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Spherical First Passage Time: A tool to investigate area-restricted search in three-dimensional movements

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ABSTRACT

A better understanding of animal movements is of crucial importance for investigating numerous ecological issues. Developments in bio-logging technologies largely contributed to the observation and recording of animal displacements. Recently, several devices were developed to track animals in a three-dimensional space. However, given the larger number of variables, these advances generated new analytical problems and currently, few methods exist to analyse 3-D movements. In this study, we present a new technique, the Spherical First Passage Time (SFPT), to determine the scale of search behaviour in a volume. Building on the development of the First Passage Time (FPT) approach, SFPT measures the time required to cross a sphere along a 3-D path. We used simulations as they provide an opportunity to better understand processes involved in a system. Moreover, they offer the advantage of considerably increasing sample size in cases where empiric data remain scarce. However, in order to be more realistic, simulations were constrained within the physiological and behavioural features inherent to a diving animal, in this case beluga whales. First, we modelled three-dimensional movements as a correlated random walk for which the vertical and horizontal dimensions were considered simultaneously. One restricted search event was included in each simulation. Spatial scales obtained with the SFPT approach were compared to those obtained from the classical FPT analysis over the corresponding horizontal path. Results indicate a significant difference between the two approaches, suggesting that, in most cases, an approach in 2-D misrepresents spatial scale of search behaviour occurring in 3-D. Although we tested the SFPT with the example of a diving marine mammal, we argue that this method is applicable for all animals moving in a three-dimensional space.

1. Introduction

A majority of living organisms utilize three-dimensional spaces to complete their yearly cycle. The analysis of these movements can provide insights into various aspects of behaviour and biology. Over the last three decades, developments in bio-logging technologies have made significant contributions to our understanding of animal displacements relative to their physical environment (Hooker et al., 2007). Different kinds of loggers have been used to study foraging strategies (e.g., Ropert-coudert et al., 2004), migration (e.g., Tanaka et al., 2005), attendance patterns (e.g., Manlove and Hepp, 2000), distribution (e.g., Smith et al., 2000), diving behaviour (e.g., Hays et al., 2001) and flight patterns (e.g., Weimerskirch et al., 2003) of many taxa. In most cases where remote-sensing devices have been employed to study animal activities, information has often been difficult to obtain in any other way. In terrestrial domains, animal movements are concentrated within a two-dimensional space, whereas in aerial or aquatic domains where flying or diving animals live, the third dimension makes their approach to space use fundamentally different.

Until recently, vertical and horizontal coordinates have rarely been collected and analysed simultaneously, reducing the environment to a two-dimensional space. However, the development of devices to track diving animals in three dimensions has allowed the collection of more detailed information on behaviour than was previously possible. Using altimetry of Global Positioning Systems (GPS), acoustic systems, geomagnetic intensity, dead reckoning or digital tags (DTags), authors retrieved information about three-dimensional paths of many species of birds or marine mammals (e.g., Weimerskirch et al., 2002, 2005; Harcourt et al., 2000; Hindell et al., 2002; Mitani et al., 2003, 2004; Davis et al., 2001; Johnson and Tyack, 2003). These advances in data collection have also generated new analytical problems. There is a need to find ways to analyse one more variable and to measure scales of change in 3-D movement patterns to determine space use and identify intensive search behaviour in a volume.

According to the theoritical framework of foraging ecology, predators should adjust their movements in response to prey

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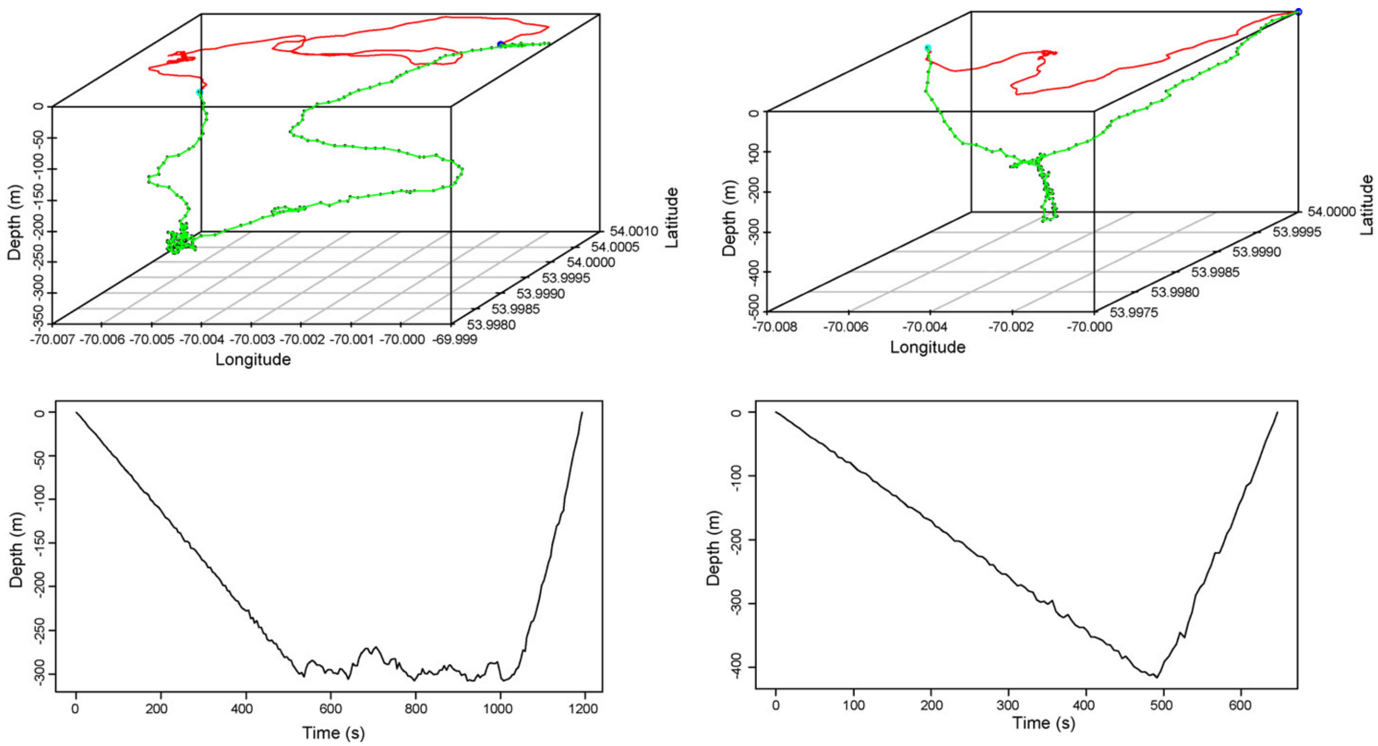

Fig. 1. Two examples of simulated dives. The path in 2-D is represented in red, the one in 3-D is in green. The equivalent 2-D dive profiles are represented in the bottom. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

capture or environmental conditions (e.g., Johnson et al., 1992; Bailey et al., 1996; Fauchald, 1999; Pinaud and Weimerskirch, 2005). For example, predators should increase turning rate and decrease speed when they have encountered prey or when they detect favourable environmental conditions (Cézilly and Benhamou, 1996; Fauchald, 1999). In an environment, which is not spatially uniform, resources usually occur following a non-random and aggregated distribution (patches), which is affected by physical parameters. Predators in patchy environments should increase search effort after detecting a prey item before continuing wider-range exploration, because of the high probability of encountering other prey items nearby (e.g., Pinaud and Weimerskirch, 2005). This scale-dependent search behaviour, which has been termed area-restricted search (ARS) (Kareiva and Odell, 1987), is often a central component of movement pattern analyses (e.g., Bovet and Benhamou, 1991; Marell et al., 2002; Fritz et al., 2003; Pinaud and Weimerskirch, 2007).

First Passage Time (FPT) is a scale-dependent measure of search effort (Fauchald and Tveraa, 2003), which identifies the spatial scale and position of the ARS. While FPT analyses have been applied to many species, most of the studies using this approach concerned terrestrial animals or flying seabirds, and focused on foraging movements in horizontal dimensions (Frere et al., 2002; Fauchald and Tveraa, 2003; Pinaud and Weimerskirch, 2005). A recent study has shown, for a diving marine predator, that when the vertical dimension is included in FPT analyses, movement patterns at the surface inadequately represent search activity at depth (Bailleul et al., 2008). However, this last approach remained two-dimensional, as the vertical and horizontal dimensions were not considered simultaneously.

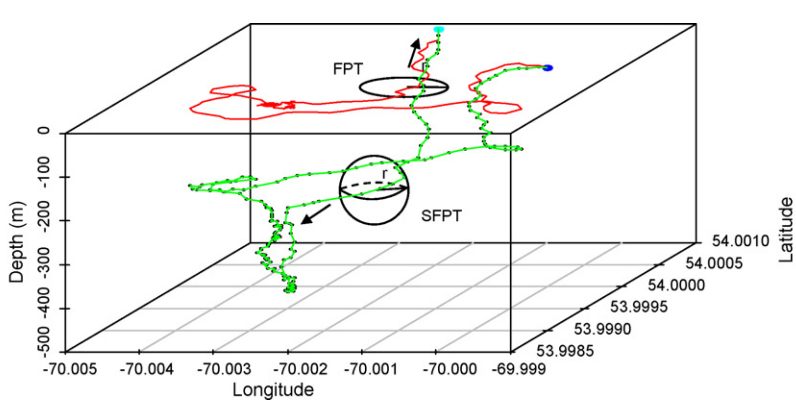

Fig. 2. Example of a simulated dive. The circle corresponds to the FPT analysis realized on the surface track. The sphere indicates the use of SFPT through the 3-D path. *r* corresponds to the radius both of the circle and the sphere. It varies from 2 to 400 m. Black arrows indicates the displacement of the circle or the sphere along the track respectively at surface and at depth.