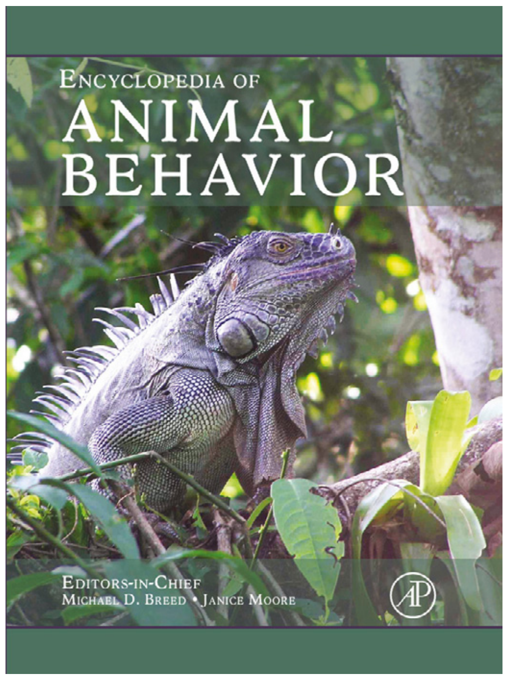

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Spatial Orientation and Time: Methods

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The study of animal space use and movement is a rapidly growing area in animal behavior. New technologies such as GPS (global positioning system) tags allow researchers to obtain unprecedented amounts of information about how animals move through and interact with the landscape, and with each other. Animal movement and spatial behavior is an exciting research area, and one that often bridges the fields of animal behavior, population ecology, and conservation biology. For example, animal behavior researchers may be interested in the influence of mechanistic and ecological factors on the dispersal behavior of individual animals. The data gathered in such a study of dispersal behavior may also apply to questions about population redistribution across the landscape, or the prediction of how endangered species will respond to habitat fragmentation and modification. The number of tools and techniques available for analyzing animal spatial data is rapidly expanding; in this article, we present a subset of the available methods. We assume that the data for each tracked animal consist of (at minimum) a series of X, Y coordinates and associated time stamps; an almost infinite number of additional measurements, such as habitat type, elevation, and distance to water or roads, may be associated with each location.

Data Collection Considerations

Before spatial analyses can be conducted, the data must be collected in a manner appropriate to answer the study question. For this reason, and because it is often costly (in terms of both equipment and researcher time) to conduct a tracking study, we recommend that researchers think carefully about several issues before beginning data collection. There are matters to consider both in tag deployment and in tag reading. Tag deployment issues include which, and how many, animals to tag. Tag reading considerations are how frequently to collect locations, at what time of day to track, how many locations to obtain, and location error. Because studies of spatial behavior are so diverse in terms of both objectives and study species, decisions made about tag deployment and reading will depend greatly upon the specific study.

Which animals to track will depend on the study question: a researcher interested in natal dispersal will track juvenile animals, and a study of sex differences in home range areas will require tracking both male and female adults. The number of animals that can be tracked is often restricted by financial concerns, but despite financial constraints, one must ensure that a large enough sample size will be obtained to adequately test hypotheses. Ad hoc power analysis may be used to determine the required sample size.

Data collection frequency will depend on both tag constraints and the question of interest. Small tags (for small animals) often have limited battery life, requiring that locations be collected frequently over a relatively short period of time. In addition, obtaining detailed movement paths requires a high frequency of data collection, and the timing of data collection will depend on the movement speed of the study animal. The time of day for data collection will depend upon the goal of the study – if it is to characterize the inclusive space use of an animal, data must be collected at all hours of the day and night. However, many studies require data collection only during the animal's active period (i.e., during the day for diurnal animals or at night for nocturnal creatures). How many locations to collect per individual will also depend upon the goals of the study; for example, when analyzing home ranges of resident animals, a good rule of thumb is that at least 30–50 locations should be collected per individual. Finally, researchers should consider and measure location error. Location error may be due to a variety of factors, including the distortion of VHF radio signals due to 'signal bounce' off physical obstacles (such as hills) and errors in GPS locations when GPS tags are located in densely vegetated areas. If the error is large relative to the size of the study area or the animal movements, the data collected may be of limited use.

Categories of Spatial Analyses

We address two primary types of analyses in this article: (1) space use by resident animals (home ranges) and (2) the analysis of movement paths. The spatial behavior of resident and nonresident animals may be quite different from one another and will often require different methods of data collection and analysis. For example, studies of the spatial behavior of resident animals often focus on delineating and quantifying the home range area (the area typically used by an animal in its daily activities) or the territory size (the area defended by an animal). However, the home range concept does not apply to nonresident

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animals – in fact, the space used by a migrating animal may change on a daily basis. It is important to carefully consider the objectives (i.e., describe home ranges of adults, or follow the movement paths of dispersers) of a study of spatial behavior before data collection begins, to ensure that the study design will result in data appropriate for the analysis method.

Analysis of Space Use by Resident Animals

Many methods, consisting primarily of home range estimators, are available to describe space use by resident animals. Because of the large number of home range estimators, which are highly variable in their data requirements, ease of use, and suitability, we focus our discussion here on the two most widely used methods: the minimum convex polygon (MCP) and the kernel density estimator (KDE). MCPs and KDEs share some assumptions about the manner in which data are collected, the most important of which is the assumption of temporal independence of locations. For many years, achieving a lack of temporal autocorrelation between the locations of successive points was considered a primary goal of data collection for home range studies. The focus on temporal independence was due to the fact that in addition to violating the assumption of independence of data points, temporally autocorrelated points also yield less information about space use than do independent points. More recently, it has been realized that complete temporal independence is not necessary for most studies, but it is still true that data points should be collected across the animal's active period, with a reasonable amount of time between locations. To illustrate why the temporal spacing of data points is recommended, consider that a researcher will obtain much more information about the activity of a diurnal animal if ten locations are collected throughout the daylight hours than if all the ten locations are recorded between 3 pm and 4 pm. Home range analysis methods can be implemented in a variety of computer programs, and the most commonly used programs by researchers in animal behavior and wildlife ecology are ArcView 3.x (using the Animal Movement Extension), RANGES, and CALHOME, although other programs, including ArcGIS, GRASS, and MapInfo are also used.

Minimum convex polygon

The oldest, and perhaps the most widely used, home range estimator is the MCP. The MCP is calculated by connecting the outermost points at which an animal was located, which results in a two-dimensional polygon representing the home range (Figure 1(a)). In practice, researchers often discard 5% of point locations when calculating the home range, which results in a 95% MCP (Figure 1(b)). The rationale behind this approach is that discarding 5% of locations should eliminate outliers. However, the 5% figure is arbitrary, and researchers may calculate MCPs, using any percentage of the available data. For example, 50% MCPs may be used to represent 'core areas,' and 100% MCPs may be used by those who do not want to miss any space used by an animal (but note that 100% MCPs may include area that is not used by the animal at all; see Figure 1(a)). MCPs were developed before the widespread availability of computers and are thus computationally quite simple – a researcher may even physically plot locations on a map and draw the borders of the home range by hand, but most now use computer programs that quickly plot locations and calculate home range areas.

Because of the intuitive nature of the MCP, its ease of calculation, and widespread historical use, this method is still employed by many researchers. However, there are quite a few drawbacks to the MCP. Technically, MCPs may be drawn with as few as three unique locations, but recent simulation studies have suggested that as many as 100–300 locations may be required to achieve an accurate representation of the home range, using MCP estimators. Because the MCP method results in a two-dimensional polygon with no indication of the relative use of different areas within the home range, too much weight may be assigned to points on the edge of the range. That is, the presence of a few locations occurring far from the bulk of the points may result in a substantially larger range than would otherwise be obtained (compare Figure 1(a) and 1(b)). Finally, MCPs do not generate estimates of centers of activity. Some researchers now suggest that home range studies report the results of both the MCP and at least one additional home range estimator, the rationale being that the MCP is comparable among studies and allows comparison with results from the older literature. However, other researchers disagree, and suggest that the disadvantages of the MCP method are so great that this method should not be used at all. We leave this decision up to the researcher.

Kernel density estimators

The use of KDEs has become quite widespread in the past decade. Unlike MCPs, KDEs allow researchers to determine the animal's relative use of different areas of the home range, and allow for the determination of multiple centers of activity. KDEs estimate the intensity (or probability) of use at particular locations (the utilization distribution, or UD). KDE home ranges may be represented in three dimensions as map contours, with higher 'peaks' in areas with a greater probability of use (Figure 2). Software packages generate KDEs by evaluating a probability density function: a mathematical formula that incorporates a kernel function, the number of point locations, the smoothing parameter, and the coordinates at which the animal was located. The probability density function estimates the animal's probability of using a particular point on the landscape. Researchers often implement KDEs with the most-intensely used 50% of locations to estimate core areas, and 95% KDEs

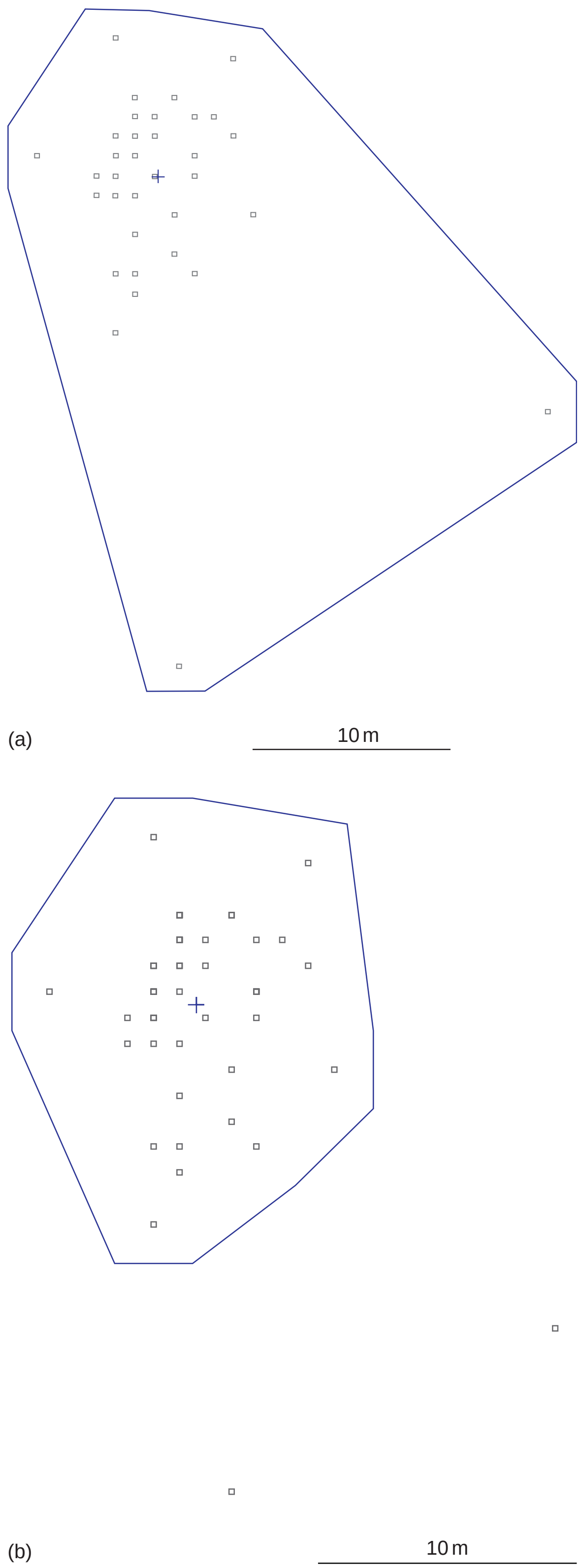

Figure 1 (a) 100% MCP home range of a male prairie vole. Note the large influence of the two points at the bottom of the range. The area of this home range is 625.5 m^2. (b) 95% MCP home range, generated from the same data shown in (a). Without the inclusion of the two distant points, the area of this home range is 194.5 m^2.

to estimate the larger home range area. A critical issue when calculating KDEs is the choice of smoothing parameter *h* (also called bandwidth; see Figure 2(b)–2(d)). If the value chosen for *h* is too small, a fragmented home range may be generated (Figure 2(b)). Alternatively, if *h* is too large, an overly smoothed single peak may be generated (Figure 2(d)). The choice of *h* is important because home range size estimates derived from fragmented KDEs may underestimate the home range area, while estimates from overly smoothed KDEs may overestimate the home range size and habitat use. The two major categorizations of smoothing parameter are fixed and adaptive. Fixed kernels utilize the same smoothing parameter across the entire area, while adaptive kernels use a different bandwidth for each location. KDEs are currently the standard methodology in home range estimation, and have relatively few disadvantages. The primary weakness of the method is the large influence that the choice of smoothing parameter can have on home range estimates.

Mechanistic home ranges

Both the MCP and KDE home range estimators are primarily descriptors of space use. Unfortunately, such statistical home range estimates have little or no predictive value. In contrast, the recently developed mechanistic home range analysis methods reviewed by Moorcroft and Lewis allow researchers to use correlated random walk movement models to integrate empirical field studies and predictive theory about animal space use. For example, researchers may make predictions about how space use will change over time, given changes in predator presence or food availability. However, this approach is still very new, and implementing mechanistic home range methods is considerably more involved than utilizing existing statistical home range methods.

Social behavior

In addition to determining the size of an area that individuals use, home range analyses may also be used to investigate social behavior. Researchers often use home range overlap to quantify the strength of association between two animals. For example, in Figure 3, a female prairie vole's (animal A) home range is overlapped by the home ranges of two males (animals B and C). The relative strength of A's association with B versus C may be quantified by comparing the percentage of A's home range that is overlapped by the home range of animal B with the percentage of A's home range that is overlapped by animal C's home range. Many home range analysis programs will output pair-wise home range overlap for any two animals in a data set. It is important to consider the directionality of home range overlap measures – because any two home ranges are likely to contain different amounts of area, the percent overlap of home range A on home range B will often be different from the overlap of B on A (Figure 3).

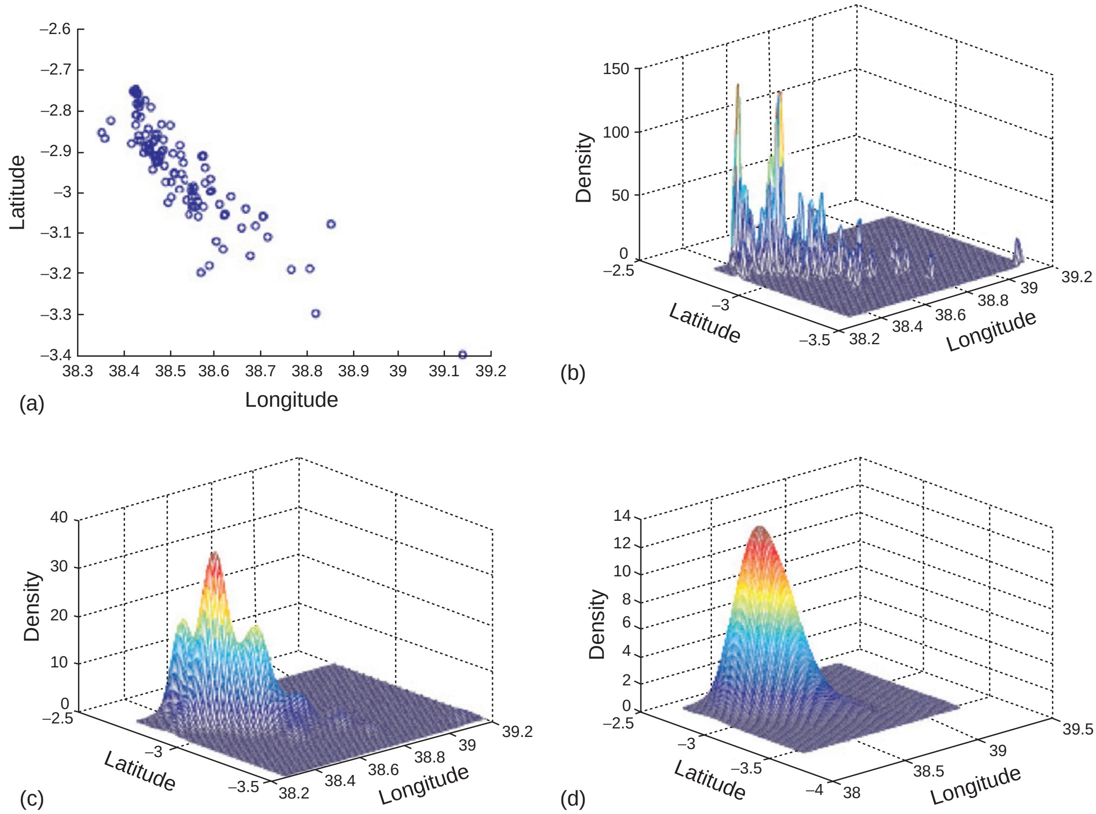

Figure 2 Quantifying the home range of an African elephant using a KDE. (a) The spatial locations of the animal in two dimensions. (b) KDE with $h = 0.008$. (c) KDE with $h = 0.03$. (d) KDE with $h = 0.08$. The figure was created using Matlab. Details of the functions used can be found in Martinez W and Martinez A (2002) *Computational Statistics Handbook with MATLAB*. Boca Raton, FL: Chapman & Hall/CRC.

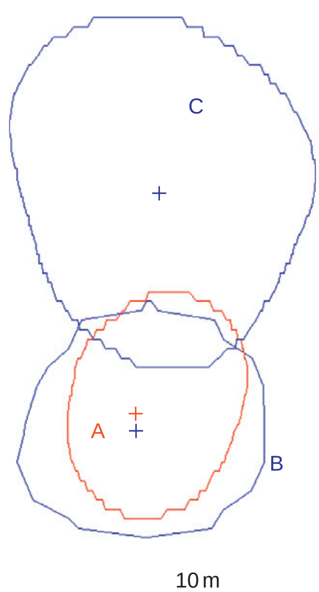

Figure 3 An example of two male prairie vole home ranges (B and C) overlapping a single female's range (A). Male B's home range overlaps 93.87% of female A's, while male C's home range overlaps just 24.80% of female A's. Note that the overlap value depends upon which animal is the focal: overlap of B on A = 93.87%, but the overlap of A on B is just 65.64% (because B's home range is larger than A's).

It is also relatively simple to determine the number of conspecifics with which an animal shares space, by counting the number of home ranges (or core areas) that coincide. If the objective of a study is to calculate a mean value of home range overlap (e.g., mean percent overlap of male home ranges on female home ranges) for an entire population, researchers must be careful to simultaneously track all animals of interest, because untracked individuals will bias the results.

Habitat use

Home range analysis is also useful for describing habitat use. By overlaying a home range on a habitat map of the study area, researchers can determine whether an animal uses particular habitat types more or less than would be expected based on the availability of those habitat types. Such an analysis of habitat use requires some type of geographic information system (GIS) habitat database. Digitized habitat maps may already be available for a study area; if not, researchers may digitize existing maps, or carry out habitat surveys. Alternatively, many sources now provide satellite images that can be used as the basis for creating digital maps. Two examples are Landsat and Satellite Probatoire d'Observation de la Terre (SPOT), which provide satellite images of most of the world. Very fine information on the height of habitat features at a scale of 15 cm can be obtained from light detection and ranging (LIDAR) surveys. LIDAR data provide information on topography, canopy heights, and biomass measurements. A researcher may also be interested in examining the effect of temporal changes in weather, climate, vegetation, or ocean productivity on animals' spatial behavior. To examine these questions, measures such as normalized difference vegetation index (NDVI) that quantify vegetation productivity may be obtained from sources such as NASA, SPOT, and NOAA (National Oceanic and Atmospheric Administration).

The choice of the appropriate level (i.e., individual, population, landscape) at which to evaluate habitat use and availability is critical to any habitat use study. For example, a researcher might compare the habitat used by an individual animal at a certain time to the habitat available within its home range, or the habitat composition of the entire home range to the habitat available across the landscape. Before analyzing a use–availability data set, researchers must think carefully about how much and what type of habitat is available to an animal. Researchers may compare habitat use and availability, using a variety of statistical approaches, including traditional statistical methods, such as χ^2 tests and logistic regression, and more complex analysis methods such as compositional analysis, which applies MANOVA (multivariate analysis of variance) to compare use and availability. Compositional analysis is now very widely used and may be conducted in various programs, including the adehabitat Package in R, and the Compos Analysis add-in for RANGES.

Analysis of Movement Paths

Researchers are often interested in analyzing the movement paths of individuals, rather than stable home ranges. The movement path analysis methods presented here are particularly useful for quantifying the movements of nonresident animals (i.e., dispersers, migrants, and experimentally displaced individuals), but some may also be applied to resident animals (i.e., those with stable home ranges). Unlike home range analysis, wherein a few techniques are widely accepted by most researchers, there are fewer 'rules of thumb' for choosing from the many options available for the analysis of movement paths. Here we review some broadly useful movement path analysis methods, including measures of path length, movement speed, directionality, and path tortuosity.

As we have already mentioned, the different objectives of researchers studying the movements of resident and nonresident animals may necessitate different tracking protocols. For example, most home range analyses assume that consecutive locations are temporally independent (see above). However, some degree of temporal autocorrelation may be desirable in a study of animal movements, where the objective is to obtain as complete a representation of the movement path as possible. Temporal independence between successive points may yield undersampled movement paths. The appropriate temporal resolution must be considered before data collection begins – animals must be located often enough that a reasonable depiction of the path is obtained, without oversampling. In addition, certain sampling methods (e.g., radio tracking and image analysis based tracking of lab animals) may contain sampling errors and noise. Smoothing techniques, such as moving windows, that spatially average a subset of locations for each time step can be used for creating more accurate movement paths.

Movement distance and speed

It is relatively easy to calculate simple measures such as path length and movement speed from spatial data. Path length (the total, or cumulative, linear distance traveled) is calculated by adding together the lengths of all segments generating a path. Logically, the longer the period over which locations are obtained, the longer the observed path length will be. Thus, path data must be standardized before making comparisons between animals. Data may be standardized by truncating all paths to include only as many observations as are contained in the shortest path (i.e., if the shortest path consists of four moves, use only the first four moves of all paths in the data set). However, truncating movement data is often not feasible because it would lead the researcher to discard much of the collected data – there are almost always some individuals for which very few observations are available. This problem may arise when individuals quickly lose their tags, or suffer predation. A more reasonable way to standardize path length data is to divide the path length by the amount of time over which the individual was observed; this would result in the distance moved per unit time, or speed, which may be compared among animals. Many of the previously mentioned software packages calculate path length and movement speed at the click of a button.

Directionality of movement

Researchers are often interested in describing the directionality of animal movement; for example, one may wish to determine whether a dispersing animal is consistently heading in a particular direction. Because directional headings are measured in degrees, which are distributed around the circular compass, traditional statistical tests are not appropriate for these data. To illustrate this problem, consider the difference in direction between compass bearings of 2° and 350°. Simple subtraction yields a difference of 348° (or −348°), when in fact these two bearings differ by just 12°. The difference between calculations arises because of the circular distribution of compass bearings – there are 360° around the compass, which means that there is a difference of a single degree between bearings of 359° and 0° (due north). Circular statistics are quite useful in the analysis of movement data, but many introductory statistics books and popular general statistics programs do not include information about circular tests. Circular statistics may be implemented in the Animal Movements Extension for ArcView 3.x and the circular statistics program ORIANA 2. Batschelet gives additional information about circular statistics may be found.

Path complexity

The complexity of a movement path may be quantified as path tortuosity, which incorporates the length of moves and the turning angles between subsequent moves to generate a measure of how complex, or tortuous, a path is. More tortuous paths are often assumed to correlate with more thorough search of an area, with relatively straight paths assumed to occur when animals move quickly through an area. Path tortuosity may be measured in different ways, but is frequently quantified as fractal dimension (D). Fractal D ranges from 1 to 2; a perfectly straight line has $D = 1$, while a path that is so complex that it turns back on itself repeatedly to completely cover a plane has $D = 2$. There has been a great deal of discussion on the validity of using fractals to describe animal movement, with much of the controversy hinging upon whether animal movements are scale-invariant. Some researchers argue that because true fractals are scale-invariant (i.e., D is the same, regardless of the spatial scale at which the path is measured), while most animal movements are not scale-invariant, it is inappropriate to apply fractal analysis to animal movement data. Others argue that D is useful for

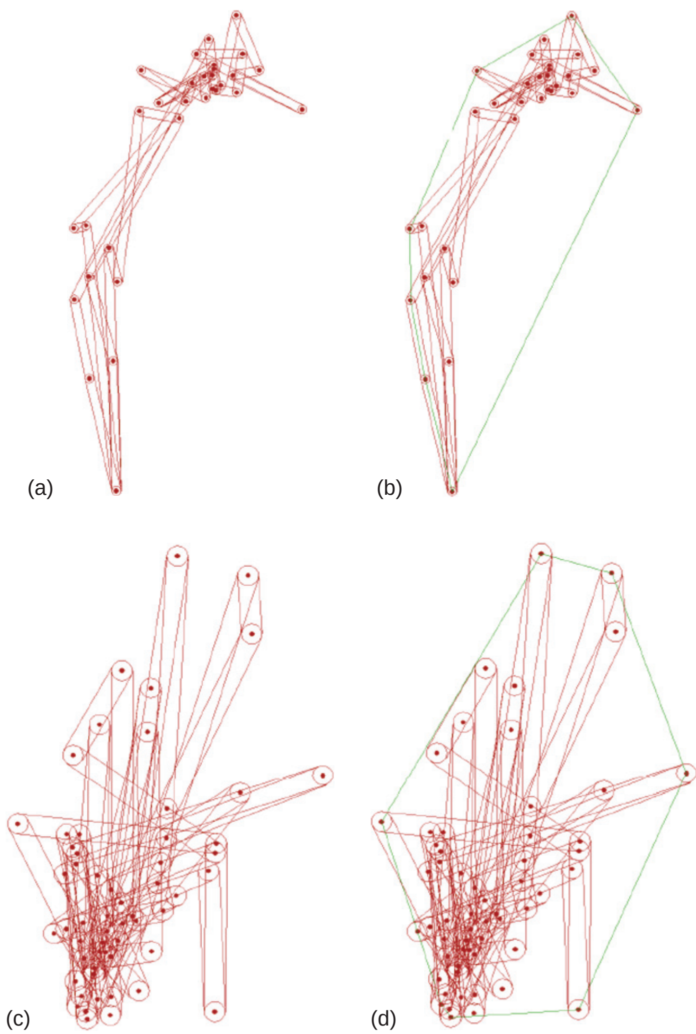

Figure 4 Dispersal range analysis of the dispersal paths of two juvenile brush mice. (a, b) Show an animal that explored a large area fairly superficially, while (c, d) show an animal that explored a smaller area rather thoroughly. (a) Individual locations are linked to form a path of total length = 1297 m. Incorporating an assessment radius (AR) of 2 m results in an assessment corridor (AC) area of 3300 m^2. (b) The MCP (outline) of all locations is 10 700 m^2, resulting in an AC/MCP ratio of 0.31. (c) Individual locations are linked to form a path of total length = 1644 m. Incorporating an AR of 2 m results in an AC area of 2129 m^2. (d) The MCP (outline) of all locations is 3324 m^2, resulting in an AC/MCP ratio of 0.64.

comparing movement paths measured on the same spatial scale. FRACTAL is a freely available computer program that calculates *D*, along with several other measures of path complexity.

Dispersal range analysis

Home range methods offer a relatively standardized way to quantify area use by resident animals. But how should researchers quantify the area used (or perhaps more appropriately, searched) by nonresident animals? Some researchers have applied home range methods to analyze data on the movements of dispersing animals, but several problems with this approach have been pointed out. For example, many home range analyses begin by eliminating outliers (i.e., 95% MCPs); however, those 'outliers' are often the most important and interesting data in dispersal studies. Erik and Veronica Doerr developed a suite of variables that can be used to quantify search behavior from tracking data. Here we present two of these variables: search area and search thoroughness. The calculation of search area is based upon the assumption that as animals move through an area, they are able to assess the surrounding habitat within a certain distance, dictated by their perceptual range (the assessment radius (AR)). If both the movement path and the width of the AR are known, these data can be combined to generate an assessment corridor (AC) of width = 2(AR) surrounding the movement path. The search area can then be estimated as the area contained within the AC (**Figure 4(a)** and **4(c)**). Search thoroughness may be quantified as fractal *D*, or as the ratio of the AC area to the area of the MCP containing all of an animal's locations (AC/MCP; **Figure 4(b)** and **4(d)**). Low AC/MCP values indicate low thoroughness, and ratios approaching 1 indicate very thorough search. DRAP, or Dispersal Range Analysis Program, is a freely available program that calculates these and other measures of dispersal behavior.

Theoretical Models of Individual Movement Behavior

Much effort has been devoted to the theoretical modeling of animal movements, primarily from an ecological (rather than a behavioral) perspective. The modeling literature is vast, and much of it concentrates on questions of population redistribution, rather than on the mechanisms influencing individual movement behavior. An awareness of recent advances in the field of modeling animal movements is beneficial but somewhat beyond the scope of the current article. For an excellent introduction to models of movement behavior, we direct the reader to Turchin's book.

See also: Remote-Sensing of Behavior.

Further Reading

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Relevant Websites

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http://www.absc.usgs.gov/glba/gistools/animal_mvmt.htm – Animal Movement ArcView Extension.

http://www.esri.com/ – ESRI (GIS software).

http://nsac.ca/envsci/staff/vnams/Fractal.htm – FRACTAL (free software to analyze movement paths).

http://grass.ibiblio.org/index.php – GRASS GIS (free GIS software).

http://landsat.gsfc.nasa.gov/ – NASA Landsat Program.

http://www.noaa.gov/ – National Oceanic and Atmospheric Administration (NOAA).

http://www.movebank.org/ – MOVEBANK (online repository of movement data).

http://kovcomp.co.uk/oriana/index.html – ORIANA (circular statistics software).

http://www.r-project.org/ – The R Project for Statistical Computing.

http://www.spatialecology.com/index.php – Spatial Ecology software.

http://www.spot.com/ – SPOT IMAGE.