

Testing for habitat detection distances using orientation data

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Understanding how organisms move through landscapes is important for predicting the effect of landscape structure on population dynamics and distributions of organisms (Merriam 1984, Johnson et al. 1992, Wiens et al. 1993, With 1994, Ims 1995). The various components of movement behaviour influence how organisms move through a landscape. What landscape elements are used and avoided? What are the rates of movement and tortuosity of movements in different landscape elements? Are learning and memory involved in moving through landscapes? The way that organisms move through landscapes may also be influenced by their ability to detect suitable habitat from some distance. A species that could perceive habitat from a distance would have less trouble finding habitat and moving through a novel, fragmented landscape. Little is known about this perceptual ability in vertebrates (Lima and Zollner 1996).

Zollner and Lima (1997) have attempted to fill the gap in our knowledge about the ability of real organisms to detect habitat at a distance. In a recent paper, they have introduced a novel approach that they believe will demonstrate how to detect perceptual thresholds in small mammals. They suggest that the movement of white-footed mice (*Peromyscus leucopus*) is influenced by their limited ability to visually recognize "preferred" habitat (woods) from relatively long distances (> 10 m). However, there is a possible flaw in their design and analysis that we feel others should be made aware of before emulating Zollner and Lima's study.

Analysing directional data: concerns with null expectations

For Zollner and Lima the question was: do white-footed mice perceive woods differentially with distance? They attempted to answer this question by releasing mice dusted with fluorescent powder in non-preferred

habitat (bare fields and soya fields) and then measuring their orientation as the angle between release and final known position (either where the mice entered the woods or where the trail of fluorescent powder was lost). The first statistical test they applied to their data was a log-likelihood contingency test (*G*-test), which tested the null hypothesis that all of the classes (in this case, release distances) had the same frequencies (in this case, proportion of released mice successfully reaching woods) (Zar 1996). This use of a *G*-test suggests a null hypothesis that mice at all release distances have an equal probability of reaching the woods, which, as we show later, may be incorrect. Since the *G*-test was only marginally significant ($p = 0.08$) Zollner and Lima went on to look at the orientations of the released mice.

Zollner and Lima tested if orientations were clustered in the direction of woods for each release distance. They used mean vector lengths (r) as a measure of the clustering of the orientations and *V*-tests to test whether that mean vector was significantly oriented toward the woods (Batschelet 1981). They found an increasing tendency for mice to be oriented toward woods at closer release distances and concluded that this supports the hypothesis that mice are perceiving habitat within 10 m of woods. However, perceptual ability may not be the only explanation for the observed patterns. Since movement paths were terminated once mice reached the woods, all mice (even if they could not perceive woods until they were in them) could eventually wander into the woods and all orientations would be clustered in the direction of the woods, given enough time. With a limited amount of time, imperceptive individuals would tend to have orientations clustered in the direction of habitat and not be uniformly distributed (because some mice would encounter habitat by chance and stop). Furthermore, individuals released closer to habitat would have a greater chance of encountering habitat than individuals released further from habitat and, therefore, the cluster-

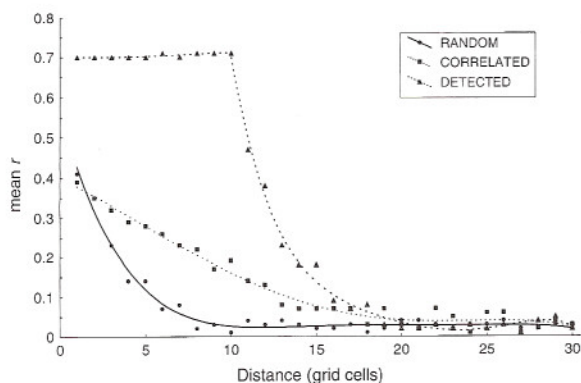


Fig. 1. Change in the length of the mean vector (r) of orientation (angle between release and final position) of 1000 random walkers released at increasing distance from a wooded edge. There were three classes of random walkers: 1) a true random walk (no response to woods, a uniform distribution of turn angles), 2) correlated random walk (no response to woods, turn angles concentrated around 0°), 3) random walkers that can detect woods (orient toward woods at a distance of 10 cells or less, otherwise a uniform distribution of turn angles).

ing of orientations should be more pronounced for individuals released closer to habitat than a group released further from habitat.

We illustrate this point with a computer simulation of non-perceptive, purely-random walkers that are released at a starting point in non-habitat. At some distance from the starting point there is a straight forest (preferred habitat) boundary which is more than twice as long as the maximum movement distance attainable by the random walkers. This very long border emulates the situation under which Zollner and Lima conducted their experiments; the forest edge was much longer than the maximum distance a mouse could move before the trail was lost. Walkers move for up to 100 steps, and movement paths were terminated if an individual reached the forest edge. This simulation is not intended to mimic the movements of Zollner and Lima's mice (we do not have enough information to try to do that) but to illustrate how the patterns interpreted as evidence of perceptual ability may be generated by a non-perceptual process. We find that the proportion of walkers that encounter the boundary increases with decreasing distance between the release point and the boundary. Therefore, the tendency of orientations to cluster in the direction of woods (as indicated by the magnitude of r and the significance of a V -test) also increases with decreasing distance, even though the walkers do not orient toward the woods (Fig. 1, random line). If we also model walkers with a perceptual distance (10 cells away), within which they orient toward the woods, there is a threshold at the perceptual distance where clustering of orientations starts to decrease with increasing distance between woods and release point (Fig. 1, detection line). The data that Zollner and Lima present (1997, Fig. 1) for orientation angles at

three different distances could be explained by either model, that is, their empirical data do not distinguish between the null model of random movements with respect to the woods and the alternative model of directed movements toward the woods. Thus, the random movement of individuals that lack perceptual ability produces the same qualitative patterns as those presented by Zollner and Lima. The analysis (V -test) that Zollner and Lima used to suggest that mice orient toward woods at 10 m or less merely tests whether the orientations are more clustered toward the woods than would be expected from an underlying uniform distribution (Batschelet 1981). The null hypothesis Zollner and Lima tested does not match the null model: they should have been testing whether the orientations were *more* clustered in the direction of woods than would be expected by mice moving randomly and not responding to woods from a distance. This same concern of attributing patterns that may have been generated by random movement to non-random behaviour has been raised about long-distance homing experiments in rodents (Joslin 1977). The suggestion that there is a 10-m perceptual range for white-footed mice is not adequately demonstrated by Zollner and Lima as claimed.

How the movement behaviour is modelled influences the relationship between release distance and clustering of the path orientations. For example, if we repeated the simulation described above, but this time modelled the movement with a greater concentration of turning angles in the forward direction, we observe a slower decline in r with release distance (Fig. 1, correlated line). Therefore, the appropriate null hypothesis (value of r) changes as the nature of the movement (e.g., concentration of turning angles in the forward direction) changes. Thus, if Zollner and Lima were to analyse their data taking this into account they would need to determine how the distribution of orientations would look under a null model (with no perception) and attempt to reject the appropriate null hypothesis (r equal to some value greater than 0). Zollner and Lima (1997: 53) mapped the actual trails of the mice that would provide movement data (e.g., turning angles) and could, therefore, be used to estimate the null r value using simulation modelling. However, the accuracy of the estimated null hypothesis would be hard to determine and would decrease the accuracy of subsequent statistical tests. This illustrates how important it is to determine the correct null hypothesis before testing for dynamic processes from static distributions.

Other approaches

One can avoid complicated null hypothesis (requiring estimation by simulation), by looking at initial orienta-

tions rather than final orientations. The initial orientation could be determined after each individual had made a small number of moves or moved a short distance (to allow for some orientation to be detected) but before any released individual would have a chance of contacting habitat. In this case, since habitat does not stop movement causing orientations to cluster in the direction of habitat, the null hypothesis is truly a uniform distribution of orientations. Therefore, observed orientations can be tested for a tendency to cluster toward the woods using a *V*-test. This approach has been used to test if yellow-bellied pond slider turtles (*Trachemys scripta*) orient toward water (Yeomans 1995) and if female cabbage butterflies (*Pieris rapae*) orient toward host-plant patches from a distance (Fahrig and Paloheimo 1987). Of course, mice stressed due to handling might respond differently than unstressed mice with regard to movement within non-preferred habitat. Thus, any results derived from this type of experiment may not give a true picture of *Peromyscus* movement behaviour and this impact of handling should be assessed.

It may be more insightful to see if movement behaviour changes as individuals wander closer to preferred habitat patches. It would be possible to contrast movement behaviour at different distances from habitat both quantitatively and qualitatively. This would require analysing individual movement trails for an increasing tendency for forward movement toward habitat (versus more random movement) at some distance from habitat. It would then be possible to look at a group of individuals to see if that change in movement behaviour occurred at a consistent distance from preferred habitat. Investigators interested in insect responses to host-plants have used a similar approach where they compare the tortuosity of movement paths in the presence and absence of host-plant cues (e.g., Visser 1988). Taking this approach with mice may require additional tracking methods (possibly radio-collars and triangulating antennae). Mice would be released in the centre of the non-preferred habitat, possibly with some cover. This would allow more time for mice to recover from the handling and may provide more natural movement behaviour in the field.

Another way to test for long-distance detection of habitat would be to use mark-recapture methods. To do this one would need to determine, using simulations based on measured movement behaviour, either diffusion rates or colonization rates that would be expected if the organism did not detect habitat and if they did detect habitat. Diffusion or colonization rates would need to be determined using simulations. Individuals, marked to indicate distance between release point and habitat, can be recaptured either as they approach habitat (to determine diffusion rates) or at habitat (to determine colonization rates). The observed diffusion or colonization rates could then be compared to those expected under detection and non-detection scenarios.

This approach is used in studies of insect detection of host-plants (reviewed in Stanton 1983, Finch 1986). Since mice are cryptic and their movement trails are hard to follow for long distances this approach may actually be more appropriate for studying mouse movement behaviour. Additionally, this approach could be used to study habitat detection at larger distances and has already been used in landscape ecology studies of small mammal movement (e.g., Wegner and Merriam 1979, 1990, Middleton and Merriam 1981, Merriam et al. 1989).

In conclusion, to understand how animals exist in landscapes we need to know how landscape structure and animal behaviour interact. Zollner and Lima have contributed to that understanding by empirically investigating perceptual distances. However, when analysing data gathered to investigate perceptual distances it is necessary to be extremely careful that the statistical tests used are testing an appropriate null hypothesis.

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