Using a null model approach to explore how dynamic interactions in wildlife are analyzed

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Abstract

The nature of interactions between individuals of an animal population is a fundamental aspect of a species' behavioural ecology and information on the frequency and duration of these interactions is vital to understanding mating and territorial behaviour, resource use, and infectious disease epidemiology. There have been two main ways to quantify interactions in wildlife studies: 'static interactions', which involve some quantification of home range overlap (and are therefore just spatial), and 'dynamic interactions' which are defined as occurring within a spatial and temporal threshold. Dynamic interactions can provide information on possible attraction and avoidance of individuals that are in the same area at the same time and are far more useful for understanding how two individuals interact in the context of disease transmission and behavioural ecology, but they are more problematic to measure. Few studies have tested different dynamic interaction metrics using the same data, and when they have been compared, the results have been quite variable (Miller, 2012, Long and Nelson, 2014). Most currently used dynamic interaction metrics lack a benchmarking framework that deals with null models or expected values for neutral interaction in order to facilitate more meaningful interpretation of their values (e.g., what are the values for each metric that would be associated with social behaviors be consistent with 'attraction,' 'repulsion,' or 'no interaction'?). The research presented here borrows from the null model approach commonly used in community ecology to compare observed (empirical) dynamic interaction values with distributions of expected values generated by using different null models.

Keywords: movement pattern analysis, spatiotemporal, null model, interaction, random walk.

1. Introduction

High quality movement data are increasingly available for many different types of animals, facilitating unprecedented access to insights about how movement can be used to study behaviors. In addition to increased spatial accuracy and temporal resolution of the locational information, improvements are being made to 'biologgers' that enable the collection of ancillary behavioral and physiological information as well (Rutz and Hays 2009). 'Computational movement analysis' (CMA) has recently emerged as an extension of time-geography that focuses on the development and application of computational techniques for collecting, managing, and analyzing movement data in order to better understand the processes that are associated with them (Gudmundssen et al. 2012). Although a relatively large body of research in biology and ecology has developed on

animal movement due to the long-standing necessity of using tracking technologies to study them, CMA applications have focused more often on human movement, such as using travel diaries to better understand mobility and space use and studying potential exposures to environmental hazards. Concurrently, 'movement ecology' has become a rapidly growing subfield in ecology focused on understanding the "causes, mechanisms, and spatiotemporal patterns of (organismal) movement and their role in various ecological and evolutionary processes" (Nathan et al. 2008: 19052). In spite of the fact that both subfields deal with similar issues related to spatiotemporal representation and analysis, scale, uncertainty, and inferring process from pattern, there has been surprisingly little cross-over between them.

The ability to measure interactions, or the degree to which the movement of an individual is dependent upon that of other individuals, is crucial to understanding behaviors related to territoriality and mating as well as resource use and infectious epizootic diseases. 'Dynamic interaction' (Doncaster 1990) between two individuals occurs within a spatial and temporal threshold and can provide information on possible attraction and avoidance of individuals that are in the same area at the same time, which is important in the context of investigating disease transmission and spatial ecology.

In spite of the importance of measuring dynamic interactions, they have not been a main research focus in movement analysis. Few studies have tested different dynamic interaction metrics using the same data, and when they have been compared, the results have been quite incongruous (Long et al. 2014; Miller, 2012). This research borrows from the null model approach commonly used in community ecology to compare observed (empirical) dynamic interaction values with distributions of expected values generated by different null models.

2. Quantifying animal interactions

Many of these interaction metrics were originally developed in wildlife and behavioural ecology for use with direct observations of individuals (point-based) where observations were classified as one of four types: individual α and β together; α without β; β without α; or neither α nor β (see Cairns and Schwager, 1987 for review). Most of the interaction metrics described below have extended this concept by defining "together" either in terms of home range overlap or a spatio-temporal threshold.

While a few path-based dynamic interaction metrics have been introduced recently (see Long et al. 2014), path-based methods do not address relative spatial location and are more appropriate for measuring path similarity than the degree to which individuals encounter each other. As this work is primarily focused on measuring spatially proximal interaction, I focus on point-based metrics. Table 1 briefly describes the dynamic interaction metrics that are tested here, along with an indication as to whether they explicitly incorporate an expected value in their calculation.

The dynamic interaction metrics (DI metrics) listed in table 1 are important ways to measure level of interaction between two individuals. However, each of them has sufficient limitations that prevent robust and meaningful analysis of interactions. Point-based interaction metrics often require the calculation or selection of highly subjective factors such as home ranges or a distance threshold (d_c). Most importantly, these metrics lack a benchmarking framework that deals with null models or expected values for neutral interaction in order to facilitate more meaningful interpretation of their values.

The research presented here borrows from the null model approach commonly used in community ecology to compare observed (empirical) dynamic interaction values with distributions of expected values generated by using different null models in order to interpret the interaction metrics, as well as limitations associated with their current implementation.

Table 1: Point-based dynamic interaction metrics tested here.

DI metric	What is "interaction"?	Input	Expected values?	Interpretation
Prox	Ratio of $ST_{\alpha\beta}$ fixes to simultaneous ($T_{\alpha\beta}$) fixes.	t_c and d_c	--	• Ranges from 0 (avoidance) to 1 (attraction); • No significance test
Risk-ratio	Proportion of $T_{\alpha\beta}$ fixes that are within d_c to proportion of non-simultaneous (unmatched) fixes that are within d_c	t_c and d_c	Non-simultaneous fixes (n^2-n)	• RR< 1: avoidance • RR> 1: attraction • Uses 2x2 contingency table from Doncaster test, which can be assessed with χ^2 test
Lixn	Relative use of OZ by A and B together ($T_{\alpha\beta}$ fixes) compared to their respective $T_{\alpha\beta}$ fixes outside of OZ.	t_c, HRA, HRB, and OZ	Proportion of OZ to the unshared portion of HRA and HRB	• Lixn> 0: attraction • Lixn< 0: avoidance • $\chi2$ test
Cs	Compares the mean distance between $T_{\alpha\beta}$ fixes and mean distance between non-simultaneous fixes	t_c	Non-simultaneous fixes (n^2-n)	• Ranges from -1 (avoidance) to 1 (attraction) • Separate paired signed-rank tests for attraction and avoidance
HAI	Compares $ST_{\alpha\beta}$ fixes to number of times A is in OZ without B and B is in OZ without A	t_c, d_c and OZ	--	• Ranges from 0 (avoidance) to 1 (attraction) • No significance test
IAB	Compares mean distance between $T_{\alpha\beta}$ fixes in OZ to mean distance between temporally shifted fixes in OZ.	t_c, d_c and OZ	Wrapping the time series of serial locations for a series of temporal shifts	• Pseudo-p value for each case of attraction and avoidance calculated by comparing observed to expected values.

3. Testing null models for interpreting dynamic interactions

Using GPS collar data from five brown hyena dyads in Northern Botswana (see Miller 2012) this research explores the use of four different types of null models with which to compare the existing dynamic interaction metrics:

- *Random dates-* refers to methods that involve using coordinate values of actual locations, but randomly shuffling them or measuring interactions for pairs of coordinates that did not actually occur at the same time.;
- *Rotated trajectories-*involves randomly rotating and shifting actual movement trajectories so that a path is maintained but it is located randomly in the study area;
- *Correlated random walk-* involves simulating trajectories that are parametric, but include 'persistence' by specifying a turn angle concentration and a step length parameter;
- *Bivariate Brownian movement-* involves simulating a purely random trajectory that has only a dispersion parameter that is empirically estimated.

32 "null" trajectories are generated for each of the ten hyenas from each of the four null models, and the subsequent pairing up of 32 x 32 trajectories for each dyad results in 1024 unique pairs of null trajectories for which each of the six dynamic interaction metrics will be calculated. Dynamic interaction metrics are interpreted as representing attraction, avoidance, or no interaction by comparing the observed value to the distribution of expected values generated from the four null models.

Results indicate that these widely used dynamic interaction metrics are quite incongruous in terms of the type and degree of interactions that they measure, both across dyad, null model, and DI metric. Purely distance based DI metrics such as *Cs* performed poorly when compared using null models that were not constrained to the minimum bounding rectangle. L_{IXN} was susceptible to both type I and type II errors. The null model approach greatly enhanced the ability to interpret DI metrics that did not involve an inherent significance test such as *HAI*. In general, these results suggest a need for developing new DI metrics or improving the ability to interpret existing ones, as the ability to understand how individuals interact has important implications for understanding the spread of disease as well as behavioural ecology for less observable individuals.

4. References

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