Foraging strategy of a neotropical primate: how intrinsic and extrinsic factors influence destination and residence time

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Summary

1. Most animals need to actively search for food to meet energetic requirements and live in heterogeneous environments where food resources have complex spatio-temporal patterns of availability. Consequently, foraging animals need to find a balance between effort and resource allocation while accounting for intrinsic and extrinsic factors, which are often overlooked when modelling foraging behaviour.

2. We identified the decision rules for foraging in black howler monkeys (\textit{Alouatta pigra}), according to food preferences, locations of high-quality patches and previously eaten trees, phenology of food resources and hunger state. We depicted foraging in two stages: (i) the choice of the immediate next tree and (ii) the time spent on this tree. We used a recently developed model for inference of movement processes, incorporating resource selection functions into a Markov chain framework.

3. We found that monkeys tend to move to preferred tree species at each step. However, we did not find conclusively that, at each step, monkeys direct their movements to reach high-quality patches. In fact, they were using these patches intensively, thus limiting the possibility to move towards other high-quality patches. Time spent on a tree was positively and strongly affected by the presence of preferred food items, but not by its species. We also showed that time spent on trees increased as a function of satiation state. We suggest that the strategy adopted by black howlers tends to be efficient because choosing preferred trees at each step and spending more time where preferred resources are available should favour energy intake and restrain movement costs.

4. This study showcases a modelling framework that can be widely used in ecology to describe movements as a combination of multiple attraction and repulsion sources, such as mates and competitors.

Key-words: \textit{Alouatta pigra}, dietary preference, food competition, foraging, movement monitoring, residence time, resource selection function

Introduction

Most animals move to satisfy intrinsic needs that insure their survival. Observed movement patterns are the result of complex interactions between an animal and the characteristics of its environment, such as food distribution, competition and predation (Nathan \textit{et al.} 2008). One major driver of animal movement is foraging, because most animals must actively search for food resources to satisfy their energetic requirements. Yet, most animals live in fluctuating environments, where food resources are seasonal and have complex spatio-temporal patterns of...
renewal and deterioration. To survive in variable environments, animals must adopt efficient foraging strategies to find their food resources.

Optimal foraging theory states that natural selection should retain foraging strategies that maximize fitness, which is often translated into maximization of energy intake per unit time and minimization of energetic expenditures (MacArthur & Pianka 1966). This theory has led to the exploration of many aspects of foraging decisions, such as (i) optimal food patch choice; ii) optimal time allocation to patches (known as the marginal value theorem; see Charnov 1976); (iii) optimal food choice and (iv) optimal movement pattern between resources (Pyke, Pulliam & Charnov 1977). According to these models, an optimal forager should choose a food type that maximizes energy intake per unit of time, choose a patch that maximizes the return, that is, the net energy gain of the patch when the energy expenditure required to move to this patch is considered and leave the patch when its return becomes lower than the average return in the environment (Stephens, Brown & Ydenberg 2007). It is also expected that interpatch movements are efficient, that is, that the movement pattern maximize resource encounter given the spatio-temporal distribution of the resource (Cody 1974; Pyke 1978).

These foraging models simplify the foraging process and their assumptions are rarely met (Pyke 1984; Stephens, Brown & Ydenberg 2007). For example, these models assume that the individuals have complete knowledge of the availability and location of food items or patches so that the foraging decisions are optimal (MacArthur & Pianka 1966; Charnov 1976; Pyke, Pulliam & Charnov 1977). However, animals in natural contexts are expected neither to forage optimally nor to be omniscient. Consequently, these models have received mitigated support from empirical studies (Stephens, Brown & Ydenberg 2007). Many adaptations have been proposed to make optimal foraging models more representative of observed foraging strategies. Such adaptations include the consideration of central-place foraging (Pyke 1984), digestion limitations (Jeschke, Kopp & Tollrian 2002) or stochasticity in search patterns (Bartumeus & Catalan 2009). Many other intrinsic and extrinsic factors such as motion capacities, hunger and environmental conditions outside food patches, can greatly affect the movement patterns (Nathan et al. 2008; Martin et al. 2013). As noted by Holyoak et al. (2008), most movement studies, including those describing foraging processes, often neglect the role of certain factors, especially intrinsic ones. Moreover, most models in optimal foraging studies focus on patch or resource depletion and tend to disregard the effect of intrinsic and extrinsic conditions found outside patches on interpatch movements (Bartumeus & Catalan 2009).

The goals of this study were threefold. First, we aimed to describe the foraging strategy of an endangered neotropical primate, the black howler monkey (Alouatta pigra Lawrence 1933) using both intrinsic and extrinsic factors. Second, we wanted to characterize the foraging performance of the monkey troops based on the general predictions provided by the optimal foraging theory. Finally, we aimed to provide a statistical approach for inference of movement processes that could be widely used in foraging studies but also in other movement studies. Black howlers offer great opportunities for the study of foraging strategy in a natural context. They use relatively small home ranges (0.4–21 ha; Loudon 2000; Gavazzi et al. 2008; Rizzo & Stahler 2009). They have a fairly inactive lifestyle and move relatively slowly compared to other primate species (Pavelka & Knopff 2004). This allows an observer to follow them easily and distinguish movements that are related to foraging from other movements. Moreover, they show marked preferences for some tree species and food items, which they may actively seek in their territories. Fig (Ficus sp.), sapodilla (Manilkara zapota (L.) P. Royen) and Mayan breadnut (Brosimum alicastrum Sw.) are reported to be key species in the black howler’s diet, especially for their fruits (Silver et al. 1998; Pavelka & Knopff 2004; Rizzo 2004; Rivera & Calmê 2006). Since these resources are patchily distributed in the environment in both space and time, monkeys are faced with the problem of where and how to search for their food efficiently.

We hypothesized that black howlers would be efficient foragers (i) by moving directly towards high-quality patches of trees; (ii) by allocating more time on trees with potentially high rewards and (iii) by not revisiting feeding sites, which would tend to maximize net energy gain (Stephens, Brown & Ydenberg 2007). Direct movements towards high-quality patches of trees should lead to the use of nonpreferred trees as stepping stones to reach high-quality patches. We also hypothesized that intrinsic factors such as food preferences and hunger would determine foraging strategy by affecting the attraction strength of food resources. To test our hypotheses, we designed a model depicting the movement of individuals as a function of intrinsic (dietary preferences, hunger state, motion capacities) and extrinsic factors (distribution of food resources and patches and possible paths based on motion capacities). We predicted that black howler monkeys would move with (i) higher probability to high-quality patches of trees; (ii) equal probability to preferred and nonpreferred trees used as stepping stones towards high-quality patches; and (iii) lower probability to trees upon which they have already fed. We also predicted that black howler monkeys would spend more time (iv) on trees of preferred species, (v) on trees bearing preferred food items and/or (vi) if they were hungrier. We assumed that:

Knowledge of the location of preferred trees should drive monkey movements at large spatial scales, that is, out of their detection range. Home range localization and size is defined by the animal’s capacities to sample and remember the information about its resources, stored in a cognitive map, and to use this information for its own benefit (Van Moorter et al.
Thus, black howlers must have a good knowledge of the spatial distribution of the resources in their home range, especially if home range is small and less information must be stored;

2 The species and food item preferences represent a favourable choice. It has been suggested that the energetic content of food items influenced dietary preferences (Provenza 1995). Black howlers’ preferred species and food items are known to be either highly nutritious (i.e. *Brosimum alicastrum* and *Manilkara zapota*; Estrada & Coates-Estrada 1985) or less nutritious but available year-round (*Ficus* spp.; Janzen 1979);

3 After a feeding bout, howlers remain generally on the same tree for resting, a behaviour associated with their slow-digestion characteristics (Milton 1981).

**Materials and methods**

**STUDY SITE**

The study was conducted in and near the Calakmul Biosphere Reserve (CBR), located in the south-central Yucatan Peninsula of Mexico (18°07′21″N, 89°47′00″W). Elevations in the CBR range from 260 to 385 m. The climate is tropical with mean annual temperatures fluctuating between 22 and 26 °C. Annual rainfall is highly variable, but generally ranges between 900 and 2000 mm. Each year includes two distinct seasons: the wet season (June–November) and the dry season (December–May). The vegetation is composed of low and medium semievergreen forest, low and medium semideciduous forest, and high evergreen forest (Vester et al. 2007).

**STUDY TROOPS**

Three troops of black howler monkeys were selected; two troops were located at the Calakmul archaeological site, within the southern section of the CBR (18°07′21″N, 89°47′00″W), while one troop was on the Conhuas communal forest area, at the northern edge of the southern section (18°32′06″N, 89°53′40″W). Study troops were composed of 4–9 individuals, with at least one adult male and one adult female (N = 20). Monkeys were individually identified using sex, size and specific traits, such as fur characteristics and scars. Troop habituation to the presence of observers was not required for the troops at the archaeological site because of their regular contacts with the CBR staff, tourists and other researchers. However, 3 days of habituation were required for the Conhuas troop before monkeys stopped fleeing from observers or howling in their presence.

**MOVEMENT MONITORING**

Since black howler monkeys are strictly arboreal and move relatively slowly compared to other arboreal primates, we were able to follow closely their daily movements and make direct observations on their behaviour. We monitored the troops from September to December 2009 and from February to April 2010, covering a wet and the following dry season. Each troop was followed for a maximum of 7 hours per day and 4 days each month, for an average total of 105-7 hours per troop. We assumed that movements of an individual represented the movements of the whole troop because black howlers form cohesive groups and do not separate while moving (Byrne 2000). Therefore, we followed only one individual at a time, preferentially the individual that was leading the troop’s movements (N = 16 focal individuals). If this individual went out of sight for more than four trees in a row, another individual was randomly chosen among those remaining visible.

We recorded 54 trajectories, which we divided into 112 subtrajectories. A subtrajectory was defined as the continuous movement record for a given focal individual; a new subtrajectory started when another focal individual had to be followed or when trajectories were interrupted by movements that were not related to foraging. Trees in subtrajectories were located with a global positioning system (GPS, <10 m precision), with their distances and azimuths from the GPS-positioned tree recorded to maintain precision. We identified the species, measured the diameter at breast height (DBH, cm at 1-3 m) and evaluated the phenological state (proportion of young and mature leaves, presence of buds, flowers and ripe or unripe fruits) for all trees that were visited, even those upon which monkeys did not feed. Positions of all trees for which the crowns were directly connected to those of visited trees were also registered to evaluate all possible movement options for howlers.

**BEHAVIOURAL OBSERVATIONS**

Continuous focal observations of behaviours were simultaneously conducted to locate feeding activities both spatially and temporally, and to distinguish foraging movements from other movements. Observed behaviours were classified into four categories: feeding, moving, resting and other (Appendix S1). When feeding behaviours were recorded, items that were consumed were identified. All movements not related to foraging, that is, those associated to the category other (e.g. confrontation between troops or fleeing) were removed from the analysis.

**PHENOLOGICAL MONITORING**

To explore phenological tracking of resources by black howlers, we monitored fruiting peaks for each species that was known to be consumed and tested if monkeys preferentially moved to certain trees belonging to these species during their fruiting periods. Every week during the study, we monitored the phenological state of 400 trees that were located within the troops’ home ranges. We used the number of trees bearing fruits as a function of time since the beginning of the study as a proxy for general phenological variation throughout the study period (further details are provided in The Model section).

**ATTRACTION TO TREES, FOOD ITEMS AND FEEDING PATCHES**

To quantify the feeding preferences of black howlers for tree species and food items, we constructed two indices of attraction. The attraction index for tree species (referred to as the rank index) was based on a selectivity index that had been previously calculated for black howlers in the CBR (Rivera & Calmé 2006). The selectivity index used by Rivera & Calmé (2006) was calcu-
related with the Chesson’s index ($e_i$, Chesson 1983), which considers the proportion of a species in the diet, weighted by its proportion in the environment, and the sums of these proportions for all species evaluated. This index ranges from -1 (negatively selected species) to 1 (positively selected species). From the Rivera & Calmé (2006) selectivity index, we attributed an attractiveness value ranging from 0 to 4 to all species that were recorded to having been eaten during our study, with four being the most preferred species. We modified the Rivera & Calmé (2006) index because several species used in their calculations did not appear to be consumed during our study. Since Chesson $e_i$ is affected by the total number of species included in the analysis, we converted the original selection values into more simple ones that were still representative of the order of selection.

We also calculated an attraction index for the food items that were recorded as being eaten during the study (referred to as the food item index), based on preferences outlined in previous studies on howlers (Silver et al. 1998; Pavelka & Knopff 2004; Rivera & Calmé 2006). This index was calculated by dividing the rank of the food item by the total number of items that were known to be consumed for a given species in our study. It ranged from 0 to 1, with 1 corresponding to the most preferred. Tree species and food items that were consumed during the study, and their associated attractiveness ranks are presented in Appendix S2.

We also expected that large trees belonging to preferred species, and the trees surrounding them, were more likely to be visited than other trees. Thus, we delineated areas, named hereafter as patches, which consisted of trees belonging to the three most preferred species ($Ficus$ sp., $Manilkara zapota$ and $Brosimum alicastrum$) with a DBH $> 50$ cm (discriminating 77% of all the trees visited during observations). The patches also included all trees that were located within a radius of 40 m, a distance that generally included all immediate trees surrounding the main tree.

### THE MODEL

We modified a recently developed movement model, which incorporates resource selection functions into a Markov chain framework (Colchero et al. 2011). We modelled movements that were recorded in subtrajectories as a series of discrete steps, $t$. Each step was divided into two distinct stages: (i) the movement from one tree to the next (destination tree); and (ii) the time spent on the destination tree. We constructed the model so that at each step, we could determine whether the tree of destination reduced the distance to the nearest high-quality patch. Although the original model proposed by Colchero et al. (2011) used a Bayesian framework to better account for missing data and measurement error, our data set did not have any of these data limitations and, therefore, it was sufficient to draw inferences on both processes from a maximum-likelihood approach (Geyer 1992; Brooks et al. 2011).

Let $x_i$ represent the location of tree $i$ and $X_{o,t}$ be a random variable for the location of troop $g$ at step $t$. The first stage of the model evaluates the multinomial probability that troop $g$ moves from a tree of origin $i$ to a tree of destination $j$ within a time interval $\Delta t$ and within an observation window $w_j$, centred on tree $i$. We defined the observation window $w_j$ as all trees for which the crowns were connected to the crown of the tree of origin, not including the tree of origin such that $i \notin w_j$. We deemed it sufficient to only include close neighbouring trees since howler monkeys usually move between trees by walking along connecting branches. We considered that the time required to leave a tree and enter the next is negligible. Thus, we assumed that $\Delta t$ is constant. The multinomial probability of movement from the origin tree to the destination tree is

\[
p(X_{o,t}, \Delta t = x_j | X_{o,t} = x_i, z_{ij}, b, c) = \frac{\exp[m(z_{ij}, b, c)]}{\sum_{c=1}^{s} \exp[m(z_{ij}, b, c)]}
\]

where $m(z_{ij}, b, c)$ is a link function that relates the vector of covariates, $z_{ij}$, associated with tree $j$ with the probability of moving from the tree of origin to the tree of destination. Vectors $b$ and $c$ represent parameters linking these covariates to the movement process. This link function is calculated as

\[
m(z_{ij}, b, c) = b_1R_j + b_2D_j + b_3P_j + b_4E_j + \sum_{s=1}^{s} [c_sH_jI_j]
\]

where $R_j$ is the attraction to the species of the destination tree $j$ (Rank), $D_j$ is the distance between the trees of origin and destination (Dist), $P_j$ is the Euclidean distance between the tree of destination and the closest patch of highly attractive trees (Patch; set to 0 when monkeys were using a patch), $E_j$ is the distance between the tree of destination and the closest tree where monkeys had previously eaten during the whole study period (Eaten), $H_j$ represents the time since the start of the study in days, $I_j$ is an indicator that assigns 1 if the tree belongs to species $s$ and 0 otherwise and $S$ is the total number of species recorded in the study. These last variables were used to estimate the effect of phenology on the attractiveness of the trees of destination, measured by the species-specific parameters $c_s$. Alternatively, to account for nonlinear (i.e. quadratic) phenological changes, we tested the following link function

\[
m(z_{ij}, b, c) = b_1R_j + b_2D_j + b_3P_j + b_4E_j + \sum_{s=1}^{s} [c_{1,s}(H_j - c_{2,s})^{2}I_j]
\]

where parameter $c_{1,s}$ measures the strength of attractiveness of the species $s$ of tree $j$ as a function of time, and parameter $c_{2,s}$ measures the time when this attractiveness reaches its maximum. Due to the poor performance of this alternative model (all parameters $c_{2,s}$ were larger than the duration of the study), we only report results from Eqn. 2a.

The second section of the model considers the time that troop $g$ spends in the tree of destination $j$ at step $t$, which we label as $y_{g,i,t}$. We assumed that the time spent in the destination tree declined exponentially as a function of the covariates, for which we used an exponential generalized linear model (GLM; Nelder & Wedderburn 1972) of the form $y_{g,i,t} = \exp(\lambda_{j,t})$, where $\lambda_{j,t}$ is the rate parameter for which the inverse represents mean time spent in each tree. We modified the canonical link to accommodate negative parameter values, such that

\[
\lambda_{j,t} = \exp(-q(y_{g,i,t}, a))
\]

where $q(y_{g,i,t}, a)$ is a link function with parameter vector $a$ that relates the vector of covariates $y_{g,i,t}$ to the time spent on tree $j$. This link function was calculated as

\[
q(y_{g,i,t}, a) = a_1R_j + a_2F_j + a_3K_j
\]

where $R_j$ corresponds to the species attractiveness rank as explained above, $F_j$ is the attractiveness rank of the most preferred food item that was available in the destination tree during
the recording day (Part), and \( K_{xy} \) is a proxy for satiation state. This proxy for the satiation state was calculated as the amount of time spent eating earlier in the day, weighted by the time spent foraging actively, which included eating and searching for food in a tree (Eaten2). If we assume that the time spent eating is a function of the amount of food ingested, this ratio represents the return on the food ingested earlier in the day, and thus approximates the satiation state of the animal. Since howlers eat regularly and have slow gut-passage times compared to other species (Milton 1981), we included in the analysis all previous feeding events in the same day, not only the last one. Definitions and expected effects of covariates are presented in Table 1.

As mentioned above, the data structure allowed us to draw inference for movement processes from a maximum-likelihood approach. Thus, we constructed the likelihood function as

\[
L(\mathbf{a}, \mathbf{b}, \mathbf{c}, \mathbf{x}, \mathbf{y}, \mathbf{W}, \mathbf{Z}, \mathbf{V}) = \prod_{g=1}^{G} \prod_{i=1}^{T_g} \pi(x_{ij}, D_i, W_i, Z_i, \mathbf{a}) \pi(y_{ij} | y_{ij}, \mathbf{a})
\]

where \( G \) corresponds to the total number of groups (i.e. 3), \( T_g \) is the total number of steps per group, \( \mathbf{a}, \mathbf{b} \) and \( \mathbf{c} \) are parameter vectors to be estimated, \( \mathbf{x} \) is the vector of all destination trees, \( \mathbf{y} \) is the vector of times spent on each destination tree, \( \mathbf{W} \) is a matrix of observation windows, and \( \mathbf{Z} \) and \( \mathbf{V} \) are design matrices of covariates for processes of movement to, and time spent within, the destination trees. Maximum likelihood estimates (MLEs) for all parameters were obtained using a Metropolis algorithm within a Markov chain Monte Carlo method (Geyer 1992; Beerli & Felsenstein 2001; Clark 2007; Brooks et al. 2011) with 50 000 iterations and a burn-in of 5 000 iterations. We tested 10 different combinations of the seven covariates that have been described above (Table 2). For model selection, we used Akaike Information Criterion (AIC, Akaike 1974). We performed all statistical analyses in R 2.12.2 (R Development Core Team 2011) and required the libraries \texttt{mvtnorm} and \texttt{msm} (Genz, Bretz & Hothorn 2006; Jackson 2011).

### Results

Two models among our candidates performed as well in explaining the data, with a difference in AICs of <2 (Table 2). The model receiving the most support included all covariates except the effect of general species phenology on the probability of moving to the destination tree (model 1), while the second model ignored this covariate and the attraction to tree patches. Model probabilities among the set of models that were tested were 0.43 and 0.33 for models 1 and 2, respectively, suggesting that both models supported the data equally well. However, the slope parameter associated with the distance to the nearest high-quality patch, \( b_{\text{patch}} \), which appeared in model 1 but not in model 2, did not significantly differ from 0 (mean: 0.003 \pm 0.003, \( P = 0.056 \)). We considered model 2 to be more parsimonious and to explain better the observed data on movement to, and time spent on, the destination tree.

The probability of moving to the destination tree decreased with increasing distance between the tree of origin and the tree of destination (Table 3). High attractiveness ranks (most selected species) of the destination tree increased the probability of moving to that tree; the

| Table 1. Descriptions and expected effects of covariates on the probability of moving to a destination tree or to leave the destination tree |
|-----------------------------|-----------------|---------------------------------|-----------------|
| Probability of moving to a destination tree | Covariates | Description | Expected effects |
| Rank | Distance in metres between tree of origin and tree of destination. Attractiveness rank of tree of destination, based on an independent electivity index of tree species consumed by Alouatta pigra in Calakmul Biosphere Reserve (Rivera & Calmé 2006). Ranks range from 0 to 4, with 4 being the most strongly selected species. | Negative |
| Part | Distance between destination tree and nearest patch border. Patches were defined as discrete areas of attraction, centred on patches of species with rank of 4 and DBH > 50 cm, and covering a 40 m radius around attraction centres. | Negative |
| Phenol | Linear model of phenology as a function of time since the beginning of the study (15 September 2009). Since it was impossible to assess phenological states for all trees for all dates, time since the beginning of the study was used as a proxy for general phenological variation throughout the study period. | Species-dependent |
| Probability of leaving a destination tree | Rank2 | Attractiveness rank of the destination tree (see Rank). Attractiveness rank of the most preferred food item available in the actual tree, ranging from 0 to 1, with 1 being the most preferred part. This attractiveness rank is species-specific and only applies to tree parts known to be consumed by Alouatta pigra. | Positive |
| Part | Attractiveness rank of the most preferred food item available in the actual tree, ranging from 0 to 1, with 1 being the most preferred part. This attractiveness rank is species-specific and only applies to tree parts known to be consumed by Alouatta pigra. | Positive |
| Eaten2 | Satiation state, which is the amount of time spent eating earlier in the recording day, weighted by the amount of time spent foraging actively (which included eating and searching for food items in the same tree). | Negative |
probability of moving to a tree with the maximum ranking was one-third greater than that of moving to a tree with the lowest ranking (Fig. 1). The distance between the destination tree $j$ and the nearest tree where monkeys had been seen eating previously during the study period had a weak and positive effect on the probability of moving to that tree.

The time spent by howlers on a tree strongly increased with the availability of highly ranked food items, while it slightly decreased with the attractiveness of the tree (Fig. 2a, b). Also, the time spent on a tree increased when the groups had spent more time eating during the day (Fig. 2c).

**Discussion**

This study aimed to describe the foraging strategy of black howler monkeys, to consider the performance of this strategy and to provide a statistical approach for modelling animal movements as a result of multiple attraction and repulsion sources that could be applied in various ecological contexts. We present here a discussion for the two movement stages, which is the movement to a destination tree and the time spent in this tree. Then, we discuss these results with the perspective of foraging performance and consider the strengths of our modelling approach.

**MOVING TO A DESTINATION TREE**

The movement to a destination tree was influenced by the distance separating the origin and destination trees, the preference rank of a destination tree, the distance to trees where monkeys had been seen eating earlier during the study and, to a lesser extent, the distance to the nearest high-quality patches. First, monkeys preferred moving to closer destination trees. Because all destination trees were connected by their crowns to the tree of origin, shorter distances can be interpreted as monkeys either choosing small trees that were closer to one another or choosing trees that were not necessarily smaller but had strongly overlapping crowns. Unfortunately, our data do not allow us to distinguish between these two possibilities.

### Table 2. Tested covariate combinations for movement and time spent on a tree, and their associated AIC and ΔAIC values that were obtained by likelihood maximization. Suffixes pr and pr represent the probability of moving to a destination tree and leaving a destination tree, respectively. The S value in the number of parameters column refers to the number of tree species recorded during the study.

<table>
<thead>
<tr>
<th>ID</th>
<th>Model</th>
<th>Number of parameters</th>
<th>AIC</th>
<th>ΔAIC</th>
<th>Model weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>prm(Dist, Rank, Patch, Eaten), pr(Rank2, Part, Eaten2)</td>
<td>7</td>
<td>23451</td>
<td>0</td>
<td>0.53</td>
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<td>2</td>
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<td>6</td>
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<td>0.5</td>
<td>0.42</td>
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<tr>
<td>3</td>
<td>prm(Dist, Rank, Patch), pr(Rank2, Part, Eaten2)</td>
<td>6</td>
<td>23456</td>
<td>5.2</td>
<td>0.04</td>
</tr>
<tr>
<td>4</td>
<td>prm(Dist, Rank), pr(Rank2, Part, Eaten2)</td>
<td>5</td>
<td>23485</td>
<td>6.4</td>
<td>0.02</td>
</tr>
<tr>
<td>5</td>
<td>prm(Dist, Rank, Patch, Eaten, Phenol), pr(Rank2, Part)</td>
<td>6 + S</td>
<td>23554</td>
<td>103.0</td>
<td>0.00</td>
</tr>
<tr>
<td>6</td>
<td>prm(Dist, Rank, Patch, Eaten, Phenol), pr(Part, Eaten2)</td>
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</tr>
<tr>
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<tr>
<td>8</td>
<td>prm(Dist, Rank, Patch, Eaten, Phenol), pr(Rank2, Eaten2)</td>
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<tr>
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<td>6 + S</td>
<td>35297</td>
<td>11845.4</td>
<td>0.00</td>
</tr>
</tbody>
</table>

### Table 3. Means and standard errors of the parameters related to the choice of destination tree ($b$ parameters), and the parameters associated with the time spent in destination tree ($a$ parameters) for the model offering the best fit to the observed movement data (model 2).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Mean value</th>
<th>Standard error</th>
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<td>$a_{\text{Dist}}$</td>
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<td>$a_{\text{Rank}}$</td>
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<td>$0.0016$</td>
</tr>
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We showed that tree species preferences affected the foraging decision of the troops, but not in the way we expected. While we expected monkeys to move directly to high-quality patches and use trees on the way only as stepping stones, we found that they moved with higher probability to preferred tree species at each step. Our model showed that the location of high-quality patches had a weak effect on the monkeys’ movements ($P$-value = 0.056). There are two important reasons why we believe that, although weak, the signal is real. First, by taking a closer look at the spatial utilization of territories, we found that monkeys were actually using high-quality patches most of the time (Fig. 3). Movements in patches were more frequent than movements outside patches, thus masking the attraction effect of patches on the monkeys’ movements. On the other hand, we were able to depict a range of movement decisions at each step that, in some cases, would certainly deviate them from approaching high-quality patches, such as moving to preferred tree species.

We also found that black howlers tended to minimize revisitation by moving away from trees that had been previously visited for consumption. Studies on memory of food resources suggest that when a given resource is consumed, information about it is stored as unavailable for next use, thereby minimizing revisitation to unavailable resources (Sulikowski & Burke 2010). This may explain why monkeys tended to avoid revisiting trees on which they had already fed. In addition, we observed that fruit production was particularly low during the study period compared to previous years, thereby enhancing the effect of fruit rarity on resource depletion. Nevertheless, our modelling approach implied that resources were not visited before the beginning of the study, which is likely inaccurate, and many visits or revisits of trees must have gone unnoticed because of our sampling design. Therefore, tree revisitation rate is most likely underestimated, and the effect of previous visits for consumption on foraging patterns must be cautiously interpreted.
Finally, our results indicated that the choice of destination tree made by black howlers was not explained by the phenological state of the species across the study area. In variable environments, an animal may either choose to regularly sample its environment to reduce uncertainty or to minimize the cost of uncertainty by being more flexible in its foraging strategy (Dall & Johnstone 2002; Stephens, Brown & Ydenberg 2007). Acquiring phenological information by sampling and maintaining the cognitive apparatus for this process is costly (Stephens 1987; Bell 1991; Dukas 1999) and so is the development and maintenance of abilities that include alternate foraging strategies or diets (Dall & Johnstone 2002). The strategy adopted will depend on the net energy gains associated with the strategy in a given environment and on the predictability of this environment. Tracking is considered as an efficient tool to enhance foraging performance in variable but predictable environments (e.g. highly seasonal environments; Stephens, Brown & Ydenberg 2007). Although the tropical forest of Calakmul is highly seasonal and fruit production should be predictable (Vargas-Contreras et al. 2009), we did not find evidence for phenology tracking. There are two possible explanations for this result. First, fig trees, the most preferred tree species, have asynchronous and year-round fruiting patterns (Janzen 1979; Milton et al. 1982). Thus, the availability of fruits in a fig tree is not a good predictor of the fruit availability of other fig trees across the home range. Second, black howlers are facultative folivores (Silver et al. 1998). Hence, preferred tree species, even when they are not fruiting, may constitute better feeding destinations over other tree species (Rivera & Calmé 2006). The highly unpredictable nature of the black howler’s preferred species and the flexibility of their diet makes phenological tracking not worthwhile to increase their foraging performance (Stephens 1991).

TIME SPENT ON DESTINATION TREE

The time spent in a tree by black howlers was influenced by the preference for that tree species and the food item available, and by our proxy for their satiation state. Monkeys stayed slightly longer in less preferred trees, presumably because of the lower quality (i.e. delayed energetic gains) of available food found in these trees. Previous studies suggest that the energetic content of food items influenced dietary preferences (Provenza 1995) and this is true for black howlers (Janzen 1979; Estrada & Coates-Estrada 1985). Nevertheless, howlers can eat a great proportion of less nutritious food items such as leaves. This process is time-consuming, and the passage time of food for howlers is longer than for strict fruit-eating primates (Milton 1981). Therefore, leaf consumption in less preferred tree species may delay satiation and energy gains, increasing the time spent on those trees. In contrast, monkeys were more likely to stay longer on trees bearing preferred tree parts and to feed on them when passing through.

Monkeys were also more likely to stay longer in a tree if they had substantially fed before reaching the tree. This response was most probably due to a change in ‘state’, from searching to resting; troops would spend more time resting after feeding, before starting a new searching bout (S. Plante, unpublished results). Therefore, the foraging strategy observed was influenced by the satiation state of individuals. Satiation state has been proven to be an important component in foraging, affecting movement rate, search duration or resources selection (Bell 1991). Our results are consistent with this hypothesis; hunger may have stimulated a search for food, leading monkeys to spend less time on trees (i.e. moving faster) when they were hungrier.

FORAGING STRATEGY AND PERFORMANCE

The foraging strategy adopted by an animal is the result of complex interactions between its internal requirements and its environment (Stephens, Brown & Ydenberg 2007; Nathan et al. 2008). For black howler monkeys, it appears that both intrinsic (hunger and food preferences) and extrinsic factors (spatial distribution of preferred species, food items and high-quality patches) drive their foraging movements. Food preference emerges as the main driver of the black howlers’ foraging, by directing movements and by inducing considerable use of high-quality patches. We expected black howlers to be efficient foragers and our results support this idea. They attempted to maximize energy gain by selecting preferred tree species at each step and by staying in high-quality patches. Black howlers also tended to minimize travel costs while foraging by staying in locations of high food density such as high-quality patches (see Rivera & Calmé 2006) and by avoiding trees already visited for feeding. We did not consider feeding and depletion rates and neither did we evaluate the availability of resources through their entire home ranges. Therefore, we cannot evaluate the optimality of the foraging strategy observed in relation to this specific environment nor compare the performance of several alternate strategies (Pyke 1984). Nevertheless, we suggest that the black howler’s foraging strategy is efficient because it favours preferred food resource acquisition and limits movements towards unprofitable trees.

Our modelling approach allows us to identify important components of the black howler’s foraging strategy, but we may have omitted other significant components of their foraging. A potentially important factor that we did not account for was the presence of spider monkeys (Ateles geoffroyi yucatanensis), a major food competitor. The aggressive behaviour commonly displayed by spider monkeys towards howler monkeys was observed when the two species shared Ficus sp. and B. alicastrum, especially in high-quality patches (S. Calmé 2003 & S. Plante 2009–2010, personal observation). Fruit encounter rates of
spider monkeys are likely higher than those of howlers, because their daily ranges are larger and they move more rapidly (Chapman 1988; Suarez 2006). Thus, black howlers suffer from aggressive encounters with spider monkeys and asymmetric consumptive competition (Schoener 1983). It is also known that competition for food resources can greatly affect the foraging strategies that are adopted by both competitors (Alatalo et al. 1987; McNamara & Houston 1992; Stephens, Brown & Ydenberg 2007; Noser & Byrne 2010). Spider monkeys introduce uncertainty into the information on resource availability, which in turn may affect black howlers’ foraging decisions (McNamara & Houston 1992).

The fast development of movement ecology has enabled researchers to explore different techniques for statistically treating individual movement data. However, most methods either lack generality or do not integrate empirical data to support movement models (Holyoak et al. 2008). We have provided a movement model that is based on empirical data of high spatial and temporal resolution and that incorporated both intrinsic and extrinsic factors affecting foraging movements such as recommended by Nathan et al. (2008). We used continuous observational data, which is rare, highly informative and more powerful than sampling relocation data for quantifying and inferring movement processes (Turchin 1998). Detailed information on foraging movements can greatly improve our understanding of foraging strategies adopted by wild animals. Our approach also integrates the spatial and temporal distribution of resources, such as clusters of resources in patchy environments and the phenological state of resources. The spatio-temporal dynamic structure can thereby be added to the foraging model. We suggest that our modelling approach could be widely used in ecology to describe movements not only as a combination of intrinsic and extrinsic factors such as food preference and distribution, but also as a more general combination of multiple attraction and repulsion sources (e.g. mates and competitors).

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