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Developing a deeper understanding of animal movements and spatial dynamics through novel application of network analyses

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Summary

1. Determining how animals move within their environment is a fundamental knowledge that contributes to effective management and conservation. Continuous 'round-the-clock' animal movement data are frequently gathered using biotelemetry technology, providing discrete data packages on the presence–absence of animals at known locations through time. Current analyses of such data do not generally account for the interconnectivity of locations as animals move between them and consequently do not integrate graphically or statistically a temporal component to spatial changes.

2. Here, we describe the novel application of network analyses to electronic tag data whereby nodes represent locations and edges the movements of individuals. We demonstrate some of the descriptive and quantitative approaches for determining how an animal's movement interconnects home range habitats. Telemetry data from arrays of recorders provide movement data of individual animals, and as examples of the method proposed, we examine the movements of two distinct shark species, the small-spotted catshark (*Scyliorhinus canicula*) and the Caribbean reef shark (*Carcharhinus perezi*). In doing so, we consider both local and global network properties from an animal movement perspective and simulate the effects of node disruption as a proxy for habitat disturbance.

3. Comparative visual representations of two catshark movement networks suggest, for example, potential differences in space use. Multiple regression quadratic assignment procedure shows that habitat is a significant predictor of movement behaviour.

4. Null modelling of *C. perezi* movement data, corrected for the spatial restriction of static nodes, demonstrated a significant, non-random distribution of directed movements among sites. Additionally, the connectivity of this animal's movement network is significantly reduced through targeted disruption of a site of high centrality but not through disruption of a randomly selected site.

5. Network theory is a well-established theoretical framework and its integration into the fast developing field of animal movement and telemetry might improve significantly how we interpret animal space use from electronically recorded data. This technique has potentially wide application in animal behaviour but may also inform the management of habitat harbouring threatened or endangered species via the simulation, modelling and intuitive visualisation of animal movement interactions.

Key-words: acoustic telemetry, animal movements, fish behaviour, network analysis, space use, tagging

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Introduction

Understanding how and why animals move and migrate is fundamental to the effective management and conservation of wild animal populations. The spatial and temporal structure of movement cycles are based on evolutionarily successful behavioural decisions in response to numerous physical, biological and environmental stimuli (Patterson *et al.* 2008; Sims 2010). As human impacts on natural habitats become more widespread, understanding the cyclical trends involved in movement and the driving forces behind them are vital to the identification and potential mitigation of anthropogenic disruption (Southwood & Henderson 2000).

There are acute difficulties associated with observing and recording data for highly mobile and wide-ranging species in their natural habitats. As such, behavioural ecologists are increasingly relying on animal-borne electronic tags designed to store and in some cases transmit data relating to an animal's movement, speed, direction or environment (Rutz & Hays 2009). In recent years, advances in biologging and telemetry techniques have enhanced considerably our understanding of space use in a variety of animals from a broad range of environments (Cooke 2008). Ecologists now rely on such technology to estimate population density, home ranges or identify localised movement patterns. Current approaches for gathering such data include radiotelemetry (Harris *et al.* 1990), spatial arrays of static acoustic receivers (Heupel, Semmens & Hobday 2006), electronic data-logging (archival) tags, satellite-linked archival tags and Global Positioning System (GPS) tags (Sims 2010). Such advances in technology can provide 'round-the-clock' monitoring of individuals, and it is not unusual for this type of data set to contain tens of thousands of individual data points (Fancy *et al.* 1989; Heupel *et al.* 2010). These data, however, often share a generic feature, namely a time series of presence–absence data with each individual's time stamp and location creating a single data point.

The size and complexity of telemetry data sets can be challenging to visualise, analyse and interpret. In virtually all contemporary analyses (for review see Sims 2010), presence–absence data at known locations are viewed as separate entities, the abundance and frequency of which can be correlated to biotic or abiotic variables. Descriptive analyses such as frequency distributions of detections and multiple tag presence–absence graphs offer a useful approach for exploring common patterns within a population. The most frequent examples of these types of analyses are found in the marine environment where static array telemetry is widely used to track coastal marine predators (Dawson & Starr 2009; Speed *et al.* 2011). Basic inferential analyses include the generation of temporally and spatially structured residency indices which can be empirically compared (O'Toole *et al.* 2011). A more complex method for defining space utilisation and home ranges of animals is kernel utilisation distribution (KUD), widely used in both marine and terrestrial ecology providing key information on 'core areas' (e.g. Speed *et al.* 2011). These types of analyses offer powerful insights into the movements and habitat use of animals; however, there is still a wealth of information held within these large data sets which, to our knowledge, is not yet being fully exploited. Further development and refinement of analysis techniques is required not only to identify core areas using presence and absence data, but also to identify, quantify and compare empirically linkages and movements between core areas, for example.

For some time, ecologists have advocated the use of graph theory for explaining metapopulation structure and the impact of landscape connectivity on conservation (Urban & Keitt 2001). Graph theory considers the local and global structure of networks constructed from pairwise interactions of connected elements in a graphic format using nodes linked by one or a series of edges (see Materials and methods for more detail). More recently, a desire to better understand how the internet or transport routes are connected has given rise to the exploration of spatial network structures (Gastner & Newman 2006; Kaluza *et al.* 2010), and in a few cases, biological spatial networks have tracked this progress. For example, the spatial network topography of both freshwater ponds and roosting trees interconnected by amphibians and bats, respectively, has been examined (Fortuna, Gómez-Rodríguez & Bascompte 2006; Fortuna *et al.* 2009), but not for individual animal movement. These studies provide new insight into the importance and connectivity of specific habitat features on the aggregation and disease transfer of the animals moving between them. Individual-based telemetry data present an opportunity to utilise graph theory and enhance the potential for hypothesis-driven, telemetry-based field studies. This is particularly important because the frequency at which an animal or a group of animals occur at a given location does not necessarily underlie the ways in which animals move between locations. We propose that an integrative and holistic approach that accounts for the connectivity of locations has the potential to significantly improve our understanding and interpretation of animal movement and habitat use. Thus, we might begin to use electronic tag data to address a number of important hypotheses regarding the movement of an individual or group of animals (see Table 1 for examples).

The aim of this paper is to encourage an interdisciplinary approach to the analysis of animal movement and tracking data. We demonstrate the potential application of network analyses to improving the visualisation and statistical analyses of presence–absence data gathered by the wide variety of telemetry devices currently in use. We demonstrate this accessible approach using two distinct telemetry data sets of shark

Table 1. Example hypotheses (*H*) that could be addressed using network analysis of movement data obtained from animal biotelemetry data

H_1	Animals demonstrate repeatable movement patterns/show site fidelity
H_2	Movements and space use differ significantly between time of day/year or between sex/age class
H_3	Environmental variables can be used to predict movement between areas or general movement patterns
H_4	Habitat disturbance at key locations will impact animal movement

movements within two separate static acoustic arrays in temperate and tropical ecosystems. We compare movement tracks within and between individuals and apply null modelling and node disruption simulation to determine space use and vulnerability assessments for our given animals. Furthermore, the application of this technique is discussed in the context of hypothesis-driven animal telemetry and the future management and conservation strategies of a wide variety of terrestrial and aquatic taxa.

Materials and methods

In an attempt to illustrate the potential benefits of using network analyses to analyse, visualise and interpret these vast and often disparate packets of data, we interrogate two distinct data sets from the marine environment where static array, acoustic telemetry is widely used (Sims 2010). The movements of two predatory shark species are investigated: the small-spotted catshark (*Scyliorhinus canicula*) tracked within a small, deep-water acoustic array at Whitsand Bay, Cornwall, UK (Fig. 1) and the Caribbean reef shark (*Carcharhinus perezi*) tracked using a large acoustic array (32 receivers) in the shallow waters off the coast of Cape Eleuthera, Bahamas (Fig. 2). Methodological details of the capture, tagging and acoustic tracking of sharks are provided in the Supporting information (S1 and S2). The data here represent individual, unreplicated animal tracks which are used to demonstrate the specific application of this approach. These data have been selected to illustrate how network analyses account for the interconnectivity synonymous with telemetry data and furthermore how statistical analyses of these animal tracks can be explored in their entirety or in a restricted format enabling specific hypothesis testing.

WORKING WITH NETWORK DATA

Network theory relies on the notion that complex interconnected systems are made up of *nodes* connected by *edges*. Nodes may represent anything from individual organisms, physical locations or centres of information and may be dynamic or static within their environment. Edges, whether binary (0 or 1) or weighted (continuous values between 0 and 1), are equally variable and might encapsulate physical or emotional interactions or associations between network nodes (social networks), directional flow of information or disease, or the mobility of organisms between fixed locations. Nodes and edges are assimilated into a network of interconnected nodes from which a number of quantitative metrics can be calculated that can describe both local and global network structure. In particular, node-based metrics (local properties) can be used to describe the influence individual nodes (*i*) have on the overall network structure and are determined from the level of interaction one node has with any other node, either directly or via intermediaries. In the present study, an interaction would constitute the movement of an individual or group between two areas with the weighting of this movement edge relative to the frequency with which this directed movement is made by an

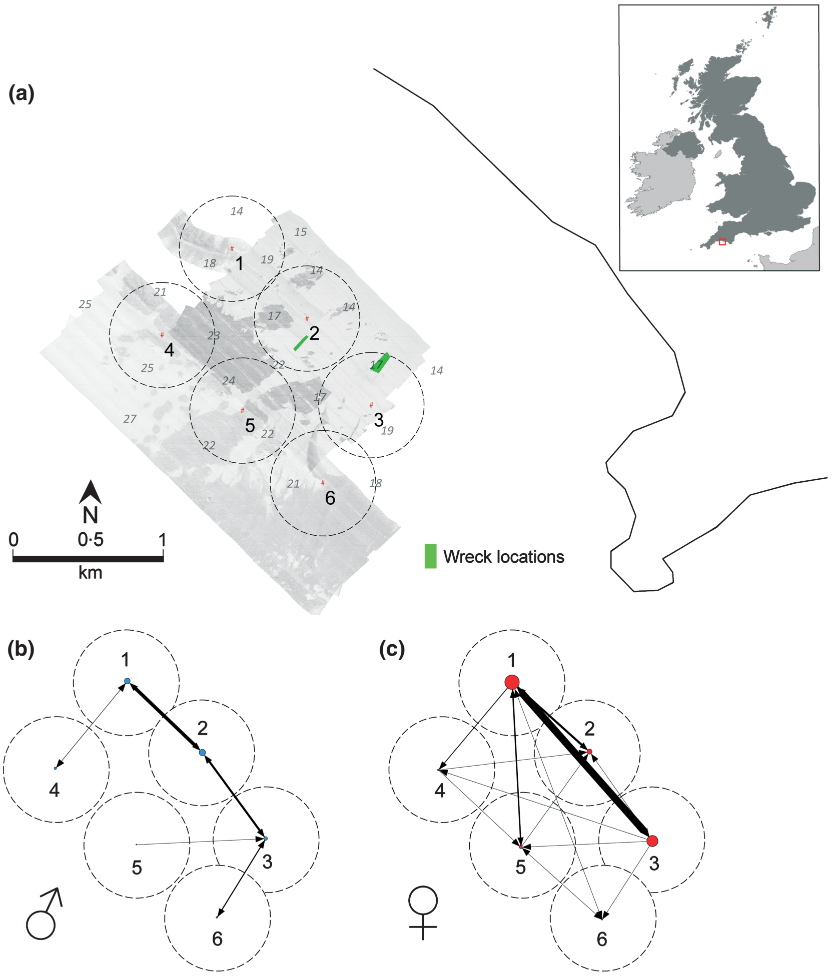

Fig. 1. Spatial layout and topography of an acoustic receiver array (with six datalogging receivers) at Whitsand Bay, Cornwall, UK (black line denotes coastline) (a) in which male (b) and female (c) small-spotted catsharks were tracked during 2010. Networks represent absolute interaction data (total counts) of movements between receiver locations (i.e. greater edge weight shows more frequent interactions). Node size indicates detection frequency. Dotted circles around receivers indicate approximate detection range.

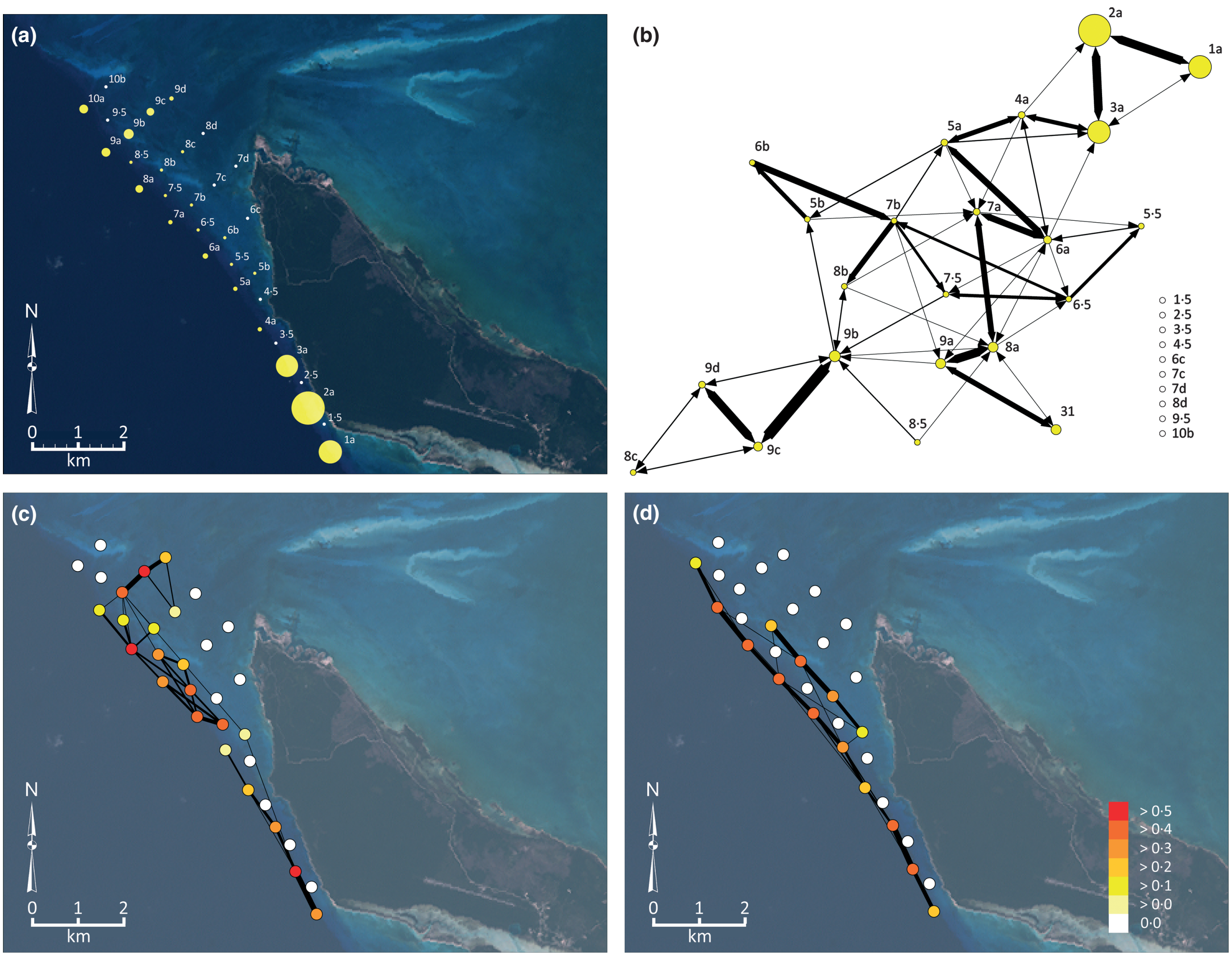

Fig. 2. Spatial layout of acoustic receivers and the detection frequencies (a) of a male Caribbean reef shark tracked within an array situated off the coast of Cape Eleuthera, Bahamas. The relative interaction data (< 1 h filtered), weighted track of this individual is represented without spatial reference using spring embedding and node repulsion (b) and then with spatial reference during the first (c) and last (d) 7 months of the acoustic track to demonstrate changes in space use through time. Node colouration represents degree (k) and ranges between 0·57 (high centrality) and 0·00 (no centrality).

individual. Common node and edge-based metrics are summarised below.

Centrality

Measures of local centrality indicate a nodes' importance directly via its level of connectedness. *Degree* (k_i), for instance, is a local measure of the number of direct links or edges attached to a node, and therefore, *degree centrality* gives an indication of the reachability of a node or location. Degree may be further refined to account for *In-degree* (k_i^{in}) and *Out-degree* (k_i^{out}) to explain entry and exit points or gateways to an area of interest or conservation concern. An area with a high degree centrality, for example, would suggest strong site fidelity by wide-ranging animals. In this instance, animals may return from many different areas but always back to the same location, as described for the home ranges of Galápagos sealions, *Zalophus wollebaeki* for example (Wolf *et al.* 2007).

Betweenness

Betweenness (B_i) offers another local property based on the number of paths that pass through a specific node, from one node to another via the shortest path length. Transient or migratory species for example may divert to a specific habitat, such as a watering hole, *en route* to another location (Wolanski & Gereta 2001). These areas of high betweenness might provide access to a limited resource or be important for the social exchange of information and therefore are likely to promote aggregation (Krause & Ruxton 2002; Jacoby, Croft & Sims 2011). Such localised node metrics may prove beneficial in assessing the relative importance of specific locations to the core movements of site faithful or territorial animals.

Degree distribution

Equally, there are global properties of these movement networks, such as the degree distribution $P(K)$ across all habitat locations, which reveal important structural components within the network. These can be used to model the possible effects of disturbance on the current space use of an animal (see Rhodes *et al.* 2006 for example).

Average path length

Another global property worth considering is the average path length (L) between all nodes. This metric provides a measure of how easily, or indeed likely, an animal moves between locations on average and is useful for comparing networks between individuals or age classes.

Density

Finally, *Edge density* (E) represents the proportion (or percentage) of actual edges present, out of the total number of edges possible in a given network ($E = 1$). This measure is likely to inform analyses of random and non-random space use in animals.

DATA PROCESSING

The large amounts of data produced from biotelemetry techniques can today be explored in spreadsheet or database programs for a variety of statistical analyses. Modern programs offer a range of functionality and algorithms for sorting, sampling and randomising data, and it is relatively straight forward to automate searches or run queries within the data to pick out interactions or movements of different animals between receivers or locations. Spreadsheets or simple text files of interaction data can then be fed directly into one of several programs developed specifically for analysing interaction or association data. In this study, SOCPROG, a MATLAB-based program designed for analysing social structures in animal groups (Whitehead 2009), and UCINET (Borgatti, Everett & Freeman 2002) are used, both of which offer a comprehensive set of network analysis tools (see Data S1, S3 for links to programs and manuals). These programs were used to manipulate the data into full matrices of directed shark movement interactions (Data S1, S4) between receivers within their respective arrays, upon which all further analyses were conducted. Once the data are entered into a program, there are a number of considerations to bear in mind when creating a movement interaction matrix.

Absolute or relative edge weighting

The matrix can either comprise absolute values where weighted edges represent a total count of movements between two nodes or a relative proportion of the number of times a movement is made between node A and node B, divided by the total number of movement edges in the network (see Data S1, S4 for Supporting information). Absolute interaction data (hereafter AID) and relative interaction data (RID) are likely to produce very different movement networks as RID controls for the time spent within the monitored area. However, AID can provide a useful insight into temporal space use in animals. Both RID and AID, each containing directed movements, are used in the following analyses to illustrate the potential uses of count and proportional data for biologically meaningful exploration.

Sampling rate

When an interaction measure relates to a physical movement, we are primarily working with dyadic pairings (two locations and an edge between them), in the form of directed movements between one node and another. Therefore, each sample will simply relate to each movement step made between a pair of locations. Weighted and directed movements are considered in this paper.

Filtering/restriction

It is at this stage in the data preparation that a network/matrix can be easily filtered or restricted using various column headings in the raw data file to consider only certain aspects of the data set. This might include restricting a network to purely immediate movements between locations, by filtering at an edge duration (E_t) of ≤ 1 h or 30 min for example. Additionally, temporal restrictions can be placed on the data to consider specific seasonal movements or alternatively tagged animals might be categorised for quantitative comparison of movement networks between classes.

NETWORK VISUALISATION

Suppose the data now comprise a complete or filtered matrix format, visual exploration of the data is highly recommended. This can be achieved in both SOCPROG and NETDRAW, the latter being a visualisation component of UCINET, by simply loading the file containing the interaction matrix. Furthermore, a list of node-based properties, often referred to as 'attributes', can be entered parallel to the interaction matrix. Node attributes within a movement network, for example, might include habitat type, canopy cover, water depth or number of animals present. Node size and colour can be altered in accordance with these attribute data to illustrate detection frequency, sex or specific geographic variables. Additionally, visual filtering of edge weight (e.g. NETDRAW allows the switching on and off of nodes and edges) in some movement networks might reveal clear distinction between home ranges and exploratory movement behaviour. Network visualisations can then be laid out in a number of different ways based on the structural properties of the network in question (see Results, Fig. 1). Equally useful, however, is the ease with which nodes in these programs can be moved around or referenced to specific locations or environmental features, facilitating the overlay of a network on a map using mapping tools such as GIS. Alternatively, movement networks might not require spatial reference, in which case there are a number of functions such as multidimensional scaling or spring embedding that will aid visual representation of networks based on edge weights and measures of centrality. As such, network analyses offer a vast and intuitive array of visual manipulation techniques which are extremely useful for informing further quantitative analyses.

Model visualisation 1

The AID for the annual movement of two example small-spotted catshark individuals (9114, male) and (9127, female) were drawn up into comparative network visualisations using NETDRAW. Node size was manipulated to reflect the residency times throughout the year based on the frequency of detections at each acoustic monitor (Fig. 1).

Model visualisation 2

The Caribbean reef shark array represents a dynamic system of 32 receivers. The annual space use of a juvenile male reef shark (0·89 m TL) represented as RID is given in Fig. 2 and includes a spring embedded visualisation of the network (Fig. 2b). Here, node colour was manipulated to indicate the core areas or home ranges of this animal during the first and last 7 months of its total track (Fig. 2c,d) using the centrality metric described above (K_i).

STATISTICAL ANALYSES AND NULL MODELLING

Model analysis 1

Calculation of node-based metrics were carried out in UCINET using the 'Network > Centrality > Degree/Betweenness' functions, which are a small subset of an extensive range of analyses designed to calculate different structural properties within network data. Some of these analyses, not presented here, are also likely to prove suitable for analysing interaction data on animal movements.

Node-based metrics of betweenness (B_i) and directed in- and out-degree (k_i) were calculated and compared between the male and female (RID) catshark movements (Fig. 1b,c) to illustrate how replication of movement tracks between different sexes might yield interesting insight into behavioural strategies. Network measures are summarised in Table 2.

Model analysis 2

The inherent nature of network data rules out the use of many traditional statistical analyses because of the violation of the common assumption of independent data points. As such, current statistical approaches largely rely on generating null network populations by randomly permuting various aspects of the data set (Croft *et al.* 2011). The observed network structure is then compared to the distribution of a large number of randomly permuted networks generating a *P* value of significance. Clearly, general biological conclusions about species-specific movements also require multiple individual tracks. Incorporated within the network programs discussed above are a number of other statistical analyses designed to handle non-independent, matrix data. Multiple regression quadratic assignment procedures (MRQAP) are designed for permuting multiple linear regression coefficients of data in square matrix format (Dekker, Krackhardt & Snijders 2007).

Using the double Dekker semi-partialling procedure built in to UCINET, MRQAP was used to determine the environmental variables linked to individual-directed catshark movements within the acoustic array. Environmental data attributed to each of the six acoustic receivers were converted into similarity matrices using the 'Data > Attribute to matrix' function whereby absolute differences between receivers yielded positive values of the distance between the attribute scores of a pair of nodes (or locations). The attributes included were (i) inshore or offshore receiver location, (ii) mean depth of the area within detection range of each receiver, and (iii) a habitat complexity score based upon averaging arbitrary, but consistent, values of rugosity and habitat substrate. These similarity matrices were then regressed against the RID on the annual, direct movements (< 1 h) and space use of the two catsharks throughout 2010.

Model analysis 3

There are several methods for carrying out statistical analyses of network data using null modelling and randomisation of real movement data that can be interpreted intuitively from a movement analysis perspective. Comparing some structural property of the movement network, such as mean density (*D*), centrality (*C*) or path length (*L*) to a suite of random networks is a useful method for determining whether an animal is using an area in a random manner and is likely to prove useful, when combined with the above regression analyses, for testing specific hypotheses (see Table 1). There are, however, a number of ways in which interaction matrices can be permuted to create random networks and these might differ from how some networks of social interaction are randomised (Whitehead, Bejder & Andrea Ottensmeyer 2005; Croft *et al.* 2011). Given that the network nodes are spatially restricted in telemetric movement networks (i.e. direct movements between one pair of nodes is more likely than another because they are nearer one another), it would be unwise to permute either nodes or edges in the random networks without accounting for this spatial bias. Therefore, the random networks need to preserve aspects of the most likely spatial arrangement of the network structure.

To determine whether the model Caribbean reef shark showed random use of the acoustic array, the variance in degree (k_i) for the < 1 h filtered AID was calculated for the observed track disregarding any nodes which were not visited by this individual (see Fig. 2b). This observed value was compared to the frequency distribution of the same test statistic calculated on a series of permuted (randomised networks). To preserve spatial structure in the data, observed individual movement events (n = 624), which contributed to overall edge weighting, were permuted to create replicated (weighted) movements from the raw data. Reassignment of these individual-directed movements during each permutation was constrained to only directional edges between pairs of locations which occurred in the empirical movement network (see Fig. 2). The permutation was done using a Monte Carlo simulation in POPTOOLS (an Microsoft Excel add-in; Hood 2010) creating a distribution of 10 000 random networks against which variance in degree (k_i) of the empirical data was compared to generate a *P* value. This provided a conservative test, based only on the known movements from the observed data, for which to determine whether the frequencies of movement between specific receivers were likely to have occurred under random movement.

Model analysis 4

It is probable that if an animal is demonstrating non-random space use of an area over extended periods of time, then there are attributes associated with those areas that are favourable to that animal during its current phase of development, whether it is protection, food

Table 2. Comparative summary of the node-based metrics betweenness, in-degree and out-degree for the male and female catshark throughout 2010. Male and female sharks made intermittent use of the habitats covered by the acoustic array for 277 and 317 days, respectively

	Male (9114)			Female (9127)		
Receiver	B_i	k_i^{in}	k_i^{out}	B_i	k_i^{in}	k_i^{out}
1	10	0·28 (17)	0·30 (18)	5·5	0·45 (84)	0·47 (86)
2	10	0·40 (24)	0·40 (24)	2	0·10 (19)	0·09 (17)
3	7	0·23 (14)	0·18 (11)	1·5	0·32 (59)	0·35 (65)
4	0	0·02 (1)	0·05 (3)	0	0·03 (6)	0·01 (2)
5	0	0·00 (0)	0·017 (1)	2	0·07 (13)	0·07 (13)
6	0	0·067 (4)	0·05 (3)	0	0·02 (4)	0·01 (2)
Mean	4·50	0·17 (10)	0·17 (10)	1·83	0·17 (31)	0·17 (31)
Network centralisation (%)	19·77			22·40		

Values represent network analyses of RID, relative interaction data with AID, absolute interaction data given in parentheses.

availability or appropriate temperature ranges. It is useful then to attempt to predict how an animals' movement might be impacted by disturbances in habitat at different locations. The disruption of nodes in a movement network (i.e. removal of edges connected to a node) might serve to simulate the impact that habitat destruction is likely to have on an animal's space use and can be used to model the effects of natural and anthropogenic disturbance on animal movements, particularly among animals with high levels of site attached behaviour. Consequently, this technique has the potential to be used for impact assessment and strategic conservation measures by determining how likely an animal or group of animals is to disperse from an area if one or several nodes become unavailable (Rhodes *et al.* 2006). It does not, however, account for the potential for animals to adapt to such disturbances.

The ecological basis for this type of 'knockout' analysis is perhaps most suitable for movement between more isolated and diverse habitat locations, and as such, the relatively small-scale *C. perezi* movement track presented here does not necessarily offer a real-world example where a knockout is expected to have population consequences. It does, however, serve an illustrative purpose, indicating the potential use of this approach to conservation measures whilst also highlighting the importance of considering interconnectivity in telemetry data, over analyses of static individual locations. Using the full, < 1 h filtered, RID interaction network, edge betweenness (B_e) was calculated between nodes in a matrix format and compared before and after the targeted disruption of a node with a characteristically high centrality (9b) and that of a randomly generated node (9a). Matrices of B_e for the targeted and random node-disrupted networks were compared to B_e from the full movement network to determine whether network connectedness was significantly impacted. This was achieved using the 'Network > Compare densities' function in UCINET. Statistical tests were one tailed as we would expect connectedness to reduce to some extent with the removal of any movement edges. Random sub-sampling (20 000 bootstrap samples) of the network provided a way of estimating variance within these tests.

Results

SMALL-SPOTTED CATSHARK DATA SET

Model visualisation and model analysis 1

Comparative descriptive analyses of the example, unreplicated male and female *S. canicula* movement data reveal distinct differences in habitat use and residency times within the area under acoustic observation (Fig. 1b,c). Node size and edge weight, representative of detection frequency and frequency of movement interactions (AID) respectively, suggest that this particular female is utilising the area to a greater extent than the male. Individual node-based metrics support this idea (Table 2), revealing greater overall network centralisation or density (E) in the female movements (female: 22·40%, male: 19·77%), but interestingly, a higher mean betweenness centrality in the male network (female: 1·83, male: 4·50). This value of B for the male shark track appears to be heavily influenced by exclusive and persistent movements along the inshore half of the array. Even at this scale, using model data, there is apparent segregation in space use and movement between locations as evidenced by the stark differences in degree (k) at node 2 (Table 2).

Model analysis 2

Using more quantitative analyses, RID on the directed movements of the male and female catsharks were regressed against the environmental attributes of each of the six receiver stations to address the potential influence of habitat type on shark behaviour. Attribute similarity matrices were entered into a MRQAP which was run against individual movement networks. The regression coefficients individually were non-significant predictors of either movement track. As a model, however, the difference between the edges, in terms of habitat similarity, can be used to predict the strength of the movements made by both the example female ($R^2 = 0{\cdot}181$, $P = 0{\cdot}018$) and the male shark ($R^2 = 0{\cdot}166$, $P = 0{\cdot}036$), perhaps with a suggestion that in these cases, habitat type is a stronger determinant of the female's behavioural strategy.

CARIBBEAN REEF SHARK DATA SET

Model visualisation 2

Using a single shark track from a much larger, more dynamic telemetric data set, a number of other animal movement and space use analyses are explored from a network perspective. The RID for a Caribbean reef shark (*C. perezi*) track has been visually represented in several different ways (Fig. 2) which can be used interchangeably depending upon the type of data exploration required. Figure 2a shows the spatial arrangement of the array with the detection frequencies for each of the receivers overlaid on top. Spring embedding of the network (Fig. 2b) disregards the spatial arrangement of the receivers, but demonstrates the centrality of some locations over others based upon individual node-based metrics. These visualisations are easily manipulated to mirror the exact spatial arrangement of the array (Fig. 2c,d) and further insight is gained by representing receiver attributes across nodes. Visual analyses of the movement patterns of this juvenile shark, between the first and last 7 months of tracking, illustrate interesting changes in space use and home range of this animal throughout time and ontogeny.

Model analysis 3

Null modelling, which preserved the spatial network structure, was used to create a frequency distribution of the variance of k_i across 10 000 random networks. Significance values were produced from direct comparison of the observed data to this frequency distribution. The variance distribution of edge weighting amongst the observed shark movement network was significantly higher than would be expected from random space use ($P < 0{\cdot}001$).

Model analysis 4

The targeted node disruption ($i = 9$b) had the effect of significantly reducing network connectedness [Paired sample *t* test; $t(31) = 1{\cdot}904$, $P = 0{\cdot}044$], whereas assigning a random node for disruption ($i = 9$a), despite being adjacent to the targeted node, appeared not to impact connectedness significantly and, thus, the animal's movement pattern [Paired sample t test; $t(31) = 0{\cdot}675$, $P = 0{\cdot}210$]. Interestingly, both nodes had a similar number of detections suggesting detection frequencies, often relied upon quite heavily in more traditional analyses of telemetry data, are not necessarily indicative of the underlying movement network of an individual. Standard error for this analysis was calculated using 20 000 bootstrap samples and the results are summarised in Table 3.

Discussion

This study examines the novel use of network analyses to understand and interpret animal movement and space use gathered via passive electronic tagging equipment. Traditional analyses of animal biotelemetry data appear largely to ignore the connectivity between areas preferring instead to evaluate presence–absence data in a non-dynamic, static format. Given that biologging and biotelemetry techniques are currently undergoing rapid development (Rutz & Hays 2009), there is a need to address this connectivity in relation to how tagged animals are moving within and between these data collection points (Urban & Keitt 2001). The conversion of data into a movement network/matrix format provides edge-based data to complement static node telemetry time stamps. This allows researchers to capture both the spatial and temporal dynamics associated with animal movement in a holistic analysis of, what are often, very large, complex data sets.

Static array acoustic telemetry data were used to illustrate some of the many approaches offered by network analyses to this type of data. The handling and sorting of raw data, followed by the visual exploration of animal tracks, is discussed and examples given (Figs 1 and 2). A range of statistical analyses which can be conducted on matrix data are also described allowing comparison of individual tracks and environmental variables or null modelling and simulated predictions of movement under different scenarios. These tools offer greater flexibility to identify movement patterns associated with habitat use and furthermore can help to model the space use shifts in the event of critical habitat loss. It is important to emphasise here that we encourage the use of these analyses for studying and comparing behaviours across multiple individuals (i.e. replicating movement tracks) to draw general conclusions about how species are using an area.

Table 3. Statistical comparison of edge betweenness (B_e) as a measure of connectedness between the full Caribbean reef shark relative interaction data (RID) movement track (14 months) and the same track with the simulated random and targeted disruption of one node

Network	Node removed	E	$E–E_{\mathrm{sim}}$	Detections (n)	P*
Full	–	**1·207**	**0·000**	–	–
Random	9a	1·129	0·079	462	0·210
Targeted	9b	0·754	0·454	550	0·044

RID, relative interaction data.

Standard error (SE) estimates were produced from 20 000 bootstrap samples.

*Values indicate one tailed significance tests as mean B_e is expected to reduce with the removal of edges.

SUMMARY OF VISUAL AND STATISTICAL APPROACHES

The unreplicated movements and space use of a benthic catshark (*S. canicula*), a species for which the biology, physiology and ecology have been the subject of wide research (Ellis & Shackley 1997; Sims 2003; Jacoby, Busawon & Sims 2010), were assessed within a deep-water acoustic array. The movement tracks of the two example sharks reveal obvious differences in the temporal space use within a relatively small area of an open coastal bay. MRQAP analyses, at least in the case of these individuals, suggest that habitat features such as complex structures are significant predictors of an individual's movement, a finding which is supported by short-term continuous tracking and underwater surveys of this species (Sims, Nash & Morritt 2001). Further exploration of individual node-based metrics of each of the six receivers (Table 2) reveals high male betweenness, suggesting a roaming strategy in comparison to what is likely a refuging (philopatric) strategy in the female; such behaviour has also been documented from direct observational studies (Sims 2003). These node-based metrics on directed movements might also be used to explore the entry and exit points of an open water array such as this. Replication of male and female movement tracks for this species will no doubt prove interesting for future work.

By contrast, data collected on the comparatively wide-ranging behaviour of a larger species of coastal shark, the Caribbean reef shark (*C. perezi*), revealed that detection frequency can be a deceptive and inaccurate predictor of an animals' underlying movement strategy (i.e. differences in edge betweenness impact between random and targeted node disruption despite similar detection rate, Table 3). This is an important result given the largely static nature of current analyses of electronic tag data. Spring embedding and other network visualisation are explored (Fig. 2), and node manipulation is used to demonstrate differences in home range between the first and second half of the movement track, as this male shark grew and its movement became more orientated towards the coastal shelf. On land, radiotelemetry has also been used to explain sex differences and seasonal changes in home-ranging behaviour in terrestrial mammals such as the Eurasian lynx (*Lynx lynx*; Herfindal *et al.* 2005) or the Sichuan snub-nosed monkey (*Rhinopithecus roxellana*; Li *et al.* 2000); as such, there is now the potential to analyse such data with some of the statistical approaches outlined in this study.

Null modelling of *C. perezi* movements demonstrated that this animal is not using this area in a random manner favouring instead to move between several well-connected locations (receivers). Furthermore the likelihood for dispersal is significantly greater if one of these few, highly interconnected nodes becomes impacted beyond use. This result does not, account for adaptation to disturbance and perhaps needs to be explored in greater detail given the nature of this particular acoustic array and the likelihood of individual node disturbance at such a small scale. It does, however, provide support for the differential influence of specific areas within an animal's home range movements, and the techniques we apply here on movement data could be extended to include assessments of disturbance in other systems. For example, Amstrup & Gardner (1994) use radiotracking of individuals to assess the effects of industrial development and increased hunting on the temporal and spatial distribution of polar bear (*Ursus maritimus*) denning sites. In a more recent study, Rhodes *et al.* (2006) explored the robustness and fragility of bat roosting networks from targeted and random node removal. These types of simulations, as we have shown, can be used to predict the impact of habitat disturbance on individual behaviour and overall community space use by anticipating displacement and susceptibility to dispersal, thus indicating priority habitat for conservation (Rhodes *et al.* 2006).

ANALYSIS ACCESSIBILITY

Currently, there are a variety of programs, outlined above, which can be used to determine the movement of animals from static telemetry data. However, descriptive and quantitative analyses for these data were carried out across different programs using different platforms, which highlights a need to consolidate ideas and analyses for this type of data into a single more holistic program. Current developers of network programs, however, make it particularly easy to download and use their software and manuals (Borgatti, Everett & Freeman 2002; Whitehead 2009; Data S1, S3) providing all the necessary tools needed for the non-specialist to conduct these types of analyses. An appreciation of these analytical approaches might, in addition, be useful during the planning stages of an experiment and could perhaps help to refine the hypotheses leading a telemetry-based study of animal movement.

FUTURE DEVELOPMENTS

The field of movement ecology has seen the development of rapid, convergent approaches to the study of animal movement. Using a wide range of animal-borne electronic tags is one way in which to condense these species-specific movement differences, into simplified presence–absence data, GPS locations and the environmental variables associated with these tracks. Radiotracks of mountain lions (*Felis concolor*), for example, were analysed to determine movement 'signatures' revealing specific types of behaviour when hunting, feeding or mating (Beier, Choate & Barrett 1995). Equally, within the marine environment, smart positioning and temperature logging tags (SPOT tags) are used to track large marine predators that surface relatively frequently (Sims 2010) and have been used to explore niche expansion in salmon sharks (*Lamna ditropis*; Weng *et al.* 2005). Alternatively, small injectable radio frequency ID tags or passive integrated transponder (PIT) tags can be used to track the movements of very small birds, mammals and amphibians. Pyrenean brook salamanders (*Calotriton asper*), for instance, have been successfully tagged with PIT tags to enhance the efficiency of determining individuals at different habitat locations (Cucherousset *et al.* 2008). How animal tracks are interpreted remains open to debate (Cooke 2008); however, the need to visualise better and statistically analyse the spatial and temporal relationship inherent in animal movement remains a key barrier in movement ecology. Incorporating the interconnectivity of habitat locations into such analyses using node and edge-based metrics as here is likely to prove beneficial to the study of movement of many terrestrial and marine organisms. Furthermore, with the burgeoning development of animal social network analysis (Croft, James & Krause 2008), there seems great potential to explore the role of biological spatial networks and movement analyses, in the context of animal social networks.

Conclusion

Exploring the spatial and temporal dynamics of the ways in which animals move is a particular challenge. With availability of 'round-the-clock' tracking of animals using sophisticated biotelemetry technology, we now have the capacity to gain a real insight into the behaviour and stimuli influencing an animal's movement patterns and habitat use. To our mind, the analysis of this data currently requires greater consideration of how temporal dynamics interact with spatial parameters. The use of visually intuitive network representations and statistical analyses which account for the interconnectivity of habitat locations is one way to achieve this goal. We have demonstrated how well-established network analysis techniques can be manipulated to explore electronic tag movement data and have used actual acoustic data to discuss the considerations required to clean and filter the data into a biologically meaningful format. Specific analyses were chosen to indicate the possible ecological, conservation and management benefits of this approach, whilst attempting to highlight the potentially broad appeal of these techniques to different species and types of study.

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Supporting Information

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

Data S1. Developing a deeper understanding of animal movements and spatial dynamics through novel application of network analyses.