9. RESEARCH ARTICLE:

Parameterization, Development and Ecological Implications of a Seed Dispersal Model by Howler Monkeys

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**ABSTRACT:** Seed dispersal distance values represent key information that should be incorporated to climate change species distribution modeling; however, this information is very difficult to obtain empirically. Howler monkeys are important and effective seed dispersers of tropical forests, but still much debate exists regarding their ability to produce long-distance seed dispersal events, and concerning their clustered patterns of seed depositions in latrines. Mechanistic models of seed dispersal that include theoretical concepts, empirical data and animal behavior and movement assumptions, can help address particular hypotheses and predict outcomes to help understand the role of howler monkeys for different scenarios of canopy tree species abundance, spatial distribution and seed sizes. Thus, we created a model based on parameters obtained from literature review and field observations, and our results suggest that distances of seed dispersal can be reached up to 550m from parental trees, and although LDD events may occur of up to 3 km, howler monkeys contribute mostly to local seed dispersal. Food availability modeled by fruiting tree abundance has an effect on seed dispersal distances and number of seed dispersal events; as clustered aggregations of reproductive trees also have an effect on seed deposition patterns. Defecations in non-latrine sites led to significant longest seed dispersal distances, and the model suggests seed size to have an effect on the proportion of seeds not defecated under latrines. Howler monkeys are important seed dispersers and even though their dispersal abilities have limitations, their contribution to forest structure, its regeneration and the regional survival of some trees species has been proven more than once. Our MonkeySeed model is a promising tool for the study and comprehension of seed dispersal distances through endozoochory, and whose results can be applied in further studies of canopy tree migration and species distributions throughout climate change scenarios.

*Key words: howler monkeys, seed dispersal model, latrines, long-distance dispersal, seed deposition patterns, dispersal events*

**INTRODUCTION**

It has become very clear in recent years that there cannot be an understanding of plant populations and community dynamics without an adequate comprehension of how seed dispersal works (Nathan & Muller-Landau 2000, Muller-Landau et al. 2008, Wang & Smith 2002). This statement is especially important in tropical rain forests, where the great majority of tree species -up to 90% of canopy species- have fruits adapted for consumption and seed dispersal by frugivorous vertebrates (Howe and Smallwood 1982, Howe 1993, Nasi et al. 2002). As it is, most frugivorous species that act as dispersal agents have their own feeding behavior, digestive rhythms, movement patterns, and ways of handling fruit; therefore affecting spatial patterns of seed deposition, seed viability, seed post-dispersal processes (Schupp 1995, Andersen 2002, Muller-Landau et al. 2008, Bravo 2012), and overall dispersal effectiveness (Schupp 1993, Shupp 2010).

Since seed dispersal effectiveness depends on the quantity and “quality” of seed dispersal (Schupp 1993); many authors have come to the realization that howler monkeys (*Allouata sp.*) represent an important, widespread, and effective seed disperser depending on the plant species and region (Andersen 2002, Martins 2006, Amato & Estrada 2010, Anzures-Dadda et al. 2011, Bravo 2012). This statement is based on the fact that these primates are distributed in the majority of tropical forest of America (from low lands to 2500m; Reid 2009),
they generally show the highest density among primate populations, and are one of the largest neotropical monkeys (Julliot 1996), which gives them the ability to disperse a high number of medium to large-seeded plant species through endozoochory (Amato & Estrada 2010); furthermore, as they travel and eat in groups because of their social behavior, they can potentially disperse greater quantities of seeds. Another very important fact to consider is their long digestive time periods (Yumoto et al. 1999, Andersen 2002), which ideally allows them to travel further and disperse seeds farther from parent trees than other frugivores, also excreting a large number of viable seeds (Chapman 1989).

In contrast, it has also been argued that *Alouatta* species can be low quality dispersers because of their long inactivity times (Pavelka & Knopff 2004) and aggregated defecation patterns that greatly affect post dispersal seed fate (Andresen 2002, Bravo 2012). In the case of howler monkeys, their cohesive social groups that defecate together, mostly under sleeping sites or latrines (Julliot 1996, Andresen 1999), could represent a disadvantage for the establishment of seed/seedlings due to density-dependent mortality issues (Howe 1993, Andresen 2002, Bravo 2012). However, single individuals can excrete at different times and places than the rest of the group, integrating a scattered component into the configuration of their seed dispersal (Bravo 2009) that could be based on “in-transit site” defecations (Russo et al. 2006) when moving from site to site. This scatter component though potentially relevant has not yet been measured, and it is unknown how often and in what context it is occurring (Bravo 2009). Also, some authors claim advantages to howler monkeys clumped defecation patterns and its associated secondary dispersal fate (see also Chapman 1989, Estrada y Coates-Estrada 1991, Estrada et al. 1993, Julliot 1997, Andersen 1999, Andersen 2001, Pouvelle et al. 2009).

Nevertheless, a big discussion exists regarding whether if howler monkeys are capable to disperse seeds long distances, or do they mostly contribute to seed deposition under latrines and local dispersal. In recent years it has become more and more evident that the study and understanding of long distance dispersal (LDD) represents an important part of the puzzle for the comprehension of plant population dynamics and structure, their movement and colonization across continuous and fragmented landscapes (Nathan 2006, Nathan et al. 2008, Levey et al. 2008, Schupp et al. 2010), and how organisms disperse and eventually migrate, to help predict in what way species adapt and persist in time and space with climate change (Cain et al. 2000, Knowlton y Graham 2010). In this sense, howler monkeys may represent a promising LDD agent, as many authors believe that when it comes to animal-dispersed seed, LDD events may rely on a small subset of large mammal species as efficient dispersal vectors (Jordano et al. 2007, Vittoz and Engler 2007, Nathan et al. 2008, Schupp 2010).

LDD studies, though crucially important for large-scale dynamics of plant communities, are difficult to implement and measure empirically (Cain et al. 2000, Clark et al. 2003, Levin et al. 2003, Russo et al. 2006, Nathan 2008, Nathan et al. 2008, Will and Tackenberg 2008, Schupp 2010). That is why this aspect of research has depended more on the use of mathematical simulation models that help predict outcomes for seed dispersal, because models require more assumptions than empirical data and therefore are easily applied (Levey et al. 2008); however, few of these studies have embraced this approach using endozoochory as a means for dispersal because of its great conceptual complexity (Russo et al. 2006, Will & Tackenberg 2008, Cousens et al. 2010, Correa-Cortes and Uriarte 2012).
In this regard, inclusion in a model of information on the behavior and movement of the dispersal agent is essential for conducting realistic simulations of seed dispersal patterns (Will and Tackenberg 2008, Correa-Cortes and Uriarte 2012). Correspondingly, it is also important to include factors that may influence the spatial distribution of seed pattern deposition, like abundance and aggregation of adult trees (Correa-Cortes and Uriarte 2012), as well as seed or fruit traits (Clark et al. 2005). This is because even in plant species with the same dispersal syndromes, variation in fruit and seed characteristics may have an additional effect on their seed dispersal patterns (Muller-Landau et al. 2008).

In synthesis, the objective of this study is to contribute to the building of knowledge of seed dispersal by howler monkeys in different scenarios of reproductive tree abundance, spatial distribution, and seed size. We constructed a simulation model that incorporates howler monkey’s behavior, feeding habits, seed retention time, and real movement data in order to simulate seed dispersal distances and seed dispersal patterns. We expect to better understand the concept of (and quantify) LDD for howler monkeys, measure its scattered component, and translate this information into its ecological significance for the resilience of different tree species and their ability to migrate and keep pace with changing climates and other aspects of global change. These results will allow us to better understand the underlying importance of the howler monkey in their still debated contributions to seed shadows, and the never-ending ecological intricacy of forest community dynamics.

Study site

The Barbilla National Park (Fig.3 B) is located in the provinces of Limon and Cartago in Costa Rica, covering an area of 11,994.74 hectares, between 200 and 1600m. Its main objective is to provide protection to a large area of tropical rainforest in pristine condition, containing great diversity of flora and fauna, and many endangered species. It is also an area that has a high water production of vital interest for the supply of drinking water to neighboring communities, and has great historical value to be found in surrounding areas populated in great part by the Cabecar indigenous group (SINAC 2012).

The study area is the lowest part of an altitudinal gradient known as Caribe-Villa Mills (Fig.3A) that is located on the Atlantic slope of the Talamanca Cordillera, with an elevation range of approximately 300 to 2800m (SINAC 2012). The altitudinal gradient has an area of 227,674 hectares, and belongs to the regime of precipitation and climatic region Caribbean Southern Caribbean (IMN 2009).
METHODS

To build the seed dispersal curve obtained by howler monkeys (*A. palliata*) we designed a rule-based stochastic model that simulates the movement of the animals through an actual or fictional landscape. Movement parameters of the monkeys were acquired in the field, for which we estimated home range, speed, distance and angle of locomotion from one tree to another. We also observed the monkeys activities patterns during day time. The amount of time the dispersal agents invest in their daily activities, and gut retention times (GRT) for different seed sizes, were obtained by literature review.

We also simulated six fruit tree abundance and distribution scenarios, as well as three seed size-GRT scenarios to inquire for the most sensitive parameter in the model and its ecological implications for different tree species that can resemble the conditions we have replicated.

Fig. 3. Study site. (A) Caribe-Villa Milis altitudinal gradient, (B) close up to Barbilla National Park.
Parameters obtained in the field

A troop of *A. palliata* and some solitary males were followed for 90 hours spread between March and July 2013. Daily observation periods were ideally 10 continuous hours. The spatial location of feeding trees and resting sites, along with their travel routes were tracked with a Garmin GPS with ± nine to eleven meters of accuracy. It should be noted that the feeding activity that was recorded only includes trees (leaves, fruits and flowers).

For speed, angles, and distances traveled by howler monkeys, we used the spatial analysis tool Geospatial Modelling Environment, GME, version 0.7.2.0 (Beyer 2012). GPS points were used to extract travel movement angles and speed of the monkeys from one point to the other (Figure 4). These values will be extracted randomly by the model whenever needed.

![Graphs showing probability density associated with movement speed and angles](image)

**Fig. 4.** Probability density associated with movement speed and angles of *A. palliata*; data obtained in the field, at Barbilla National Park, Siquirres, Costa Rica, March-July 2013.

Parameters extracted from literature

Based on literature review, information on how *Alouatta sp.* individuals spend time on their daily activities (feeding, resting, traveling, and gut retention time) was collected (see Appendix 1). The available data was standardized by the number of minutes per day that the monkeys spent on each activity for each study, and the frequency of occurrence of each activity during the day (two times a day for each activity); then by using bootstrapping we generated a vector of 250 values for every parameter to better predict the probability distribution of the time howler monkeys spend on each activity during the day time (fig. 5).
Simulation Model

We designed a rule-based stochastic model called *MonkeySeed* programmed with the R version 2.15.2 package (R Development Core Team 2011) that simulates seed dispersal by howler monkeys (fig. 6, Appendix 5); it works on the foundation of the parameters indicated in Table 2. This model simulates spatial patterns and distances of seeds dispersed in a landscape with a single dispersing agent, and constructs the respective dispersal Kernels. In this case, it has been parameterized for the howler monkey genus *Alouatta*, but it could be used for other mammals if the necessary information is available.
Table 2. Summary information on parameters used for the model *MonkeySeed*

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
<th>Value</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>$XY_{ini}$</td>
<td>Potentially initial point simulation coordinates</td>
<td>$(x, y)$</td>
<td>Random points obtained according to the biggest diameter of home ranges from literature (Chapman 1988).</td>
</tr>
<tr>
<td>$V_{tray}$</td>
<td>Movement speed</td>
<td>0.022-14.062 m/min (fig.2a)</td>
<td>Estimated from field data.</td>
</tr>
<tr>
<td>$A_{tray}$</td>
<td>Movement angles</td>
<td>0.22-353.64° (fig.2b)</td>
<td>Values obtained in the field.</td>
</tr>
<tr>
<td>$XY_{seed}$</td>
<td>Coordinates for possible feeding trees, with seeds for dispersion.</td>
<td>$(x, y)$</td>
<td>20x20m grid scenarios generated for 6 distribution and abundance types of seeded trees in the landscape.</td>
</tr>
<tr>
<td>$T_{simul}$</td>
<td>Simulation period of time (days, months, years)</td>
<td>2 months</td>
<td>Chosen depending on the phenology of the tree species of interest.</td>
</tr>
<tr>
<td>$It$</td>
<td>Iterations (simulations)</td>
<td>10000</td>
<td>According to specialist criteria a minimum of ten thousand simulations is recommended.</td>
</tr>
<tr>
<td>$Radio$</td>
<td>Search radius for trees with fruits</td>
<td>20 m</td>
<td>Chosen as the minimum space between trees.</td>
</tr>
<tr>
<td>$T_{day}$</td>
<td>Day time</td>
<td>13 h</td>
<td>Value generated from literature review (Mittermeier 1973, Garcia 1993, Stoner 1996, Estrada et al. 1999, Bravo and Sallenave 2003) and field observations.</td>
</tr>
<tr>
<td>$T_{night}$</td>
<td>Night time</td>
<td>11 h</td>
<td>Value generated from literature review (Mittermeier 1973, Garcia 1993, Stoner 1996, Estrada et al. 1999, Bravo and Sallenave 2003) and field observations.</td>
</tr>
</tbody>
</table>

In the case of this study, the models outputs are the result of ten thousand simulations, each one of a period of two months’ time (Table 2). In every iteration, the model simulates the path and activities of a single *Alouatta* individual, maintaining a sequential order in their daily actions (movement - feeding - resting); starting in the early hours of the morning until the end of the day (fig. 6 and 7), for a simulation period of time that the user can determine, and may be based on the phenology of tree species analyzed. Time probability values for each activity are chosen randomly based on a vector of values that come from the literature review (fig. 5a, b and c). The number of times that monkeys exercise each activity is based on field observations; they move, eat and rest twice daily as a group; this
The assumption was corroborated with secondary information (Mittermeier 1973, Garcia 1993, Stoner 1996, Estrada et al. 1999).

The initial position of the monkey in the landscape (a quadrant of 22 575 ha over our study site) is chosen randomly from a vector of georeferenced points that are spaced evenly according to the largest diameter for the home ranges (1173m assuming a circular shape for those home ranges) obtained from literature (Estrada 1984, Estrada and Coates-Estrada 1984, Chapman 1988; Juliott 1996, Stoner 1996, Serio-Silva and Rico-Gray 2002, Bravo and Sallenave 2003, Pinto et al 2003, Gavazzi et al 2008, Dunn et al. 2009, Amato and Estrada 2010). Also, we assumed the simulation period to start at the first sun light hour of the day (6am), but the user can decide to have the model start the simulations randomly in time.

To start a simulation, a virtual path is estimated based on an initial position, the angle and speed of travel. In turn, the distances between each of the monkey’s movements depend on time and speed parameters.
\[ X_{(t+1)} = X_{initial} + \cos(angle) + Distance \]
\[ Y_{(t+1)} = Y_{initial} + \sin(angle) + Distance \]

Where the distance is estimated:
\[ Distance = Speed \times Travel\ movement\ time \]

All these parameters are taken randomly from different data vectors (fig. 4 and fig. 5c) to estimate the next position. Given the random distribution of our movement angle values (fig. 5d), the direction of the movement that is simulated is basically a random walk.

The simulated monkey will move in the landscape calculating its path (based on a grid of points distributed equally every 20 meters) until its feeding time at any given point. At that time the model will search in a 20m radius for fruiting trees (our minimum distance between trees), if a fruit tree is not found, the model concludes that the monkey ate leaves; but, if a fruit tree is encountered, the model will start counting a gut retention time (GRT) drawn randomly from a simulated vector of possibilities obtained from literature (fig. 5d). GRT can therefore start in one simulation day and end the next (fig. 7); depending on its duration, and the monkeys movement patterns; this will influence if seeds are dropped in latrines or not.

Fig. 7. Summary of Gut Retention Time breakdown between Day Time and Night simulations. Rounded boxes represent model inputs, squared boxes exemplify daily activities the monkeys perform, circles are calculations that the model executes but does not store in its memory, and dashed boxes are model outputs. GRT=gut retention time, DT= day time, NT= night time, SDD= seed dispersal distance.
Fruiting tree distribution and abundance scenarios

The effect of fruit tree distribution and abundance in the landscape was evaluated for seed dispersal. For each type of distribution, random and aggregated, we ran the following categories for abundance: one tree every ten hectares (called Rand1 and Clust1), one tree per hectare (Rand2 and Clust2), and ten trees per hectare (Rand3 and Clust3). These scenarios were based on actual point coordinates extracted randomly from a 20 meter grid of points from the study site, with the use of GIS tools like ArcMap 10.1 and Geospatial Modelling Environment, GME, 0.7.2.0 (Beyer 2012).

Seed size-GRT scenarios

In regards to gut retention time (GRT), some authors believe that seed size is relevant to digestion time: the bigger the seed, the longer the time it takes to be excreted by the monkey (Julliot 1996). With this in mind, we took values of seed size (seed length) and GRT that have been published by Julliot (1996) and Yumoto et al. (1999) and demonstrated a linear effect between the two variables (fig. 8).

![Figure 8](image)

**Fig. 8.** Linear regression ($R^2=0.54$, $p=0.006$) estimated for seed sizes and gut retention times published by Julliot (1996) and Yumoto et al. (1999). Solid gray lines represent prediction bands, and dashed gray lines represent confidence bands.

The equation of the regression is:

$$Seed\ Size = -6.98 + [0.41 \left(\frac{GRT}{60}\right)]$$

We then created a range of values of seed sizes based on published information by Julliot (1996) and Yumoto et al. (1999) of seed size and GRT by using bootstrapping to create 250 replicates of the values, and then, with the use of a cluster analysis we generated three different groups or scenarios of GRT for the model according to seed sizes (Table 3).
Table 3. Seed size (cm) and gut retention time (GRT) groups created with a cluster analysis.

<table>
<thead>
<tr>
<th>Group</th>
<th>n</th>
<th>Mean</th>
<th>SD</th>
<th>Min</th>
<th>Max</th>
<th>GRT (h)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Small Seed (0.40-1.38cm)</td>
<td>205</td>
<td>1.14</td>
<td>0.19</td>
<td>0.4</td>
<td>1.38</td>
<td>18-20</td>
</tr>
<tr>
<td>Medium Seed (2.18-2.33cm)</td>
<td>26</td>
<td>2.29</td>
<td>0.05</td>
<td>2.18</td>
<td>2.33</td>
<td>22-23</td>
</tr>
<tr>
<td>Large Seed (3.27-5.32cm)</td>
<td>19</td>
<td>3.83</td>
<td>0.78</td>
<td>2.72</td>
<td>5.32</td>
<td>25-30</td>
</tr>
</tbody>
</table>

Model outputs

Model outputs are stored as R files (extension “.RData”; R Development Core Team 2011), where all data can be reached. In these images 4 lists are stored: the first list is a summary of total simulations with latrine and non-latrine frequency of dispersal events, mean, 1st and 3rd percentile, and minimum and maximum values of seed dispersal distances; the second list contains 10 thousand lists (one for every model iteration): coordinates (x, y) of seed deposition, distances of seed dispersal and a frequency record of latrine and non-latrine events; the third list is one of the total distances recorded for distribution amplitudes; and the last list holds the record for all frequencies of seed dispersal events for every iteration simulated.

Data Analysis

Seed dispersal kernels (frequency distributions of dispersal distances) were constructed with “density” and “kernel” functions with the R package version 2.15.2 (R Development Core Team 2011), for the sum of all simulation cycles for every scenario of the study; adjusting the nonparametric function with the amount of dispersal events in response to dispersal distances. Based on this model, the density function of a Gaussian Kernel 1D was adjusted.

We used various components of the seed dispersal curve to characterize seed dispersal distance: mean, minimum, maximum, and 50th and 99th percentiles of the total dispersal curves for each simulated scenario. LDD events were defined as those larger than the 99th percentile values of total simulations for each scenario, and frequency of LDD and all dispersal events in general were evaluated in a qualitative manner.

Spatial distributions of seed dispersal for one of the ten thousand simulations for every scenario (that represents the 99th percentile of maximum distances) were constructed with the use of the library “spatstat” (Baddeley and Turner 2005) with the R package version 2.15.2 (R Development Core Team 2011); the “K” function was also used to characterize spatial clustering or regularity of seed depositions; and with the use of the “dismap” function, other information used as metrics to categorize differences between scenario spatial patterns of seed deposition, like the mean distances between centroid of seed deposition clusters. Also, the minimum convex polygon method was used to recreate hypothetical home ranges for the simulated monkeys, again using ArcMap 10.1 and Geospatial Modelling Environment, GME, 0.7.2.0 (Beyer 2012); additionally, an analysis of variance (ANOVA) with range transformation on the Euclidean distances of the same spatial patterns of seed dispersal was performed for all scenarios to find differences within scenarios.

With the use of the “splacs” library (Rowlingson and Diggle 2013), in the R package version 2.15.2 (R Development Core Team 2011), home range (minimum convex polygons) areas were estimated, with “chull” function, for total iterations and all scenarios simulated that
presented more than six dispersal events. This data was then used to calculate linear regressions with the use of “lm” function, between home range and maximum dispersal distance log values.

Finally, an Independent t test was run to compare latrine and non-latrine dispersal distances for all nine scenarios. Percentages of latrine and non-latrine deposition occurrences were also used to compare qualitatively between different scenarios of seed dispersal by howler monkeys.

RESULTS

*Seed Dispersal Distance, Distribution and Frequency*

All howler monkey seed dispersal curves were long-tailed, highly leptokurtic and biased toward local-scale dispersal (dispersal distances between 50 and 100 m; Table 4; fig. 9); also, some multimodality can be noted by examining dispersal kernels for every individual simulation (fig. 10 and 11). Seed dispersal could reach very long distances (up to 2421 m for abundance and distribution scenarios, and 3094 m for seed size scenarios), even though the totality of the dispersal curves had 99% percentiles that did not rise above 555 m or 619 m (for abundance and distribution scenarios, and seed-size scenarios respectively; Table 4); also, given that the threshold for LDD is the 99th percentile, only 1% of the estimated dispersal curves presented LDD events for every scenario as seen in Table 4. Mean dispersal distances, 50th and 99th percentiles are displayed in Table 4 for every scenario simulated.

![Fig. 9. Seed dispersal distance frequency distributions of the sum of all 10000 iterations simulated for every scenario studied. (A) Scenarios Rand 1, 2, 3, and Clust 1, 2 and 3 symbolize random distributions of ten trees per ha, one tree per ha, and one tree every ten ha, and clustered distributions of ten trees per ha, one tree per ha, and one tree every ten ha respectively. (B) Scenarios Seed 1, 2 and 3 signify Small Seed (0.40-1.38 cm), Medium Seed (2.18-2.33 cm), and Larger Seed (3.27-5.32 cm) respectively.](image-url)
Table 4. Summary of seed dispersal distances (in meters) for every simulated scenario of seed dispersal by howler monkeys. Frequency of seed dispersal occurrence, mean dispersal distance, standard deviation, 50th and 99th percentiles, maximum distance of dispersal recorded, frequency of LDD events (larger than 99th percentile), and percentage of LDD events.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>n</th>
<th>Mean</th>
<th>SD</th>
<th>Min</th>
<th>Max</th>
<th>P(50)</th>
<th>P(99)</th>
<th>&gt; P(99)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Random, ten trees per ha</td>
<td>398110</td>
<td>88.08</td>
<td>105.74</td>
<td>0.00</td>
<td>2421.70</td>
<td>48.61</td>
<td>530.11</td>
<td>398</td>
</tr>
<tr>
<td>Random, one tree per ha</td>
<td>97030</td>
<td>96.27</td>
<td>109.50</td>
<td>0.10</td>
<td>2380.62</td>
<td>57.07</td>
<td>537.68</td>
<td>97</td>
</tr>
<tr>
<td>Random, one tree every ten ha</td>
<td>11446</td>
<td>97.87</td>
<td>109.26</td>
<td>0.56</td>
<td>1810.15</td>
<td>58.04</td>
<td>534.78</td>
<td>11</td>
</tr>
<tr>
<td>Cluster, ten trees per ha</td>
<td>232240</td>
<td>85.14</td>
<td>103.94</td>
<td>0.04</td>
<td>2087.84</td>
<td>45.87</td>
<td>526.98</td>
<td>232</td>
</tr>
<tr>
<td>Cluster, one tree per ha</td>
<td>74325</td>
<td>92.72</td>
<td>108.07</td>
<td>0.02</td>
<td>1371.67</td>
<td>53.07</td>
<td>541.74</td>
<td>74</td>
</tr>
<tr>
<td>Cluster, one tree every ten ha</td>
<td>12252</td>
<td>97.23</td>
<td>111.91</td>
<td>0.26</td>
<td>1881.30</td>
<td>57.42</td>
<td>554.96</td>
<td>12</td>
</tr>
<tr>
<td>Small Seed (0.40-1.38cm)</td>
<td>100614</td>
<td>89.66</td>
<td>104.37</td>
<td>0.13</td>
<td>3094.18</td>
<td>51.77</td>
<td>524.54</td>
<td>100</td>
</tr>
<tr>
<td>Medium Seed (2.18-2.33cm)</td>
<td>88126</td>
<td>122.92</td>
<td>130.03</td>
<td>0.17</td>
<td>2396.46</td>
<td>80.21</td>
<td>618.81</td>
<td>88</td>
</tr>
<tr>
<td>Large Seed (3.27-5.32cm)</td>
<td>82363</td>
<td>134.58</td>
<td>128.29</td>
<td>0.11</td>
<td>2650.49</td>
<td>95.30</td>
<td>618.87</td>
<td>82</td>
</tr>
</tbody>
</table>

In regards to tree abundance and distribution scenarios, it is clear that scenarios with greater potential for longer seed dispersal distances are those with the most reproductive trees (ten and one tree per ha); less availability of fruiting trees affects not only the probability of LDD but the number of dispersal events occurring in each simulation (fig.10; Tables 4, 5). Also, the number of dispersal events per simulation varies greatly between these six scenarios; there is greater asymmetry of dispersal events in clustered distribution of fruiting tree scenarios (Table 5, Appendix 2a), which indicates clustered aggregations of canopy trees are more sensitive to have less dispersal events, even with higher tree abundance. Similarly, random fruiting tree distributions with very low tree densities, suffered greatly with the loss of dispersal events (Table 5).

In the case of seed size-GRT scenarios, even though longer distances of dispersal are obtained in the first scenario with smaller seed (therefore smaller GRT; Table 4, fig 11), number of dispersal events do not seem to vary greatly between seed size scenarios (Table 5, Appendix 2b).
Fig. 10. Seed dispersal distance frequency distributions for six tree abundance and distribution scenarios. All different colored curves represent individual ten thousand simulations that contain more than ten values of seed dispersal events per iteration.

Fig. 11. Seed dispersal distance frequency distributions for three seed size-GRT scenarios. All different colored curves represent individual ten thousand simulations that contain more than ten values of seed dispersal events per iteration.
Table 5. Number of seed dispersal events for every simulated scenario of seed dispersal by howler monkeys.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Iterations</th>
<th>Mean</th>
<th>SD</th>
<th>CV</th>
<th>Min</th>
<th>Max</th>
<th>Asymmetry</th>
</tr>
</thead>
<tbody>
<tr>
<td>Random ten trees per ha</td>
<td>10000</td>
<td>39.81</td>
<td>2.92</td>
<td>7.33</td>
<td>16</td>
<td>50</td>
<td>13.63</td>
</tr>
<tr>
<td>Random one tree per ha</td>
<td>10000</td>
<td>9.7</td>
<td>3.2</td>
<td>33.01</td>
<td>0</td>
<td>25</td>
<td>3.03</td>
</tr>
<tr>
<td>Random one tree every ten ha</td>
<td>10000</td>
<td>1.14</td>
<td>1.27</td>
<td>110.71</td>
<td>0</td>
<td>11</td>
<td>0.90</td>
</tr>
<tr>
<td>Cluster ten trees per ha</td>
<td>10000</td>
<td>23.22</td>
<td>17.33</td>
<td>74.62</td>
<td>0</td>
<td>54</td>
<td>1.34</td>
</tr>
<tr>
<td>Cluster one tree per ha</td>
<td>10000</td>
<td>7.43</td>
<td>10.96</td>
<td>147.4</td>
<td>0</td>
<td>38</td>
<td>0.68</td>
</tr>
<tr>
<td>Cluster one tree every ten ha</td>
<td>10000</td>
<td>1.23</td>
<td>2.38</td>
<td>194.06</td>
<td>0</td>
<td>16</td>
<td>0.52</td>
</tr>
<tr>
<td>Small Seed (0.40-1.38cm)</td>
<td>10000</td>
<td>10.06</td>
<td>3.34</td>
<td>33.18</td>
<td>0</td>
<td>24</td>
<td>3.01</td>
</tr>
<tr>
<td>Medium Seed (2.18-2.33cm)</td>
<td>10000</td>
<td>8.81</td>
<td>2.75</td>
<td>31.18</td>
<td>0</td>
<td>20</td>
<td>3.20</td>
</tr>
<tr>
<td>Large Seed (3.27-5.32cm)</td>
<td>10000</td>
<td>8.24</td>
<td>2.51</td>
<td>30.49</td>
<td>0</td>
<td>20</td>
<td>3.28</td>
</tr>
</tbody>
</table>

Spatial Patterns of Seed Deposition and Latrines

Simulated spatial patterns of seed deposition by howler monkeys (fig. 12) help illustrate seed clustering that exemplify resting or feeding tree sites that become latrines. It also illustrates how some non-latrine depositions are located within these same clusters of seeds; meaning that a monkey could carry seeds from one eating site to another and still disperse them far from the source but not necessarily in dung low density sites. Also, only highly abundant tree scenarios (random and clustered) show significantly aggregated spatial patterns of seed deposition for the simulation evaluated (Appendix 3) for all nine scenarios, mainly because as tree abundance is reduced, so are seed dispersal events and therefore the amount of data is reduced for the K test analysis.
Fig. 12 Howler monkey spatial patterns of seed deposition for one of the ten thousand simulations (that represents the 99th percentile of maximum distances), their associated probability of occurrence, and distances between depositions for six tree abundance and distribution scenarios and three seed size-GRT scenarios. Triangles represent latrine site seed depositions, and circles are non-latrine.

Home ranges obtained from spatial seed deposition patterns (fig. 12) of with minimum convex polygons are shown in Table 6, along with other metrics that could be extracted to help quantify differences between howler monkey seed dispersal scenarios. In this regard it is interesting to see how home range values for all different scenarios tend to follow the same pattern as Euclidean distances (see below).
Table 6. Spatial patterns of seed deposition metrics for one of the ten thousand simulations for nine different scenarios (that represents the 99th percentile of maximum distances).

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Frame Area (ha)</th>
<th>Home Range (ha)</th>
<th>No. Disp. Events</th>
<th>Centroid Mean (m)</th>
<th>No. of Eucl.Dist</th>
<th>Euclidean Mean (m)</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Random 10 trees per ha</td>
<td>493.58</td>
<td>157</td>
<td>39</td>
<td>379.50</td>
<td>741</td>
<td>982.05</td>
<td>21.44</td>
</tr>
<tr>
<td>Random 1 tree per ha</td>
<td>362.84</td>
<td>94</td>
<td>11</td>
<td>363.27</td>
<td>55</td>
<td>884.05</td>
<td>64.49</td>
</tr>
<tr>
<td>Random 1 tree every 10 ha</td>
<td>100.06</td>
<td>6</td>
<td>3</td>
<td>275.81</td>
<td>3</td>
<td>580.74</td>
<td>137.93</td>
</tr>
<tr>
<td>Cluster 10 trees per ha</td>
<td>558.32</td>
<td>207</td>
<td>45</td>
<td>436.27</td>
<td>990</td>
<td>1077.83</td>
<td>21.99</td>
</tr>
<tr>
<td>Cluster 1 tree per ha</td>
<td>91.64</td>
<td>14</td>
<td>13</td>
<td>185.52</td>
<td>78</td>
<td>308.67</td>
<td>20.77</td>
</tr>
<tr>
<td>Cluster 1 tree every 10 ha</td>
<td>114.02</td>
<td>21</td>
<td>8</td>
<td>224.41</td>
<td>28</td>
<td>389.68</td>
<td>58.43</td>
</tr>
<tr>
<td>Small Seed (0.40-1.38cm)</td>
<td>157.00</td>
<td>3</td>
<td>5</td>
<td>329.21</td>
<td>10</td>
<td>608.91</td>
<td>125.19</td>
</tr>
<tr>
<td>Medium Seed (2.18-2.33cm)</td>
<td>230.28</td>
<td>72</td>
<td>8</td>
<td>311.21</td>
<td>28</td>
<td>738.23</td>
<td>70.04</td>
</tr>
<tr>
<td>Large Seed (3.27-5.32cm)</td>
<td>118.01</td>
<td>16</td>
<td>9</td>
<td>228.05</td>
<td>36</td>
<td>573.11</td>
<td>61.37</td>
</tr>
</tbody>
</table>

The analysis of Euclidean distances between dispersal events for every spatial patterns of seed depositions (fig. 12) showed that scenarios that have trees with random distribution are significantly different from those with aggregated fruiting tree distributions, except in the case of tree species of clustered aggregations that have very high tree densities per ha (ANOVA: \( F_{5,1889} = 26.82, P < 0.0001; \) fig. 13A). The third random scenario with lowest abundance of fruiting trees had only three dispersal events; therefore this analysis shouldn’t be conclusive for this scenario. On the contrary, the Euclidean distances for scenarios of seed size-GRT do not show statistical differences between them (ANOVA: \( F_{2,71} = 1.80, \) P=0.1736; fig. 13B).

Fig. 13. Mean Euclidean distance reported between every seed dispersal event for each scenarios spatial pattern of seed deposition; bars are standard error. (A) Six different scenarios for reproductive tree abundances and distribution types: scenarios Rand 1, 2, 3, and Clust 1, 2 and 3 symbolize random distribution ten trees per ha, one tree per ha, and one tree every ten ha, and cluster distributions ten trees per ha, one tree per ha, and one tree every ten ha respectively. (B) Three seed size-GRT scenarios: scenarios Seed 1, 2 and 3 signify Small Seed (0.40-1.38cm), Medium Seed (2.18-2.33cm), and Larger Seed (3.27-5.32cm) respectively.
Simple linear regression tests between home range and maximum dispersal distances confirm the existing relationship among these two variables, for all dispersal scenarios except random distribution with the lowest tree density (see Appendix 4), probably due to very few data reported for this scenario (fig. 14 and 15).

**Fig. 14.** Linear regressions based on home range and maximum dispersal distances for all simulated tree abundance and distribution scenarios of seed dispersal that contain more than six dispersal events.
Lastly, highest seed densities from total simulations occurred underneath sleeping sites or latrines (93.6%), and only 6.4% of all seed defecations occurred in non-latrine sites (that could represent the better part of in-transit seed deposition patterns). The long tail of the seed dispersal curves could have resulted from dispersal events under in-transit sites, as seeds dispersed out of latrines (non-latrine) had longer dispersal distances than those in latrines, with a mean distances of seed deposition (maximum distance reported) of 125.74m (2087.8m) and 86.38m (2421.7m) respectively. This difference proved significant within each scenario that was tested (Rand1: \( t_{27109} = 42.1, p < 0.001 \); Rand2: \( t_{6554} = 19.54, p < 0.001 \); Rand3: \( t_{725} = 5.89, p < 0.001 \); Clust1: \( t_{16314} = 34.73, p < 0.001 \); Clust2: \( t_{5106} = 17.73, p < 0.001 \); Clust3: \( t_{798} = 7.32, p < 0.001 \)).

It is interesting to see that in the case of seed size-GRT scenarios, even though the total highest seed densities occurred underneath sleeping sites or latrines (86.1%), and 14% of all seed defecations occurred in non-latrine sites; percentages of occurrence varied between scenarios (fig. 16), specially for medium-sized seeds, contrary to tree abundance and distributions scenarios that maintained percentage of occurrence almost identical between scenarios. Regardless, non-latrine seed depositions obtained significantly longest distances compared to latrine sites, with a mean distances of seed deposition (maximum distance reported) of 138.05m (2396.5m) and 110.24m (3094.2m) respectively (Seed1: \( t_{3057} = 12.93, p < 0.001 \); Seed2: \( t_{43896} = 17.88, p < 0.001 \); Seed3: \( t_{7441} = 11.25, p < 0.001 \)).
Fig. 16. Percentage of seeds deposited under latrine and non-latrine sites according to all different simulated scenarios of seed dispersal by howler monkeys. (A) Scenarios Rand 1, 2, 3, and Clust 1, 2 and 3 symbolize random distribution ten trees per ha, one tree per ha, and one tree every ten ha, and cluster distributions ten trees per ha, one tree per ha, and one tree every ten ha respectively. (B) Scenarios Seed 1, 2 and 3 signify Small Seed (0.40-1.38cm), Medium Seed (2.18-2.33cm), and Larger Seed (3.27-5.32cm) respectively.

DISCUSSION

Dispersal Distances and Frequency of LDD

Even though seeds that are ingested and dispersed through endozooocory show the longest dispersal distances compared to wind dispersal (Beaudrot et al. 2013), it is clear that most seeds, regardless of the vector, move short distances from the parental canopy (from zero to tens of meters, Howe and Smallwood 1982, Cain et al. 2000, Clark et al. 2005). Consistently to our results, other studies that have implemented mechanistic models of seed dispersal have also obtained leptokurtic, long-tailed kernels (Russo et al. 2006, Viana et al. 2013) that illustrate a strong inclination towards local-scale dispersal.

In the case of our models simulations, local dispersal is interpreted as the values between the 50th percentile and the mean dispersal distances reported for all scenarios, which predict a greater part of seed dispersal events occurring between 60 m and 100 m approximately, while maximum dispersal distances range from 1372-3094 m (Table 4). Previous howler monkey research has indicated mean dispersal distances between 89 and 500 meters (Milton 1980, Estrada y Coates-Estrada 1984, de Figueiredo 1993, Andersen 1999, Julliot 1996, Santamaría-Gómez 1999, Yumoto et al. 1999); and, maximum dispersal distances that have been reported go from 360 to 1200 m (Estrada y Coates-Estrada 1984, Estrada y Coates-Estrada 1991, Julliot 1996, Yumoto et al. 1999, Bravo y Zunino 2000, Bravo 2009). Some of the particular differences with previous studies can be based on the fact that they are empirical data, and most of the extremely low values where collected in fragmented forest.

According to Soons and Ozinga (2005), LDD plays a much more important role in influencing regional survival in plant species than local-distance dispersal. Although there is a
general understanding that LDD is a rare and sporadic event (Nathan 2006), its definition still remains arbitrary and strongly governed by the context of the study (Cain et al. 2000, Levey et al. 2008). Nevertheless, since our goal in this investigation is to have a better understanding of LDD in terms of migration and range expansion for canopy tree species that depend on howler monkeys for dispersal under future climate change scenarios, the 99th percentile of seed dispersal distances simulated give us an objective threshold that can be used for understanding howler monkeys LDD capacity.

Though differences in LDD distances weren’t really clear between random and cluster scenarios of tree abundance and distribution for this investigation, a strong tendency towards the reduction of LDD events is noted for scenarios with low abundance of reproductive trees (Table 4, fig. 10). This statement is also true for total number of dispersal events per simulation (Table 5). Simultaneously, in the case of seed size-GRT scenarios, small seeds presented a greater amount of LDD cases than medium and large sized-seeds (Table 4), but the overall numbers of seed dispersal events were not affected by variation in seed sizes. This suggests that the most important variable impacting seed dispersal events and the occurrence of long-distance seed dispersal events in the case of howler monkeys is the abundance and accessibility of fruit (and therefore seeds), which in this study is evaluated with reproductive tree abundance.

It does not seem odd that reproductive tree abundance (or fruit availability) resulted as the most susceptible variable for seed dispersal and LDD events, since the proximity of one tree to other fruiting trees is one of the extrinsic factors that influences frugivore movement and foraging behavior (Clark et al. 2005, Nathan 2008, Cousens et al 2010, Correa-Cortes and Uriarte 2012). In this regard, one would expect that monkeys with less availability of fruit would have to travel farther and thus promote LDD events; none the less, the greater the accessibility for fruit, the larger the amount of seeds that have a chance to be dispersed and to obtain longer distances of dispersal (Shupp et al. 2010). This result is important in relation to the ecological implications for rare canopy tree species, because their ability for LDD will influence their possibility for regional survival (Soons and Ozinga 2005).

Spatial Patterns of Seed Deposition and Latrines

Aggregation is a dominant and widespread pattern of tree species distribution in tropical and subtropical forest, which can be shaped by dispersal limitations among other mechanisms (Lin et al. 2009). Furthermore, animal-dispersed plant species show more clumped seed depositions in comparison to other dispersal syndromes (Muller-Landau et al. 2008), but howler monkeys contribute to the production of the largest aggregations of dung (and therefore seeds if fruit is consumed) among Neotropical arboreal mammals (Julliot 1996, Yumoto et al. 1999, Bravo & Zunino 2000, Andresen 2002, Bravo 2009). Consistently, our simulated spatial patterns of seed depositions coincide with the aggregation referred to by other authors, except in the case of low density fruiting trees, where fecal matter does not seem to be aggregated due to lower deposition densities (Table 6, Appendix 3).

The illustration of spatial patterns of seed deposition allows better comprehension of density and probability of seeds being deposited under certain sites, but also of “microsite” depositions (Correa-Cortes and Uriarte 2012) or secondary latrines in the case of howler monkeys. In our case, these microsites can be explained by the small degree of multimodality observed in individual simulations frequency distributions (fig. 10 and 11), that may represent aggregation beneath sleeping sites at different distances from parental trees.
(Russo et al. 2006). Basically, greater seed clustering for howler monkeys embodies sleeping tree sites that become latrines (Julliot 1996, Bravo & Zunino 2000, Bravo 2009); at the same time, low seed densities can happen by defecation of single individuals (Andersen 2002, Bravo 2012) during “in-transit” movements, that may also explain LDD events (Russo et al. 2006). In this sense, our model successfully accounts for clumped patterns of seed deposition by howler monkeys with the addition of its scattered component, as demonstrated by Bravo (2009).

Interestingly enough, our seed dispersal plots illustrate how some non-latrine depositions are located within the same clusters of seeds that represent latrines; meaning, a monkey could carry seeds from one eating or resting site to another and still disperse them far from the source but not necessarily in low-density dung sites. In this regard, Bravo (2009) also mentions how howler monkeys can roam across their home ranges during the day, to eventually return to their starting point or main sleeping tree; explaining non-latrine depositions within latrine areas.

As our analysis of variance of Euclidean distances of spatial seed deposition patterns shows, distribution of food resources or the arrangement of fruiting trees in space (in the case of this study) has an effect on spatial patterns of seed deposition; except in the case of very high density of fruiting trees (10 trees per ha in clustered scenario), in which case spatial patterns don’t show differences between tree distribution (fig. 13A). In this respect, Correa-Cortes and Uriarte (2012) emphasized that seed deposition patterns arise from the interaction of animal behavior and food distribution in time and space. Cousens et al. (2010), also highlights that the way animals move and deposit seeds are the result of the influence that arises from the relationship that intrinsic (social behavior, GRT) and extrinsic factors (fruit distribution, abundance, landscape structure) play, and has to be taken into account when simulating seed dispersal patterns. This said, seed size (hence GRT) appears to have no real effect on the distribution of seed deposition in space, at least within the reach of this study.

Correa-Cortes and Uriarte (2012) states that an animal’s movement is largely limited by its home range area. Bravo (2009), also confirmed in her study in Argentina that differences in seed dispersal distances reflected dissimilarities in the spatial use of the forest by howler monkeys. Consistently, our calculated approximations of home range values show a significant effect over maximum distances of seed dispersal for overall simulations in all scenarios in this investigation; however, home range area cannot be presumed to explain LDD on its own, as many other factors come into play. Low fruiting tree abundance, for instance, seems to affect this relationship more than seed size.

The proportion of latrine depositions was tremendously high for howler monkey simulations for all scenarios (94% and 86% respectively), in contrast with previous howler monkey studies, where percentage of latrine defecations range between 61% and 75% of deposition events (Julliot 1996, Andersen 2002, Bravo 2009). Differences with literature may be due to the fact that our study is based on a model that is affected by the behavior of its parameters; GRT, as explained below, impacts the proportion of latrine depositions; as does a subset of parameters that are constant during all simulations, like the time of day when we decide a monkey starts its daily activities (Tday), which in our case, by default is at 6 am. Nevertheless, it is clear that latrines comprise most defecation events, and some studies have revealed that latrines appear to be important sites for recruitment of the most common tree species, and some rare species as well (Anzures-Dadda et al. 2011, Bravo 2012).
The only variable that seed size affected in our study, is the proportion of seeds defecated over latrine and non-latrine sites. It is clear that distances of dispersal are significantly longer in non-latrine locations because, as stated earlier, “in-transit” seed deposition may also account for LDD events (Russo et al. 2006). As it is, our model indicates that medium-sized seeds have a greater probability of being deposited in non-latrine or in-transit sites because their 22-23 hour range of GRT is accountable for howlers defecating farther from their sleeping trees. Furthermore, the 25-30 hour GRT related to large seeds, as well as the 18-20 hour GRT associated with small seeds appear to coincide with the monkeys sleeping time, augmenting latrine defecation probabilities.

These results are important because tree species with small seeds usually rely on an extensive spectrum of dispersal vectors that benefit and compensate one another; but as seed size increases, the diversity of dispersers decreases (Bueno et al. 2013), converting howler monkeys into one of the few dispersers in charge of large seeded species fate. Two medium-sized seed species that can be dispersed by howlers and are found in our study site are Minquartia guianensis and Pouteria reticulata; both of these are hardwood tree species. Further studies must be made to understand the consequences for medium and large seeded canopy tree species.

The Howler Monkeys Role in Seed Dispersal and Implications for Conservation

Even though some studies have shown that howlers are able to disperse large amounts of seeds (Estrada and Coates-Estrada 1984, Julliot 1996) folivory rather than frugivory is their characteristic diet (Reid 2009). In this respect, it is important to consider that highly frugivorous animals are not necessarily better or more effective dispersers than opportunistic frugivores (Wenny 2001), because, in the case of howlers, their generalistic feeding behavior qualifies them to survive in changing environments with variation in food resources (Beasudrot et al. 2013). And even if the majority of their seed defecations end up in high-densities supporting local dispersal, its ecological importance should not be underestimated, as the more effective the dispersal at a local level, the greater the likelihood that dispersion between metapopulations is effective (Schupp et al. 2010).

Some studies have already categorized primates to belong to their own functional group apart from birds (Clark 2001, Beasudrot et al. 2013), but also have recognized that the community structure of tree associations that depend on primate dispersal are bound by dispersal limitations; because even though highly mobile, most monkeys will spend the greater part of their existence in the same area (Beasudrot et al. 2013). Schupp et al. (2010) recognize that although there are dispersal agents and dispersal assemblies of species (or functional groups of seed dispersers) that are more efficient than others, it is important to take into account that the merged seed dispersal patterns of all, determine the resilience of the dispersal system, and the possibility of LDD events. That is why, even if Alouatta species aren’t able to produce LDD of 100km (or longer) like migratory birds (Viana et al. 2013), their contribution and overall effect on forest structure should be noted.

Forest landscape fragmentation and climate change threaten the survival of our natural habitats (Pakeman 2001, Bertin 2008, Engler and Guisan 2009). Even though howler monkeys are considered persistent in disturbed habitats, Arroyo-Rodriguez and Dias (2009) have found evidence that high proportions of territory fragmentation and degradation do in fact adversely affect this species survival, mostly due to the reduction in food accessibility. Also, the bigger the forest area, the farther the monkeys will be able to move, increasing the
probability for LDD, successful germination and establishment; whereas in small fragments seeds have a higher probability of being deposited under adverse conditions (Serio-Silva and Rico-Gray 2002).

In time, the pressures of habitat reduction and hunting will affect howler monkey numbers, which will in turn have major ramifications on seed dispersal and the alteration of seedling communities, and thus recruitment of large-seeded tree species (Muller-Landau 2007, Beasudrot et al. 2013). We are looking at a scenario were these human-altering consequences distress the adaptation of those natural processes at the very time that climate change requires a responsive velocity for plant species to migrate to more suitable environments (Clark et al. 1998, Higgins and Richardson 1999, Beasudrot et al. 2013); especially those large-seeded low density canopy tree species that have aggregated distributions.

**Future development of the MonkeySeed Model**

Our simulation model of seed dispersal by howler monkeys (*Alouatta sp.*) has a few key areas for future development. In first place it is important to remember that seed deposition patterns pertain to just one simulated monkey, even though howlers live in cohesive social groups (a mean of 4-16 individuals per group has been reported, Chivers 1969, Mittermeier 1973, Gaulin et al. 1980, Brazza et al. 1981, Estrada 1982, Garcia 1993, Amato y Estrada 2010, Pavelka y Knopff 2004); concurrently, we do not take into consideration the amount of seed being ingested nor excreted, only the frequency of seed being consumed, and therefore expelled. Secondly, although we base our monkeys movement simulations on real field angle and velocity input data, radio-taking records would be most efficient for realistic seed dispersal simulations, as would be to include the position and number of attractive sites in howler monkeys habitats, as a means to embrace an animal's intentional trajectory movements through space (Will and Tackenberg 2008, Cousens et al. 2010, Correa-Cortes y Uriarte 2012). Finally, the inclusion in the model of landscape structure like dispersal barriers and altitudinal gradients should be considered for further studies.

**Conclusions from Our Model**

Our models results are highly influences by the behavior of its parameters. In terms of the parameters obtained by literature review, variation in the values and probability of occurrence of these values can be due to differences in the origin of the data (studies of very diverse contexts), or to the need of obtaining more information on the time that howler monkeys invest in their daily activities and their digestion. Interesting enough, the distribution of the values of movement angles that we obtained in the field do not reflect the patterns of travel movement or trails that these animals have; suggesting that more data must be obtained to make better conclusions. And, even if a sensitivity analysis was not conducted for our parameters, GRT proved to be the most sensitive parameter for longest dispersal distances as seen with medium-sized seeds; as well as fruiting tree abundance resulted most sensitive to the number of seed dispersal events.

Our motivation for the development of this model is to generate information that can help guide actions for the adaptation of climate change. This is why the results of dispersal distances generated with our *MonkeySeed* model can be applied in other modeling tools that
incorporate local and long distance dispersal distances to simulate canopy tree species distribution and migration across time, space, and future climate change scenarios.

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REFERENCES


Chivers DJ. 1969. On the daily behavior and spacing of howling monkey groups. Folia primat. 10: 48-102


Knowlton, J. and Graham, CH. 2010. Using behavioral landscape ecology to predict species responses to land-use and climate change. Biological Conservation 143: 1342-1354


Nathan, R. 2006. Long-Distance dispersal of Plants. Science, 313: 786-788


Soons MB, and Ozinga W. 2005. How important is long -distance seed dispersal for the regional survival of plant species ? Distrib Deversity, 11: 165-172


Wang, B.C., and Smith, T.B. 2002. Closing the seed dispersal loop. TRENDS in Ecology & Evolution Vol.17 No.8

