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A stochastic movement model reproduces patterns of site fidelity and long-distance dispersal in a population of Fowler's toads (*Anaxyrus fowleri*)

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ABSTRACT

Although amphibians typically exhibit high site fidelity and low dispersal, they do undertake rare, long-distance movements. The factors influencing these events remain poorly understood, partly because amphibian spring movements tend to radiate from breeding sites and the animals are often difficult to locate at other times of the year. In this study, we investigate whether these movement patterns can be reproduced by a parsimonious model where foraging steps follow a heavy-tailed, Lévy alpha-stable distribution and individuals may either return to a previous refuge site or establish a new one. We consider three versions of the return behaviour: (1) a distance-independent probability of return to any previous refuge; (2) constant probability of return to the nearest refuge; or (3) a distance-dependent probability of return to each refuge. Using approximate Bayesian computation, we fit each version of the model to radiotracking data from a population of Fowler's Toads, which inhabits a linear sand dune habitat on the north shore of Lake Erie in Ontario, Canada. Only the model with distance-independent, random returns provides a good fit of the inter-refuge distance distribution and the number of refuges visited per toad. Our results suggest that while toads occasionally forage over long distances, the establishment of new refuges is not driven by the minimization of energy expenditure.

1. Introduction

The movements that individual animals undertake to go from place to place are fundamental to virtually every aspect of animal ecology and behaviour. How small movements of animals at daily or hourly scales result in such larger phenomena as home-ranges, dispersal and migrations at seasonal, annual or life-time scales, however, remains a difficult problem to understand. It has commonly been observed that a high-frequency of short-distance movements combined with rare, long-distance movement events results in a movement step size distribution that is strongly leptokurtic, with a sharper peak and longer tails than expected of a normal distribution, and possibly heavy-tailed, i.e. with the long-distance probability tail extending past that of an exponential distribution (e.g., Cecala et al., 2009; Gomez and Zamora, 1999; Morales, 2002; Paradis et al., 1998; Skalski and Gilliam, 2000). Such heavy-tailed distributions in animal movement may be consistent with the Lévy flight foraging hypothesis (Viswanathan et al., 1999), according to which optimal search patterns follow a power-law distribution of step sizes, with the frequency of steps proportional to some inverse power of their length. However, tests of this hypothesis have been the subject of numerous statistical challenges (Edwards, 2011).

In actuality, animal movement is not scale-free and must be constrained by biological limits, so that the power-law distribution can only hold within a certain range of step sizes (Benhamou, 2007). Over the longer time scales that encompass multiple individual movements, such as may occur during foraging or dispersal behaviours, movement distances may also depend on the animal's memory and "cognitive map" of the environment, features that are poorly represented in movement models based on independent steps (Gautestad and Mysterud, 2013). More complex models that can accommodate both specific movement rules and memory effects may be required, but their outcomes may not be expressible in terms of analytical likelihood functions.

Although the absence of a likelihood function previously precluded formal statistical analysis, computational and statistical advances in the last 20 years have made it possible to derive

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inferences from simulation-based models (Hartig et al., 2011). Approximate Bayesian computation (ABC) is a simulation-based inference method originally developed in the field of population genetics, wherein the large number of possible genetic histories and intermediate states leading to a given outcome make explicit likelihood calculations intractable (Beaumont et al., 2002; Tavaré et al., 1997). Since analogous challenges, i.e. path dependence and a large number of unobserved intermediate states, are also encountered in the study of animal movement, ABC provides a flexible mean to test foraging and dispersal behaviour models with empirical data (Marchand et al., 2015).

Anuran amphibians, although they have generally been considered poor dispersers relative to larger, more vagile terrestrial vertebrates, can be valuable subjects for testing models of animal movement. Individuals may show a high level of site fidelity yet mark-recapture studies have also shown that anurans will undertake relatively rare long-distance movements of up to a few km in a matter of days, or as far as 35 km over the course of a season (Smith and Green, 2005, 2006). Whether site fidelity is advantageous should depend on the tradeoff between the benefit of a known location relative to the cost of returning to that location (Wells, 2007). As many amphibian species make use of refuge sites as part of their daily activity cycles, this makes discretizing movement simpler as time periods between movement steps are more or less standardized and biologically meaningful. Nevertheless, locating individual anurans outside of the breeding season can be difficult with many species as they tend to be mostly nocturnal foragers that hide during the daytime. Moreover, the small size of most species precludes the use of GPS satellite telemetry methods that can provide long-term, high-resolution movement time-series for larger terrestrial animals (Wikelski et al., 2007). Both of these difficulties can be overcome, however, with the appropriate model species.

In this study, we develop a parsimonious model that describes both site fidelity and long-distance movements, and apply this model to the movements of Fowler's Toads (*Anaxyrus fowleri*) in a population inhabiting a linear sand dune habitat on the north shore of Lake Erie in Ontario, Canada. In this environment, adult Fowler's Toads are readily locatable as they forage on the beaches at night (Greenberg and Green, 2013). Previous capture-mark-recapture data (Smith and Green, 2005, 2006) have established and quantified the heavy-tailed movement distribution curve of these toads. The toads can also be fitted with small radio-transmitters (Boenke, 2011), which allow them to be tracked to their daytime hiding places in the sand dunes fronting the beaches. Based on this radiotracking data, we use ABC to estimate the parameters of the movement model, including the scale and shape of a Lévy-stable distribution of movement steps and the probability of returning to a known refuge rather than establishing a new one.

To assess the importance of energy constraints on movement, we compare the relative fit of three versions of the return step: (1) toads return to a randomly selected previous refuge, independent of distance; (2) they return to the nearest refuge from their current location; or (3) the probability of return to any previous refuge is a decreasing function of the distance to that refuge. We hypothesize that either of the last two models would provide a better fit if minimizing energy expenditure were the primary factor determining refuge choice.

2. Methods

2.1. Study site and population

We studied the movement ecology of Fowler's Toads at Long Point in Ontario, Canada, along the beaches of Long Point Provincial Park and the Long Point National Wildlife Area Thoroughfare Point Unit (UTM zone 17 N: 550700–553000 Easting, 4713615–4714200 Northing; NAD 83 Datum). Although the dune ecosystems along the north shore of Lake Erie are highly dynamic (Gelinas and Quigley, 1973; Stenson, 1993), human disturbance at this site is minimal and movement by toads not constrained either by lack of suitable habitat or by lack of connectivity between habitat patches (Smith and Green, 2005, 2006). The toads generally take refuge in the sand dunes fronting the beach during the day and emerge to forage for invertebrate prey along the lakeshore at night.

2.2. Stochastic movement model

To reflect both the high rate of apparent site fidelity and the heavy-tailed distribution of dispersal steps present in the previous mark-recapture data (Smith and Green, 2006), we used a variant of the multiscaled random walk (MRW) model proposed by Gautestad and Mysterud (2005). The MRW is based on a power-law step length distribution, but differs from a classic Lévy flight by allowing a certain frequency of return steps, wherein the individual revisits a location chosen at random from previous points in the walk. As each successive visit to a location increases its effective weight for future return steps, the MRW model allows home range patterns to emerge without the need to specify an ad hoc homing process.

In our model, we assumed that return steps only occurred at the end of the nighttime foraging path, when the toad is at a position Δx_n away from the previous day's refuge site. At this point, the toad either takes refuge at its current position or returns to a known refuge site.

2.2.1. Return steps

Our three model versions differ in how they describe the return behaviour:

Model 1 (random return): The probability of return is constant ($p_{\rm ret} = p_0$), and the toad selects a refuge at random from all the previous days' refuges. As in Gautestad and Mysterud's model, multiple visits to a refuge increase its "weight" for future return steps.

Model 2 (nearest return): The probability of return is constant ($p_{\rm ret} = p_0$), but the toad always returns to the nearest refuge.

Model 3 (distance-based return probability): The probability of returning to a given site decays exponentially with the distance $d_{\rm i}$ to that refuge:

$$p_{ret(i)} = p_0 e^{\frac{-d_i}{d_0}}, \quad (1)$$

where d_0 is a characteristic distance to be estimated along with p_0. The probability of not returning to any previous site is the product of the complements of the $p_{\rm ret(i)}$:

$$1 - p_{ret} = \prod_{i=1}^{R} (1 - p_{ret(i)}), \quad (2)$$

where R is the number of *distinct* previous refuges.

In the case of a return event, the probability of each refuge being chosen is given by:

$$P\,(return\,at\,i\,|\,return) = \frac{p_{ret(i)}}{\sum p_{ret(i)}}. \quad (3)$$

With an additional parameter, the third model allowed us to consider intermediate cases of distance-dependence. As the characteristic distance d_0 decreases, it becomes increasingly likely that the toad will choose the nearest refuge; yet the outcome differs from that of model 2, since the probability of return is not constant but decreases with distance. In the limit where d_0 is very large, $p_{\rm ret(i)} = p_0$ and all previous sites have the same probability of return. Contrary to model 1, however, the probability of returning to any site is not constant but increases with R (as a consequence