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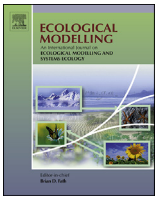

Predicting the seed shadows of a Neotropical tree species dispersed by primates using an agent-based model with internal decision making for movements

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ABSTRACT

The spatial pattern of endozoochorous seed dispersal depends strongly on the movement patterns of the disperser and the gut transit times of the seeds. In this study, we developed an individual-based simulation model for seed dispersal in the tropical tree *Parkia panurensis* carried out via two primate species (*Saguinus mystax* and *Saguinus nigrifrons*) using data collected at the Estación Biológica Quebrada Blanco in northeastern Peruvian Amazonia. From field data, we identified factors determining the movement patterns of the primates. We assumed that the need for energy (food) is the driving force for movement and that other activities are scheduled accordingly. The final movement pattern is therefore an interplay between directional travel toward fruit trees, semi-directional searching for prey and stationary resting phases.

First, we parameterized the model using a genetic algorithm such that simulated and field data converge at very similar target values for the daily path length and home range size. Second, a sensitivity analysis of several parameters in our simulation model revealed the following parameters to be the most important for producing a realistic movement pattern: the number and position of feeding trees and the energy gained from the selected food type. Finally, we introduced the gut transit times of seeds and the defecation habits of the primates, which allowed us to examine the seed shadow generated by a specific troop of primates. The simulated seed shadows of individual *P. panurensis* trees are similar to those found in nature. We conclude that agent-based modeling using behavioral data has the potential to improve home range estimation and seed shadow prediction, especially for unexplored locations.

1. Introduction

Seed dispersal is a key process in ecological systems affecting the spatial structure of plant communities and influencing colonization and population dynamics at both local and regional scales (Bullock and Clarke, 2000; Levin et al., 2003). Density-dependent mortality close to source trees (Connell, 1971; Janzen, 1970) and the need for a population to spread to assure its survival in a changing environment (Cain et al., 2000) require efficient dispersal mechanisms. Therefore, many fruit-bearing plant species rely on animals as dispersal vectors (Russo et al., 2006; Westcott et al., 2005).

Animals do not spread seeds uniformly over their home range but instead place them patchily within space (Julliot, 1994; Schupp et al., 2002). This pattern is a result of the activities of the animal dispersal vectors throughout their daily routine. It not only influences the spatial patterns of seed dispersal but also affects the regeneration pattern and the spatial-genetic structure of plant populations (Born et al., 2008; Choo et al., 2012; Fragoso et al., 2003). Animal activities that have been shown to contribute differentially to the primary seed shadow include the movements of vectors through their home ranges (Holbrook and Smith, 2000; Will and Tackenberg, 2008), patterns of resting, sleeping and defecation (Cousens et al., 2010; Julliot, 1994), the distribution of food sources and the matrix in between (Alcantara et al., 2000; Harata et al., 2012), seed size (Alcantara et al., 2000; Stevenson, 2000), gut passage time (Stevenson, 2000; Westcott et al., 2005), social and mating behavior (Karubian et al., 2012; Kesler et al., 2010) and interactions between individuals (Charles-Dominique, 1995; Scofield et al., 2012, 2011; Stevenson, 2000). Hence, predicting the seed shadows of animal-dispersed species is highly challenging because of the many factors affecting animal movement decisions and, thus, the unintentional dispersal of seeds. Due to the great

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amount of effort required to collect data on all of these parameters in the field, predictive modeling of the dispersal process should be employed to evaluate the specific importance of all of these factors prior to field data collection.

Because animal dispersal vectors often generate spatially aggregated seed deposition patterns (Julliot, 1994; Schupp et al., 2002), their mode of seed dispersal cannot be modeled appropriately as a decreasing function of distance (e.g., inverse modeling approaches). Most authors have recognized this problem and have developed mechanistic models to predict seed dispersal directly from the traits of plants and their dispersal agents. Mechanistic models of zoochory typically predict seed shadows based on seed dispersal curves that account for the gut passage times of seeds and the displacement rates of the animal dispersers (Russo et al., 2006; Wehncke et al., 2003; Westcott et al., 2005). However, in reality, the dispersal curve is an emergent property of the plant-disperser interaction (Westcott et al., 2005). Therefore, existing mechanistic models are likely to underestimate the clumping of animal-dispersed seeds (Muller-Landau and Hardesty, 2005). In particular, varying behavioral responses to different habitat features, such as various food types, physiological needs such as resting and sleeping, and social needs such as grooming have not been incorporated in these models thus far.

Many of these data are available from different studies on primates in tropical ecosystems. These primates are known to disperse the seeds of a multitude of plants mainly endozoochorously within their home ranges (Charles-Dominique, 1995; Sobral Griz and Machado, 2001; Terborgh et al., 1993). They consume large quantities of fruits but do not negatively affect their germination capacity, and they transport seeds over adequate distances (Chapman and Russo, 2007; Chapman et al., 2010; Culot et al., 2010; Knogge and Heymann, 2003; Schupp, 1993). Furthermore, the diets of many primates are well known from direct observations, and their daily routines have been monitored for several purposes. All of these data are available and ready to use. Therefore tropical tree species and their seed-dispersing primates are a good study system for developing models to achieve a deeper understanding of animal seed dispersal. It is widely accepted that the shape and size of the resulting primary seed shadows are generated through the activity patterns of the primates (Janzen, 1976), together with the gut passage time of the seeds and their defecation by the disperser (Cousens et al., 2010).

We set out to model the emergence of seed shadows as a result of plant-disperser interactions through developing a spatially explicit individual-based (SEIB) simulation model of endozoochorus seed dispersal by primates. The dispersed seeds addressed in this work come from the Neotropical tree species *Parkia panurensis* (Fabaceae). The primates involved are two tamarin species (*Saguinus mystax* and *Saguinus nigrifrons* [previously *Saguinus fuscicollis* (see Matauschek et al., 2011)]), which live in interspecific associations of 8–15 individuals. The model was parameterized using empirical data on the movements and behavior of one of these tamarin groups collected at the Estación Biológica Quebrada Blanco (EBQB) in northeastern Peruvian Amazonia by Kathrin Lüttmann in 2008. Based on these data, we identified specific patterns describing the movement of the tamarins. These patterns were subsequently employed as quality indicators of how well our simulation was able to reproduce these patterns (Grimm et al., 1996).

Our basic assumption regarding activity selection in tamarins is that the maintenance of homeostasis is the driving force. Every activity requires a specific mode of movement. These modes include directional movement toward fruit trees, semi-directional searching for prey, scent marking of trees within the home range and stationary resting phases. All of these modes together produce the group's home range and, hence, the seed shadow of individual *P. panurensis* trees.

To estimate model parameters that have not been quantified empirically, we varied several parameters that influenced the gain and loss of energy during the daily routine of our simulated group using a genetic algorithm (GA). At the time simulated and field data converged at very similar target values identified from field data, we conducted a sensitivity analysis to investigate the influence of the model parameters on the resulting movement pattern. Finally, we introduced two seed dispersal variables: gut passage times and the defecation frequency. This final model was used to predict seed dispersal distances and seed shadows for individual *P. panurensis* trees within our study area. Hence, the modeled seed shadows were compared to empirical data collected at EBQB.

Our main objectives were (1) to simulate average tamarin activity patterns on a daily basis as an individual decision process, (2) to estimate the specific influence of simulation parameters on the outcome of the movement pattern and (3) to test the prediction of seed shadows for individual *P. panurensis* trees using the optimized simulation parameters.

2. Material and methods

2.1. The natural system

2.1.1. Study site and grid system

Field data were collected at the Estacion Biologica Quebrada Blanco (EBQB) research station in northeastern Peru (4°21′S and 73°09′W). The primary forest in the study area, which is located within the Amazonian floodplain, represents a continuous matrix for the movements of the seed-dispersing tamarins. The study site is equipped with a 100 m × 100 m trail grid, covering an area of approximately 1 km^2. The exact location of every feeding, sleeping and resting tree used by the tamarins with a diameter at breast height (dbh) > 15 cm was recorded using GPS. For each tree, the species was determined.

2.1.2. Animal species and activities

The two tamarin species addressed in this work (*S. mystax* and *S. nigrifrons*) form mixed-species troops, in which they spend on 80–90% of their activity time together (Heymann and Buchanan-Smith, 2000). The activities of the tamarins begin around sunrise and are maintained for a period of 10 h on average (Smith et al., 2007). Prey foraging, feeding on fruit and resting are their main daily activities (Knogge, 1999). Social interactions (e.g., grooming) and the scent marking of trees within the home range are further components of their daily routine (Heymann, 2000; Löttker et al., 2007). The approach to fruit-bearing trees is characterized by traveling in a relatively straight line (Garber, 1989), whereas the movement steps made during prey foraging and scent marking are more or less random (Knogge, 1999).

2.1.3. Plant species and seed dispersal

We selected the legume *P. panurensis* (Fabaceae) as model species because its seeds are dispersed at our study site exclusively by the two tamarin species present. The sticky exudate surrounding each of the up to 23 seeds per pod represents a major food source for the tamarins between June and September (Knogge and Heymann, 2003; Peres, 2000). The seeds are swallowed along with the surrounding exudate and voided with the feces. The germination rate and latency of the seeds are not affected by the gut passage (Knogge et al., 2003).

2.1.4. Field observations

The dataset used for parameterization and model calibration was obtained during a field trip conducted by Kathrin Lüttmann in 2008 at the EBQB. The position and the activity of the tamarin group