periods. In analysing between-step measurements, the results are often compared to theoretical distributions as a means of interpretation, such as the Lévy walk, random

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walk or correlated-random walk (Viswanathan et al. 1996; Edwards et al. 2007; Humphries et al. 2010). Methods focusing more specifically on the temporal aspects of the data have made use of time series analysis, in which between-step measures (e.g. distance or turning angle) are examined through time to test for autocorrelation in movement behaviour (Dray et al. 2010). Kernel methods have also been applied, classically to (x, y) locations in two-dimensional space, to derive the probability of occurrence on a landscape, and has recently been extended to estimate probability of occurrence in space and time (Keating & Cherry 2009).

Using animal movement data, we were interested in developing a measure to characterize an animal's use of habitats; specifically, to measure the spatiotemporal variation in use of sites within a habitat. In examining movement data, or following an animal in the field, it is often apparent that some sites are used more intensely and more often than others. It is possible that there exists a cyclical pattern of site use, one based on seasons or depletion–replenishment of resources, so that the animal in question may or may not follow along similar routes on the landscape. The relevant method should allow the estimation of variation in these patterns of habitat use in space and time, and provide a statistically sound way to test for differences, for example, among comparable species. Existing approaches to examine spatiotemporal variation (e.g. Mantel test and correlograms; see below, *Variability and Autocorrelation in Animal Visits of a Landscape*) do not capture and compare variation between specific areas and periods, and as a whole are more global than the small-scale focus desired here. Therefore, we evaluated a new approach that uses the beta-binomial distribution (BBD) in a framework where a spatiotemporal grid is created to measure habitat use. Basically, the space and time in which the animal is moving are broken into space–time cubes in which either presence or absence of passage (i.e. Bernoulli trial) is recorded. Space–time cubes have been introduced as sampling units in the field of time geography, and have been used to map spatiotemporal data for subsequent analysis (Miller 2005). Subdividing the space–time cubes into cells within sampling units following the BBD opens the door to the quantification of spatiotemporal aggregation at smaller scales.

The BBD was applied by Hughes & Madden (1993) in an epidemiological context for investigating the aggregation of diseased plants on agricultural landscapes. These authors showed that when there is uneven chance of finding an infected plant through the landscape (i.e. it is more likely to find an infected plant near another infected plant), the BBD can be useful in quantifying the spatial aggregation of infection occurrences. In a spatiotemporal context, the BBD has been suggested for use with animal movement data (Dutilleul 2011, Chapter 4). In this approach, Dutilleul (2011) proposes an extension on the framework of Madden & Hughes (1995) that consists in measuring the displacement of a spatial unit (i.e. point) through time and quantifying the aggregation of visited areas in space and time.

The objective of our paper is to evaluate the spatiotemporal version of the BBD framework (ST-BBD hereafter), as a tool to estimate the intensity to which an animal uses its home range. We first apply the ST-BBD framework to primate movement data simulated under two behaviour models. We then apply it to movement data collected for three primate species in the field, and quantify the intensity of habitat use within each species and compare it between species. The three species chosen vary in the degrees of frugivory and folivory: spider monkeys, *Ateles geoffroyi*, rely heavily on fruit resources (frugivorous), whereas howler monkeys, *Alouatta pigra*, and red colobus, *Procolobus rufomitratus*, typically rely on leaves (folivorous). Foraging for fruits in a tropical forest requires finding the few dispersed trees that produce fruit intermittently. By comparison, when foraging for good-quality leaves, trees are thought to be less dispersed, offering food more often than do fruit trees. Given the varying distribution of resources, both spatially and

temporally, we used the ST-BBD framework to quantify spatiotemporal aggregation accordingly and determine differences in habitat use by these two folivorous and one frugivorous primate species.

Data Sets

Simulated data

We first simulated movement data with an agent-based model (ABM) of primate group foraging, which approximates primate group movement behaviour for use in a spatially explicit epidemiological study (Bonnell et al. 2010). In general, ABMs define characteristics and behaviours of individual agents (e.g. primates, fish, farmers, companies) within a simulation environment, and allow them to interact to create system-level outcomes (for use of ABM in behavioural studies, see: Hemelrijk 2002; Bryson et al. 2007). The ABM here was constructed as a general model, made to fit a wide range of primate group foraging behaviours. In this study, we focus on the effect that a foraging trait called 'weight of remembered sites' has on overall movement behaviour. This trait is a key model component that affects each primate's foraging decision making. In the model, the primate agents use a food site index to assess which site, seen or remembered, is the best site to move towards. This food site index is based on the expected amount of food and the distance to such sites, while the parameter 'weight of remembered sites' gives extra weight to sites that are familiar (i.e. remembered) to the primate agent (equation 1).

The food site index value at site (x', y') from site (x, y) is given by

$$I(x', y') = \frac{D((x', y'), (x, y))}{F(x', y') * w} \quad (1)$$

where $D(\cdot)$ represents the Euclidean distance between two points, $F(\cdot)$ is the primate's evaluation of the amount of food at a given site, and w is the weight parameter applied to remembered sites.

When preference for remembered sites is increased, simulated primates tend to use selected sites intensively, visiting familiar sites often, and travelling along similar routes connecting these sites. We will thus refer to this behaviour model as the 'routing model', because it creates travel routes. On the other hand, with low preference for remembered sites, groups show nonspecific ranging behaviours and no heavy use of a specific area. Accordingly, we will refer to that behaviour model as the 'nonrouting model'.

For each type of model, one simulated group of primates (group size = 72) was made to forage on a 1.5×1.5 km landscape for 6 months. Movement data were recorded for 5 months, after the first month was discounted to sufficiently initialize the memory of individuals in the simulated group. The position of the simulated group was taken every 30 min during the active hours of the day (0700–2000 hours), and recorded as a point (x, y) with a time component (t) . The 30 min interval was selected because it is very feasible logistically speaking and is therefore often used in field studies (Chapman et al. 2002), and it is a crude time period to avoid autocorrelation given the distances animals can cover in half an hour (Reyna-Hurtado et al. 2009). With the chosen total duration (5 months) and sampling time interval (30 min), the final set of simulated data was composed of two point patterns, each with 3900 point locations in space–time (Fig. 1).

Collected data

Our second data source consists of GPS points or tracks taken from field measurements of primate group movement. We make use of movement data collected from a highly folivorous primate (red colobus), a folivore–frugivore primate (black howler), and a highly frugivorous primate (spider monkey). Red colobus data were collected from August 2006 to June 2010 in Kibale National

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