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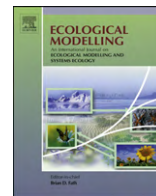
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Short communication

A new index for measuring perpendicularity of animal movements in relation to patch boundaries

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ABSTRACT

We introduce a new index for measuring perpendicularity of animal movements with respect to a boundary (e.g., a habitat patch edge), and provide a computer algorithm for its calculation. Our index, η , improves on an approach that measures perpendicularity with respect to a fixed boundary direction. This is because η accounts for moment-to-moment trajectories relative to nearest-neighbor boundary attributes at the scale of an animal's movement. Our algorithm `prp` calculates η efficiently and accurately with both synthetic data and large telemetry datasets. In addition, we have included routines in `prp` which account for scenarios inherently problematic to perpendicularity estimators.

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1. Introduction

The modelling of individual animal movements is a topic of increasing concern to ecologists (Brillinger et al., 2004; Preisler et al., 2004; Dalziel et al., 2008; Fryxell et al., 2008; Nathan et al., 2008; Morales et al., 2010; Smouse et al., 2010). Of particular interest is the movement of animals with respect to patch characteristics such as area, heterogeneity, and boundary complexity (Forman, 1995). To address this, a number of useful indices have been developed including first passage time (Johnson et al., 1992), residency time (Anderson et al., 2008), state-space models (Forester et al., 2007), and measures of movement complexity (Barraquand and Benhamou, 2008). Notably absent, however, is an effective index of perpendicularity with regard to a patch boundary. We define perpendicularity here as the orthogonality (*sensu* geometry) of the angle between a vector describing direction of animal travel and a line representing the edge of a feature of interest. Perpendicularity is important because it describes the propensity of an animal to move along patch edges (low perpendicularity) or to cross back and forth across boundaries (high perpendicularity). Such patterns may provide practical guidance for management (e.g., reducing wildlife–vehicle collisions) as well as theoretical insight into both population distributional properties (Charnov, 1976), and animal reactions to topographic and patch characteristics at different spa-

tial scales (Bowyer et al., 2001; Kie et al., 2002; Anderson et al., 2005).

Kie et al. (2005) examined movements by North American elk (*Cervus elaphus*) with respect to riverine systems by measuring perpendicularity in relation to a single dominant drainage direction. In establishing a new perpendicularity index we improve on this approach by quantifying moment-by-moment perpendicularity with respect to associated moment-by-moment patch boundary characteristics. We note that the raw change in average distance to a patch boundary is inadequate as an index of perpendicularity. Such an assessment is strongly dependent on species size, travel velocity, or first passage time, and thus only allows intraspecific comparisons. In instances of extreme sexual dimorphism (with respect to movement) this approach only allows intrasexual-intraspecific comparisons. We seek to create an index, insensitive to scale of movement, which allows general (e.g., interspecific) comparisons. For example, it has been observed that beaver (*Castor canadensis*) generally approach a body of water perpendicularly, relative to moose (*Alces alces*) (A.R. Rogers, personal communication). Our index allows quantification of such patterns.

2. Methods

To explain our approach we present a hypothetical landscape showing the movement of an organism (vector C) with respect to an ecologically important boundary, e.g., patch edge, river location, escarpment edge, etc. (Fig. 1). Our index η can be used to measure moment-by-moment animal movement relative to boundary

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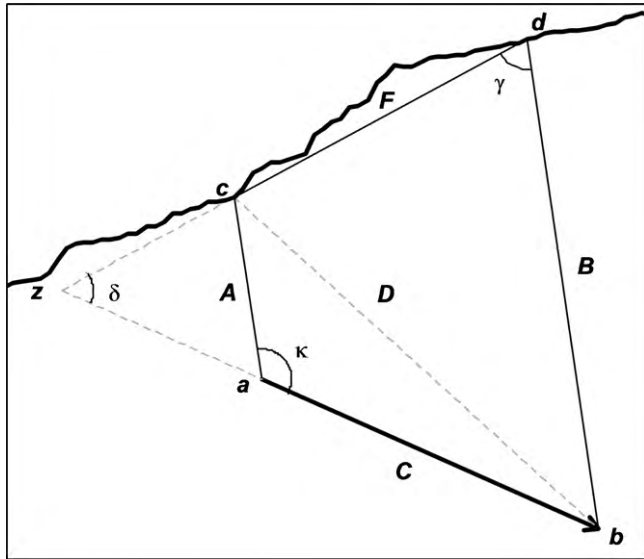


Fig. 1. Illustration of animal movement measurements with respect to an ecologically important boundary (jagged, wide line). The length of the lines A and B represent the closest distances to the patch edge from the start and endpoint of the animal movement vector, C. Points are lower case, lines are capitalized, and angles are indicated with Greek letters.

attributes. This is accomplished by first, establishing the line F between the Euclidean nearest-neighbor points (c and d) on the boundary with respect to the start and endpoints of the trajectory vector, C (Fig. 1), second, finding the angle δ between F and the trajectory vector C, and third, utilizing this angle in calculations for η (Eq. (2)).

To find the point of intersection of \vec{ab} and \vec{cd} (i.e., z in Fig. 1) we use the rules for solving systems of linear equations. Specifically, we find the x-coordinate of z by taking the linear equations describing F and C equal to each other. We then insert this x-coordinate into either equation to find the y-coordinate for z. We then calculate the Euclidean distances:

$$S = \sqrt{(x_b - x_z)^2 + (y_b - y_z)^2} \text{ and } T = \sqrt{(x_d - x_z)^2 + (y_d - y_z)^2},$$

where the Cartesian coordinates of z are (x_z, y_z) . From the law of cosines, it follows that:

$$\delta = a \cos \left[\frac{S^2 + T^2 - B^2}{2SC} \right]. \quad (1)$$

We propose the following general index:

$$\eta = \begin{cases} \delta \leq 90^\circ; & \frac{\delta}{90} \\ 90 < \delta \leq 135^\circ; & \frac{[90 - (\delta - 90)]}{90} \\ 135 < \delta \leq 180^\circ; & \frac{\delta - 90}{90} \end{cases}. \quad (2)$$

To aid in interpretability, our index converts angular azimuth measures to a 0–1 index, where an outcome of 0 indicates movement that is perfectly parallel to the boundary, and an outcome of 1 indicates perfect perpendicularity.

It may occasionally be useful to describe whether an animal moves more consistently towards or away from a boundary. For these calculations we recommend the following adjustment to Eq. (2):

$$\eta_{\text{sign}} = \begin{cases} (A - B) < 0; & -\eta \\ (A - B) \geq 0; & \eta \end{cases}. \quad (3)$$

Here the index will become negative if movement is away from a boundary edge.

2.1. The R-function `prp`

Our function `prp` calculates η and provides a number of other useful movement summaries. The function has been incorporated into the R-package `asbio` “applied statistics for biologists” <http://CRAN.R-project.org/package=asbio> (Aho, 2010), and can be run using R free statistical software <http://www.r-project.org/>. Supplemental guidance and examples are included in `asbio` help files. To access this information a user can type `?prp` in the R-console after installing `asbio` and loading the package for an R work session. The function `prp` has eight arguments, although only five are required. For clarity R-objects and arguments are given sans serif font.

```
prp<-function(Time, S.X, S.Y, N.X, N.Y, habitat=
NULL, near.angle=NULL, F.0.NA=TRUE)
```

The arguments: `Time`, `S.X`, `S.Y`, `N.X`, and `N.Y` are required. `Time` is a vector containing the times that the location of an animal is recorded. Any time-series format including a simple numerical sequence can be used. `S.X` and `S.Y` are Cartesian coordinate vectors (e.g., UTM) containing the X and Y coordinates for animal locations at each time interval. `N.X` and `N.Y` are the X and Y locations (e.g., UTM) for the nearest-neighbor points on a boundary. Nearest-neighbor coordinates can be obtained from the function `near.bound` in library `asbio` or from ARCGIS ArcToolbox Near output.

The three optional arguments allow different summaries of time-series locations with respect to patch boundaries and provide adjustments to situations that can potentially confuse `prp`. The argument `habitat` is an optional character vector that specifies which patch an animal is within at a particular time frame. The argument `near.angle` is a numeric vector containing the angle of azimuth to the nearest point on the boundary with respect to a four quadrant system (i.e., NE = 0–90°, NW is >90° and ≤180°, SE is <0° and ≥–90°, and SW is >–90° and ≤–180°). This output can be obtained from the function `bound.angle` in `asbio` or from ARCGIS ArcToolbox Near analysis. The information from `near.angle` is used along with `habitat` to determine if the boundary an animal is closest to changes (see Section 4). The argument `F.0.NA` is a logical statement (`TRUE` or `FALSE`) specifying whether or not a time interval in which $F=0$ should be made NA (see Section 4).

3. Results

We demonstrate the function `prp` using a computer-generated time series with ten observations (Fig. 2), and a high resolution (10-min interval) 2008 dataset containing telemetry data for a single mule deer (*Odocoileus hemionus*) in the Starkey Experimental Forest (U.S. Forest Service) in Northeastern Oregon. The mule deer dataset is available in `asbio` under the name `deer.296`.

Perpendicularity analysis results for the computer-generated time series are shown in Fig. 2. To analyze the Starkey mule deer data we first loaded `asbio` and brought in the dataframe `deer.296`. The code below assumes that the package `asbio` has previously been installed for workstation use.

```
library(asbio)
data(deer.296)
names(deer.296)
[1] "Time"      "X"         "Y"         "NEAR_X"    "NEAR_Y"
[6] "Hab_Type"  "NEAR_ANGLE"
```

We then ran `prp`.

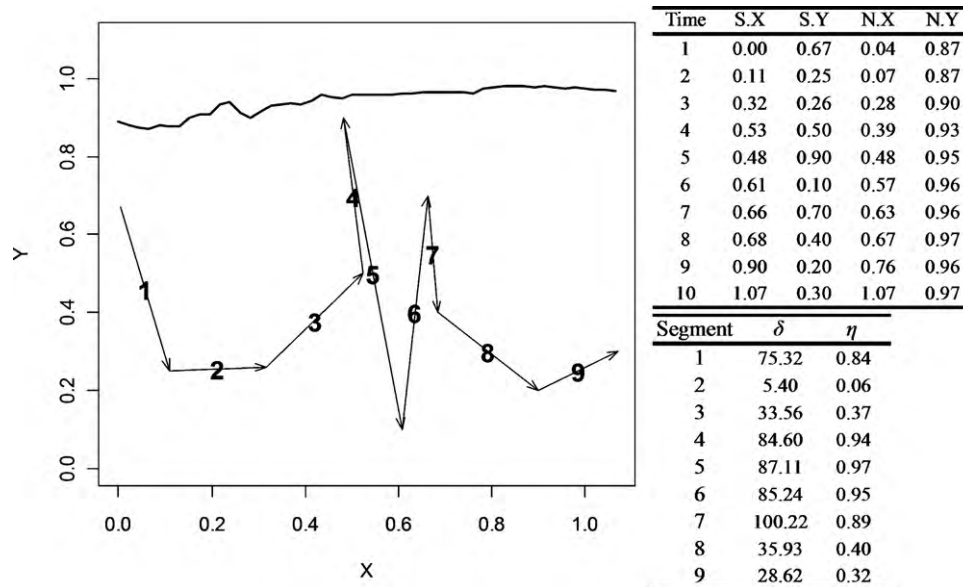


Fig. 2. A simulated telemetry time series of $n = 10$ locations resulting in 9 movement vectors (arrows). Perpendicularity is measured with respect to the boundary in the top of the figure.

```
with(deer.296, prp(Time, X, Y, NEAR_X, NEAR_Y, Hab.Type, NEAR_ANGLE))

Perpendicularity index

Binomial estimates for crossing probability
  Binomial estimates Wilson estimates
p.hat                                001156878275
S.p.hat                             000049986516

Perpendicularity summary
Mean.Eta                             SE.Eta
0.4175078                          0542290317
```

4. Discussion

By trigonometric definition δ , the basis for our index η , is the angle between C (the movement vector) and F (the general linear direction of patch edge relative to the movement fractal). Extensive testing with computer-generated datasets with known values of δ indicates that `prp` calculates this angle correctly. This is visually evident in the output of the perpendicularity analysis of the synthetic time series shown in Fig. 2. Visual confirmation is not possible for the complete mule deer dataset which contains 5422 time intervals, but `prp` output for this and 11 other large telemetry datasets indicate equally effective results. We note that system time for analysis of around 5500 time intervals is about 17.4 s for a Pentium 4 processor with 1 GB of RAM. Run time could be decreased still further by calling the language C or Fortran for looping. This change will be implemented for later versions of the function.

The print output from `prp` is an R-object of class `prp.index`. For compactness this includes only the mean and $S_{\bar{x}}$ for the $n - 1$ interval estimates of η . If `habitat` and `near.angle` are specified (as they were for the mule deer data analysis), then estimates of the probability of border crossings, \hat{p} , and its standard error, $S_{\hat{p}}$, are also returned. Both conventional and Wilson binomial point estimates (Wilson, 1927) for p and σ_p are provided (see Section 3). The latter are recommended when calculating confidence intervals for the binomial parameter p (Agresti and Coull, 1998). Additional hidden but accessible output includes the lengths of lines A , B , C , D , angles γ , κ , and δ , and the index η , for each time interval.

4.1. Problematic scenarios

There are a number of potential movement situations that may confuse `prp`, or for that matter any perpendicularity algorithm. As a result we suggest that researchers examine animal movement data before running `prp` to identify problem scenarios in advance. This step will help in setting arguments for the `prp`.

Of particular biological interest is a situation where $F = 0$ (i.e., the distance between the start and end of the line indicating the patch edge is apparently zero; see Fig. 1). This may occur for at least four reasons. First, the boundary coordinates may have a very coarse resolution. This will cause the same point to be chosen repeatedly as the nearest-neighbor boundary coordinate because there will be few other options. Second, the direction of animal movement may be perfectly perpendicular to the boundary at a particular point fractal (i.e., the animal is either moving directly towards the nearest point on the edge, or moving directly away from it; Fig. 3a). Third, a cove in the boundary may cause $c = d$ even when the animal is *not* moving perpendicularly (Fig. 3b). To be conservative, `prp` recognizes cases where $F = 0$ as NA by default. This can be changed so that $\eta = 1$ whenever $F = 0$ by specifying `F.0.NA = FALSE` (Fig. 3b). If a boundary is crossed when $F = 0$, then animal movement is perpendicular to the boundary point fractal. In this case `prp` makes $\eta = 1$ (Fig. 3c). Note, however, that this outcome will only be detectable if the optional argument `habitat` is specified (following section). Fourth, the animal is not moving. In this instance $C = F = 0$. Because no measure of perpendicularity is possible, the function `prp` makes these intervals NA.

Two final situations may be confusing to perpendicularity algorithms. These are: (1) if an animal moves from one boundary to another boundary within the same patch or (2) if an animal crosses a boundary and $F \neq 0$ (two lines may cross at non-orthogonal angles). If the first situation occurs then we have the trajectory pattern shown in Fig. 3d. Note that the line F is completely unrepresentative of the “dominant direction” of the patch boundary. Such a trajectory is detectable by `prp` if the optional arguments `near.angle` and `habitat` are specified; as a result we strongly recommend their inclusion. The function `prp` contains a subroutine called `Find.quad`, which if the arguments `near.angle` and `habitat` are provided, detects whether a quadrant switch in direc-

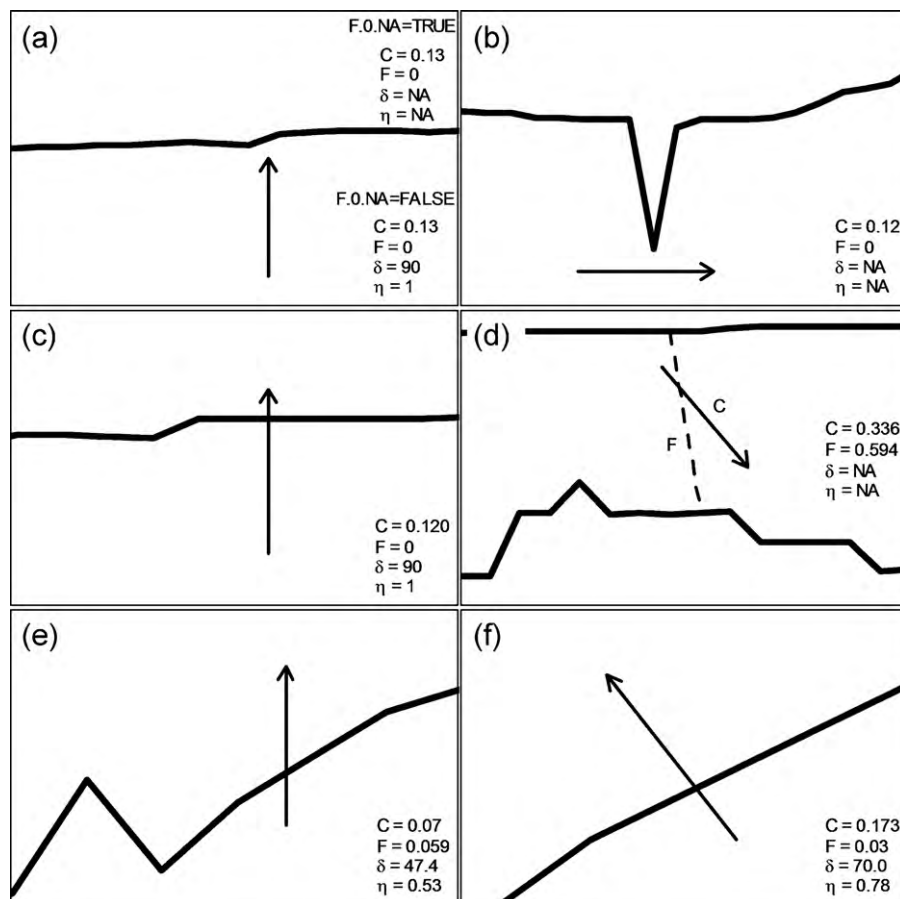


Fig. 3. Potentially confusing situations for a perpendicularity index: (a) $F=0$ because of the orthant relationship of the direction vector and the boundary, (b) $F=0$ because of a cul-de-sac in the boundary, (c) $F=0$ and a boundary is crossed, (d) the beginning and end of the movement vector are closer to different boundaries, (e) and (f) boundary crossed where $F \neq 0$.

tion has occurred between events in a time sequence. If a quadrant nearest to a boundary switches but the *habitat* character vector does not change, then it can be assumed that the animal is moving from one boundary to another within the same patch (Fig. 3d). Because η is meaningless in these situations *prp* makes these outcomes NA (Fig. 3d). The second scenario will not affect η provided that only a single boundary is crossed (Fig. 3e and f). We note that if several boundaries are crossed frequently during a single time interval then the value of η or any other measure of perpendicularity will be dubious. This may occur if the patch (or other feature) dimensions are small relative to the average distance moved in a time interval.

4.2. Application

Our angular index adds valuable information to movement measures based on distance (Diffendorfer et al., 1995), area (Anderson et al., 2005), or time (Barraquand and Benhamou, 2008). Perpendicularity measurements provided by η are useful because they describe the “degree of importance” of a boundary to an animal. Both frequent crossings (resulting in perpendicularity) and parallel movements indicate that an animal is responding non-randomly to the boundary, and signify that the boundary is of ecological importance.

Our index allows testing of a number of existing theoretical models of animal movement. We list three. First, it has been hypothesized that permeability of patches increases with edge-to-size-ratio (Stamps et al., 1987). Thus, animal trajectories should be increasingly perpendicular and protracted as patch complexity

increases while linear boundaries will act as partial barriers, resulting in prolonged parallel animal movements (Forman, 1995). The usefulness of these predictions for generalizing animal movements is obvious; however, tests of these hypotheses are largely anecdotal (Forman, Unpublished data). Second, patch shape may be an important factor in determining animal movement. For instance a lobe in a patch may result in a “peninsula effect” resulting in increased concentration of activity (Forman, 1995) and pronounced perpendicular or parallel movements. As with patch complexity, few data exist to associate animal trajectories with patch shape. Third, patch heterogeneity has been associated with a number of important movement indices including first passage time (Barraquand and Benhamou, 2008) and home-range size (Kie et al., 2002; Anderson et al., 2005). Perpendicularity provides another useful measure of the effect of patch heterogeneity on animal movement. Our index in combination with telemetry and spatial data provides a tool for addressing these and other important movement-based hypotheses.

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