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Original Article

Primates adjust movement strategies due to changing food availability

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Animals are hypothesized to search their environments in predictable ways depending on the distribution of resources. Evenly distributed foods are thought to be best exploited with random Brownian movements; while foods that are patchy or unevenly distributed require non-Brownian strategies, such as Lévy walks. Thus, when food distribution changes due to seasonal variation, animals should show concomitant changes in their search strategies. We examined this issue in 6 monkey species from Africa and Mexico: 3 frugivores and 3 folivores. We hypothesized that the more patchily distributed fruit would result in frugivores showing more Levy-like patterns of motion, while folivores, with their more homogenous food supply, would show Brownian patterns of motion. At least 3 and up to 5 of 6 species conformed to the overall movement pattern predicted by their primary dietary item. For folivorous black howler monkeys (*Alouatta pigra*), ursine colobus (*Colobus vellerosus*), and red colobus (*Procolobus rufomitratus*), Brownian movement was supported or could not be ruled-out. Two frugivores (spider monkeys, *Ateles geoffroyi yucatanensis*, and gray-cheeked mangabeys, *Lophocebus albigena*) showed Lévy walks, as predicted, but frugivorous vervet monkeys (*Chlorocebus pygerythrus*) showed a Brownian walk. Additionally, we test whether seasonal variation in the spatial availability of food support environmentally driven changes in movement patterns. Four of 5 species tested for seasonal variation showed adjustments in their search strategies between the rainy and dry seasons. This study provides support for the notion that food distribution determines search strategies and that animal movement patterns are flexible, mirroring changes in the environment.

Key words: *Alouatta pigra*, *Ateles geoffroyi yucatanensis*, Brownian walk, *Chlorocebus pygerythrus*, *Colobus vellerosus*, Lévy walk, log-normal walk, *Lophocebus albigena*, *Procolobus rufomitratus*.

INTRODUCTION

Within the new movement ecology paradigm (Nathan 2008), animal movement patterns while foraging are suggested to have evolved to

best search for food items that have specific spatial distributions. For example, it has been suggested that for species whose food resources are abundant and uniformly distributed, such as the leaves eaten by folivores, the best movement pattern is randomly-derived (i.e., Brownian movement) (Viswanathan 1996; Viswanathan *et al.* 2011). Brownian walks are characterized by irregular motion and steps of

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relatively constant length with random turning angles (step lengths show an exponential distribution, Turchin 1996). In contrast, for species whose food resources are rare and patchily distributed, such as the fruit of frugivores, non-Brownian search strategies are proposed to maximize encounter rates with food (i.e., step lengths show a negative power-law or lognormal distribution) (Ramos-Fernández *et al.* 2004; Reyna-Hurtado *et al.* 2012). When step lengths are power-law distributed, this suggests the possibility of a Lévy walk, where animals show a series of short similar-length steps interspersed with occasional very long steps, which allows them to cover large distances (Shlesinger and Klafter 1986; Viswanathan *et al.* 1996; 1999; 2008; Bartumeus *et al.* 2005). Lévy-walks are believed to have adaptive value for animals facing uncertainty in the distribution of their resources (Bartumeus *et al.* 2005), alternating extensive (between patch) and intensive (within patch) searching (Shlesinger and Klafter 1986; Shlesinger 2009).

Movement patterns have been studied for several primate species and some frugivorous species behave as predicted and are non-Brownian walkers. For example, Ramos-Fernández and colleagues (2004) found that spider monkeys (*Ateles geoffroyi*), who eat a high proportion of fruit, were typically Lévy walkers. Hamadryas baboons (*Papio hamadryas*) and chacma baboons (*P. ursinus*), with relatively randomly distributed food sources, were, as predicted, Brownian walkers (Schreier and Grove 2010; Sueur 2011). Yet, primates often have extremely flexible foraging strategies (Chapman *et al.* 2002; Chapman and Rothman 2009) and some species switch between highly localized food to very abundant resources throughout the year (i.e., primates living in seasonal forests, spider monkey in Santa Rosa, Costa Rica or Calakmul, Mexico; Chapman 1990; Hernández-Sarabia 2013). Thus, it is likely that one movement strategy is not sufficient to optimally search for resources throughout the year and that a mix of search strategies are being used by the same species in different seasons or at different locations.

Previous research has shown that animals can modify their movement patterns when food availability changes and switch searching strategies (i.e., from Brownian-walkers to Lévy-walkers) in short periods of time. In nonprimates, research on marine predators has shown that when they are hunting prey that is abundant they exhibit Brownian motion but when they are searching for sparsely distributed prey they exhibit movement that is closer to Lévy walks (14 species of predatory fish, Humphries *et al.* 2010; great white sharks, *Carcharodon carcharias*, Sims *et al.* 2012). Seasonal movement patterns have been examined in a scavenger, the Egyptian vulture (*Neophron pernopterus*), showing that search strategies were generally Brownian at the African wintering area where food was randomly distributed but were more complex and often Lévy-like at the European breeding grounds where food was predictable and patchy (López-López *et al.* 2013). For primates, Schreier and Grove (2010) have shown that Hamadryas baboons (*Papio hamadryas*) in Awash National Park, Ethiopia exhibit Brownian search strategies in one area of their home range and Lévy walks in another area of their home range, suggesting differences in food distribution in these areas.

Given that food availability and distribution is predicted to play a major role in determining animal movement patterns, here we compared species with variable diets and asked, what happens to their movement patterns when food availability and spatial distribution changes over time? We analyzed movement data from 6 primate species from Africa and America, with diets ranging from almost strict folivores (i.e., *Procolobus rufomitratus*—red colobus) to highly frugivorous (i.e., *Ateles geoffroyi*—spider monkey) under different seasonal

conditions of food availability and spatial distribution. Our aims were to determine: 1) if the search strategies of each species is predicted by their dietary specialization, 2) whether search strategies changed with seasonal food availability, and 3) whether the direction of the change is towards a more Brownian walk pattern when food was abundant and evenly distributed and towards a non-Brownian walk pattern when food was scarcer and patchily distributed. Our study is a collaboration between primate researchers working in 3 countries on 2 continents, to bring together movement data on 6 species across the primate phylogeny at 4 study sites (Figure 1), with the aim of contributing to a greater understanding of how changes in food distribution impact animal movement strategies.

Contrary to early research, recent findings have demonstrated that primate folivores can be constrained seasonally by food when the availability of high-quality leaves (high protein and low fiber) are low (Chapman and Pavelka 2005; Snaith and Chapman 2005), and that scramble competition occurs, limits group size, and affects ranging behavior (Snaith and Chapman 2005; Teichroeb and Sicotte 2009). Primate frugivores, on the other hand, have traditionally been viewed as being more constrained by food availability than folivores, as fruit in tropical forests is usually found in discrete patches that are distributed unpredictably in time and space (Terborgh 1986; Chapman *et al.* 1997). Thus, in this study, we assume that food for folivores is generally more abundant than for frugivores or for frugivore/insectivores but that all species, regardless of their dietary specialization, will be food constrained at some points in the year. We used rainfall as a proxy for changing food availability, with the general expectation that leaves and fruit should be more plentiful in tropical rainforests during periods with more precipitation (Murphy and Lugo 1986). Thus, drier periods were generally treated as more food scarce (except in the case of ursine colobus monkeys, where the opposite is true, Teichroeb and Sicotte, *in press*). We hypothesized that movements and foraging strategies would change in leaner seasons to resemble the patterns of species with different dietary specializations. So, frugivores were expected to change to more Brownian-like movement patterns in lean seasons and folivores were expected to use Lévy-like movement patterns in these seasons relative to more food-abundant times. However, each species was predicted to make changes at its specific spatial and temporal scales.

We compare 6 primate species (Figure 1). From Mexico, we included 2 sympatric monkeys, the Yucatan spider monkey (*Ateles geoffroyi yucatanensis*) and black howler monkey (*Alouatta pigra*), that differ in feeding habits with the former being mainly frugivorous (Hernández-Sarabia 2013) and the latter being folivorous (Chapman and Pavelka 2005; Hernández-Sarabia 2013). However, both of these primate species have been recorded to feed on leaves and fruit occasionally when the availability of other food items is low (Hernández-Sarabia 2013; K. Rizzo, personal communication; Chapman and Pavelka 2005). Three primates from East Africa were studied, the folivorous red colobus (*Procolobus rufomitratus*) and the frugivorous/insectivorous gray-cheeked mangabey (*Lophocebus albigena*) from Kibale National Park, Uganda that have been monitored for 25 and 20 years, respectively. The third species from East Africa was the vervet monkey (*Chlorocebus pygerythrus*), which are common inhabitants of riverine and perturbed/secondary forests. We examined movements in the population at Lake Nabugabo in southern Uganda which has been studied since 2011 and are primarily frugivorous (Teichroeb *et al.* 2015; Chapman *et al.* 2016a,b). Finally, we also include movement data from ursine colobus monkeys (*Colobus vellerosus*), a mostly folivorous species inhabiting the

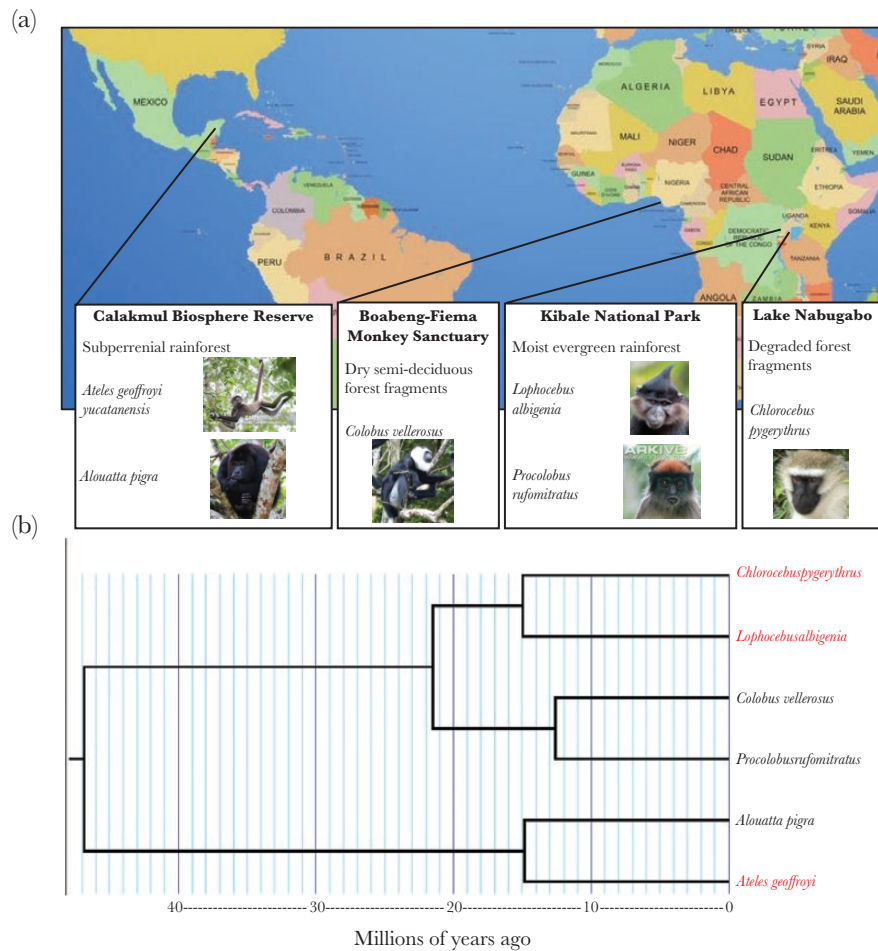


Figure 1

(a) World map showing study site locations, forest type, and species studied. Photo credits: *Alouatta pigra*, K. Klass, *Colobus vellerosus* and *Chlorocebus pygerythrus*, J. Teichroeb. (b) Cladogram showing relationships and phylogenetic distances between study species. Frugivores are indicated with red, folivores are indicated with black. Consensus tree from GenBank made in 10kTrees (Arnold et al. 2010) manipulated in Mesquite (Maddison and Maddison 2017).

Upper Guinea forests of western Africa. Our study population resides at the Boabeng-Fiema Monkey Sanctuary in central Ghana (Saj et al. 2005).

METHODS

Study sites and design

We worked at 4 sites in 3 countries, Mexico, Uganda, and Ghana (Figure 1). Spider monkeys and black howler monkeys were studied in the Calakmul Biosphere Reserve (CBR; 7238 km²; 18°06'N-89°48'W), which is located in Campeche State in southern Mexico. CBR is the largest tropical forest in Mexico and was decreed a protected area in 1989. The Calakmul climate is warm and subhumid, with a mean annual temperature of 24.6 °C (although temperature may range from 10 °C in January to a maximum of 42 °C in April; SMN 2017). There is seasonal rainfall, mainly in summer (June through September), with an annual average of 1076 mm. We calculated a seasonality index based on the variability in rainfall throughout the year following Korstjens et al. (2006) and Reyna-Hurtado et al. (2016), using the following equation: Seasonality Index = maximum monthly precipitation – minimum monthly precipitation divided by the annual average of precipitation. The Calakmul index of seasonality was estimated at 0.119. There are 4 major forest types: the

medium subperennial forest, the low-flooded forest that gets seasonally inundated after 2–3 months of heavy rains, and the medium and low semideciduous forests, which both can be classified as dry forest. In the main archeological site, there are 3 groups of black howlers that have been studied for 10 years (K.A. Rizzo, personal communication). There is also one big community of spider monkeys (>75 individuals) that was studied once previously (K.A. Rizzo, personal communication). Our research on spider monkeys and black howlers was done from January to August 2010 and June to August 2011. Data were taken from 2 groups of black howlers (6 and 8 individuals in each group) and one community of spider monkeys (>70 individuals). Spider monkeys have a fission–fusion social organization, where a community of generally affiliative interacting individuals divide into foraging subgroups that are spatially separated and move independent of one another (Chapman et al. 1995). A GPS fix taken from the center of the howler monkey group or spider monkey subgroup being followed every 15 min. Spider monkey feeding was recorded for 184 and 85 h in dry and rainy seasons, respectively (Hernández-Sarabia 2013), while black howler monkey feeding was recorded during 207 and 89 h in dry and rainy seasons, respectively (Hernández-Sarabia 2013).

Red colobus and gray-cheeked mangabeys were studied in the mid-altitude moist forest of Kibale National Park in western

Uganda (795 km²; 0°13′–0°41′N and 30°19′–30°32′E). The area experiences 2 rainy seasons (March to May, and October to December) and rainfall varies along a latitudinal/elevation gradient (Chapman *et al.* 1997). In the area used by the groups, mean annual rainfall is 1676 mm (1990–2016) and daily temperature maxima and minima averaged 23.9 °C and 15.6 °C (1990–2016). The Kibale Seasonality Index was estimated at 0.205 (following Korstjens *et al.* 2006). Kibale was gazetted as a Forest Reserve in 1932, and became a National Park in 1993 (Struhsaker 1997). There are 5 groups of red colobus in the park that were habituated to researchers 20 years ago, and 6 groups of mangabeys have been followed, initially with radio telemetry and subsequently through knowledge of their home range since 1997 (Olupot 1999; Janmaat *et al.* 2009). We studied, one large group of red colobus that has been continuously observed since 2006 and recorded movement and diet data from June 2010 to May 2012 with the help of 3 skilled assistants. A GPS fix was taken from what was estimated to be the geographic center of this group every 15 min. Five groups of mangabeys were monitored for variable periods of time from August 2010 to July 2011, but for at least 1 week every 2 months by a skilled assistant who took a GPS fix in the same fashion.

Research on vervet monkeys was carried out at Lake Nabugabo, Uganda (0°22′–12°S and 31°54′E). Lake Nabugabo (8.2 × 5 km) is a satellite lake of Lake Victoria. Nabugabo experiences 2 wet and 2 dry seasons per year with an average of 1348 mm of rain falling mostly March through mid-May and November through early December, though for this study we only collected movement data in the dry season. The average temperature in nearby Masaka is 21.1 °C with a Seasonality Index of 0.215 (www.worldweatheronline.com). The landscape around the lake consists of wetlands, grasslands, and patches of swamp forest, but a small portion on the western shore includes farmer's fields, and patches of degraded forest (Chapman *et al.* 2016b) and the study group (M group, 24 individuals) ranged in this area (Teichroeb *et al.* 2015). Movement data was collected during dawn to dusk follows over 41 days between June and July 2012. A GPS point was taken in the center of the group every 15 min during follows. Diet data were collected with scan samples of at least 5 individuals collected every 30 min by 2 trained field assistants. If monkeys were feeding during the sample the item and species was recorded.

We observed ursine colobus (*Colobus vellerosus*) in the Boabeng-Fiema Monkey Sanctuary (BFMS) in central Ghana (7°43′N and 1°42′W). BFMS is in the forest-savanna transition zone and consists of 2 dry semideciduous forest fragments of 190 ha. The sanctuary and 5 surrounding forest fragments contain approximately 365 ursine colobus (Kankam and Sicotte 2013). There are 2 distinct wet and dry periods at BFMS; the long wet season last from approximately March to July and there is a short rainy season in September. There is a short dry season in August and a prolonged one from November to February. Mean annual rainfall in the area (1985–1990) is 1250 mm (Fargey 1991) with a monthly range of 0.4–227.6 mm (Teichroeb and Sicotte 2009). BFMS seasonality index was estimated at 0.181 (following Korstjens *et al.* 2006). Average minimum and maximum temperatures (2002–2005) were 18.5 °C and 34.7 °C, respectively. This rainfall and temperature data are from the same year when movement data were collected. We analyzed the movements of a single multi-male/multi-female group (called WW - 30.5 individuals) that was followed for 13 months (July to November 2004, January to August 2005). Dawn to dusk

follows for at least two, 2-day periods per month were conducted by JAT and a research assistant, though more follows were done in some months (690 contact hours during 58 dawn to dusk follows). Scan samples were taken every 30-min to record all trees occupied relative to 50 × 50 m quadrats. During scans ($N = 1390$ scans), a location point for the center of mass of the group was recorded relative to a map of the field site (Waser 1974). For these analyses, step lengths were examined overall for WW group and during the long wet and long dry seasons. The species and plant parts eaten were noted during 125 h of focal animal sampling of randomly selected adult and subadult individuals.

Data analysis

From the sampling days that primate groups were followed we extracted all step lengths. Steps were constructed by measuring a straight line between the 2 consecutive GPS locations for a given species every 15 min for all species except ursine colobus, where samples were taken every 30 min. When groups rested in one spot, we considered a single location to represent all the time the group stayed there. This was to account for possible GPS error in measurements (which was calculated at less than 5 m). We examined consecutive step lengths at 15-min or 30-min intervals, according to the sampling regime followed for each species. With the exception of vervet monkeys, we performed separate analyses for the dry and rainy seasons as proxies for low and high food availability. We then fit 3 models to the observed step-length distributions, comparing between power law (Lévy-walk) and log-normal models versus exponential following the approach outlined of Clauset *et al.* (2009) and using the `powerlaw` package (Gillespie 2015) in R version 3.3.1 (R Core Team 2016). The R code used and our data are provided in the Supplementary Material. This approach first fits a power law model to the data, estimating a lower bound (X_{\min}) by minimizing the difference between the cumulative density function of the truncated data to that of a best fit power law distribution using a Kolmogorov-Smirnov test, where the scaling parameter α is estimated by maximum likelihood. A measure of goodness-of-fit is then calculated via bootstrapping (100 replicates) to determine whether the power law model is warranted given the observed data.

Finally, the power law fit was compared against other plausible distributions (i.e., exponential and lognormal). The optimal distribution(s) given the data was decided by likelihood ratio tests, using $P < 0.05$ as our cutoff for deciding whether one distribution was better than another. This procedure provides the best fit model(s) for each species, and species within season, allowing us to make inferences about the characteristics of their movement patterns. We then compared movement patterns between seasons, to test our hypotheses about how primate diet and season influence movement.

RESULTS

For the frugivores we examined, fruit was important in the diet through all the seasons compared. Spider monkeys consumed fruits most of the time and only switched between fruiting species with *Brosimum alicastrum* being the most consumed species (40%) in the dry season and *Ficus* spp (54%) in the rainy season. However, they consumed more leaves in the dry season (31%) than in the rainy season (17%) (Table 1). Mangabeys feed mostly on fruits and insects with low percentages of flowers and leaves in the diet. Their diet has been reported not to change with the seasons and Waser (1974)

found that during the rainy season mangabeys fed on fruits 58.1%, insects 28.7%, and flowers or leaves 13.1%, while in the dry season very similar percentages were found (fruits 61.3%, insects 29.4%, and flowers and leaves 9.3%). Also, [Olupot \(1998\)](#) found very similar percentages (fruits 59%, flowers/leaves and bark 14 % and insects and others 27%) in a subsequent study on the same groups. The vervet's diet at Nabugabo during the dry season when movement data were collected consisted of 68% fruit, 9.7% insects, 9% leaves, 4.6% flowers, and 8% other foods.

For the folivores, leaves were important year-round. Howler monkeys consistently consumed more leaves than fruits with a slightly higher percentage of fruit consumption in the rainy season (38.5%) than in the dry season (34%) ([Hernández-Sarabia 2013](#)). The ursine colobus diet in the rainy season included more mature leaves (33%) than the dry season diet (13.1%) and fewer young leaves

(48.1–57.9%), less fruit (4.9% vs. 8.1%), fewer flowers (1.3% vs. 8.5%), and fewer seeds (5.9% vs. 7.3%). Red colobus consume very few fruits over the year and seasons and during 2010 and 2011 the percentage never reached 1% (0.25%) and the quality of leaves has been show to vary little among seasons (C.A.C., unpublished data; [Table 1](#)).

Power-law distributions were supported overall and in all seasons for consecutive steps for spider monkeys ($n = 527$) and gray-cheeked mangabeys ($n = 2641$). Although, the Brownian movement pattern was not significantly discriminated (i.e., could not be ruled-out completely) for spider monkeys in the dry season or for gray-cheeked mangabeys in the rainy season ([Table 2](#) and [Figure 2](#)). Vervet monkey movements ($n = 1697$) supported a Brownian movement pattern during the dry season and the power-law was significantly discriminated. Howler monkeys consecutive steps ($n = 780$)

Table 1
Seasonal diet of each study species

Species	Season	Diet (%): Fruit	Seeds	Flowers	Leaves	Insects	Other	Reference
Spider monkeys	Dry	68			31		1	This study
	Rainy	82			17		1	
Gray-cheeked mangabeys	Dry	61.3			9.3	29.4	0.1	Waser 1974
	Rainy	58.1			13.1*	28.7	0	
Vervet monkeys	Dry†	68	4.6	0.5	9	9.7	8.1	This study
Howler monkeys	Dry	34			65			Hernández-Sarabia 2013
	Rainy	38.5			61			
Ursine colobus	Dry	8.1	8.5	7.3	74	0	2.1	This study
	Rainy	4.9	1.3	5.9	85.1	0	2.8	
Red colobus	Dry	<1			99			This study
	Rainy	<1			99			

*[Waser 1974](#) (leaves and flowers together).

†Movement data for vervets were only collected in the dry season

Table 2.
Species, feeding preferences and movement patterns found overall and during dry and rainy seasons.

Species	Feeding class+	Season	N	Power-law fit test ($P > 0.1$)	Power-law vs. Exp. r-(pwr,exp)	Power-law vs Log N r-(pwr,log)	Exp. vs Log N r-(exp,log)	Supported distribution	Trend of change (from dry to rainy seasons)*	Direction of change according to the predictions?
SM	Frug	All	527	0.34	2.15*	0.07	-2.13*	PL/LN	↑	Yes
		Dry	358	0.95	1.08	0.09	-1.06	PL/LN/Exp		
		Rainy	169	0.81	2.13*	0.07	-2.12*	PL/LN		
MB	Frug/Ins	All	2641	<0.01	3.51*	0.41	-3.43*	PL/LN	↓	Yes
		Dry	1508	0.02	3.30*	0.40	-3.22*	PL/LN		
		Rainy	1133	0.02	1.91	0.35	-1.86	PL/LN/Exp		
VM	Frug/Ins	All	1697	<0.01	-8.15*	-4.65*	0.16	Exp/LN	N/A	N/A
		Dry	1697	<0.01	-8.15*	-4.65*	0.16	Exp/LN		
		Rainy	N/A		N/A	N/A				
HM	Fol/Frug	All	780	1.00	1.52	-0.14	-1.75	PL/LN/Exp	↑	Si
		Dry	345	0.97	0.97	0.15	-1.07	PL/LN/Exp		
		Rainy	435	0.01	3.27*	-1.19	-3.88*	LN/PL		
UC	Fol	All	638	0.36	-0.54	-0.58	0.33	Exp/LN/PL	=	No
		Dry	291	0.30	-0.78	-0.71	1.13	Exp/LN/PL		
		Rainy	248	0.28	-0.47	-0.50	0.17	Exp/LN/PL		
RC	Fol	All	7957	<0.01	-0.85	-0.70	1.62	Exp/LN/PL	↑	No
		Dry	4058	0.01	-0.41	-0.71	-0.45	Exp/LN/PL		
		Rainy	3899	<0.01	0.61	-0.63	-1.67	LN/PL/Exp		

Fol = folivore; Frug = frugivore; Ins = insectivore. SM = Spider monkey; MB = Mangabey; VM = Vervet monkey; HM = Howler monkey; UC = Ursine colobus; RC = Red colobus.

The R test statistic is the ratio of the log-likelihoods of the data between the power-law and the competing model, a positive sign indicates a better fit for the power-law. * P value <0.05. An arrow pointing upward means the trend changed to a more long-tailed distribution (either Power-law or Log-normal), while an arrow pointing downward means the trend changed to a more Brownian distribution (exponential distribution). An = sign means no change is detected. The change is based in the power-law versus exponential distribution discrimination test and is based from the dry to the rainy season.

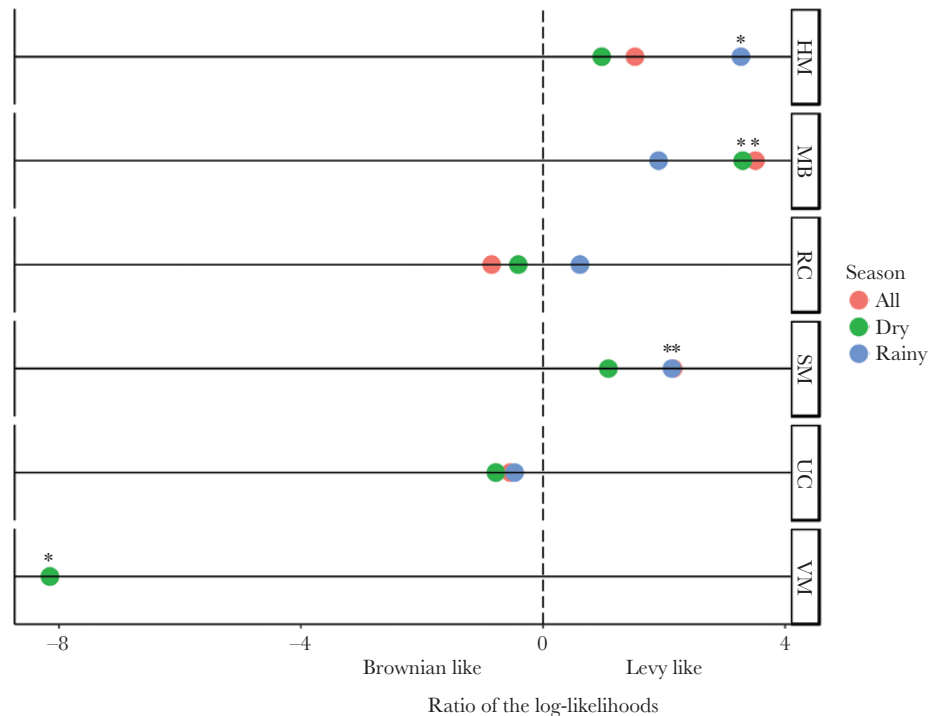


Figure 2

Ratio of the likelihood of a Brownian step length distribution (i.e., exponential) against that of a Levy step length distribution (i.e., power law). The likelihood ratio is compared between seasons (dry, rainy, and all combined) for each species: HM = Howler monkey, MB = Gray-cheeked mangabeys, RC = red colobus, SM = Spider monkey, UC = Ursine colobus, and VT = Vervet monkeys (only dry season). Increasingly negative ratios indicate a more Brownian step length distribution, increasingly positive ratios indicate a more Levy like step length distribution, and values near zero indicate difficulty in distinguishing between the two.

supported a log-normal distribution overall and during the rainy season, while the power-law distribution was the best fit model during the dry season; however, the Brownian distribution was not significantly discriminated overall and during the dry season. Ursine colobus ($n = 638$) movement patterns also supported the Brownian distribution overall and in all seasons, although the other 2 distributions were not discriminated statistically for the rainy season and the power-law was not discriminated statistically for the dry season. Red colobus consecutive steps ($n = 7957$) supported a log-normal distribution overall and during the rainy season, but a Brownian distribution during the dry season. The power-law distribution was significantly discriminated for both the dry and rainy seasons (Table 2 and Figure 2).

DISCUSSION

With data from 6 primate species, we found that overall movement patterns conformed to the distributions expected—based on dietary specializations—for at least 3 and up to 5 species. Primarily folivorous species were expected to show step lengths conforming to Brownian distributions (Viswanathan 1996; Viswanathan *et al.* 2011), which was supported or plausible for only one folivore (ursine colobus), although the exponential distribution was not totally discriminated for the other 2 species (red colobus and howler monkey). Primarily frugivorous species were expected to show non-Brownian search strategies (Shlesinger and Klafter 1986; Shlesinger 2009), and Lévy Walks were supported for 2 of the frugivores (spider monkey and mangabey). Only the primarily frugivorous vervet monkeys went against predictions. Some

of the species modified their searching patterns according to season, an index of food availability. Seasonal changes in movement patterns were evident for all species examined with the exception of ursine colobus. We predicted that movement patterns would become more or less Brownian on a seasonal basis depending on the amount of patchy (i.e., fruit, flower, seeds) versus more evenly distributed foods (i.e., leaves) in the diet, but the direction of seasonal changes in search strategies were not always in-line with our predictions. However, a more in-depth look at food distribution in these habitats may show that this general assumption about the spatial distribution of leaves versus plant reproductive parts does not always hold.

Yucatan spider monkeys, gray-cheeked mangabeys, and black howler monkeys adjusted their movement patterns when food availability changed. Spider monkey and black howlers behaved as more long-tail movers (i.e., they have a few long distance movement with many short ones) in the rainy seasons, which was opposite to what we expected. This may be due to feeding on figs (*Ficus* spp), a highly consumed tree-fruit that was readily available but had a patchily distribution, while the more abundant *Brosimum alicastrum* was uniformly distributed and more available during the dry season at Calakmul. Gray-cheeked mangabeys showed minor seasonal differences, with a longer-tailed movement pattern in the dry season compared to the rainy season. This small change from one season to another was matched by a slight increase in fruit consumption in the dry season.

Red colobus also showed seasonal differences in their search strategies with long-tail movement patterns in the rainy season and Brownian movement in the dry season. Red colobus are almost

strict folivores that never eat fruit for more than 1% of their feeding time in either season (C.A.C., unpublished data). So, this change maybe due to changes in the quality of the leaves that may be more abundant in the dry season than in the rainy season of this particular year. Ursine colobus did not modify their searching patterns despite changes in food distribution patterns. Ursine colobus always behaved as Brownian walkers despite the fact that food items were more patchily distributed in the dry season when the consumption of fruit, flowers, and seeds increased (Saj and Sicotte 2007). This could potentially be due to the importance of mature leaves in the rainy season; perhaps the search strategy that works best in the lean season is used all year long. However, ursine colobus were the only species where locations were taken every 30 min, rather than at shorter intervals and this may not have been frequent enough to show small-scale changes in movement patterns (Plank and Codling 2009).

Vervet monkeys behaved as Brownian walkers for the sole season that they were followed. This contrasts with what was predicted since vervets at Nabugabo are highly frugivorous (Chapman *et al.* 2016b). The explanation, however, may rest in the fact that they inhabit a highly perturbed habitat where the spatial distribution of fruit trees has been heavily modified, since people have lived in this area for several centuries. The vervets now often stay in one patch to eat from large fruit trees before meandering in winding patterns on the edges of agricultural fields, spreading out to hunt insects and moving to another patch of trees. Thus, most of their large group movements tend to follow a more winding course rather than direct, straight lines to new fruit trees. Though insects only make up about 10% of the diet, these are an abundant and homogeneously distributed resource and a Brownian walk would be the best strategy to take advantage of this food (Sueur 2011). Vervets are also one of the most territorial species in this study with the smallest home range (5.61 ha, Teichroeb *et al.* 2015), which may have influenced their movement patterns. Our study group had almost no overlap in home range with neighboring groups during the 2012 data collection period (J.A.T., unpublished data). In contrast, the other examined species had larger home ranges and larger overlap areas between the ranges of neighboring groups (spider monkey, Ramos-Fernández *et al.* 2013; black howler monkey, Ostro *et al.* 1999; gray-cheeked mangabey, Janmaat *et al.* 2009; red colobus, Chapman *et al.* 2002; ursine colobus, Teichroeb and Sicotte 2009; Teichroeb *et al.* 2012). The vervets often moved from one side of their home range to the other in a single day and could do so in a slow, meandering way that did not necessitate fast, straight-line movements. This could also explain why they used such a different search strategy from the other frugivores examined.

Alterations to search strategies with changes in food availability have also been found in several species of marine predators that switched from Lévy walks to Brownian walks when they changed from less productive water (more sparse prey) to more productive habitats (more abundant prey) (Humphries *et al.* 2010). In this study, 14 species of fish, among them sharks, tuna, billfish, and ocean sunfish modified their movement patterns to adjust to prey availability (Humphries *et al.* 2010). Here, we provide evidence that primates also adjust their movement patterns to optimize search when resource availability changes (see also: Schreier and Grove 2010). Similarly, Humphries *et al.* (2012) found individual variability in search strategies within black-browed (*Thalassarche melanophrys*) and wandering albatrosses (*Diomedea exulans*). In these species, individuals exhibited either Brownian or Lévy patterns of movement, with 35% and 15% of individuals respectively behaving as Lévy walkers,

while 18% and 26% behaved as Brownian walkers. As we followed groups or subgroups of primates, we did not find differences at the individual level, but groups behaved differently among seasons. We suggest that this seasonal change is related to changes in the temporal and spatial distribution and availability of food.

Our study also confirmed that spider monkeys are Lévy-walkers most of the time as was found previously by Ramos-Fernández *et al.* (2004). These authors conclude that spider monkeys may travel in subgroups when they have limited knowledge of the location of fruiting trees. Observation of spider monkeys taking straight paths just before reaching a food tree suggests a knowledge of the location of such trees (Parada-López *et al.* 2017). However, the degree of knowledge that each primate species may possess about the location and temporal availability of food items is a topic that warrants further study.

The finding that the frugivores in our sample generally used walks showing longer-tailed distributions, while the folivores used primarily Brownian search strategies, has important implications regarding how diet selects for brain size. Using a larger sample size and better statistical methods than previous studies, DeCasien *et al.* (2017) have shown that overall brain size in primates is best explained by diet, rather than group size or social system, with frugivores generally having larger brains than folivores. Cognition is an important aspect of animal foraging (Clutton-Brock and Harvey 1980; Hill 2006) but the influence of memory on animal movement strategies has been difficult to incorporate into predictions (Wolf *et al.* 2009). Lévy walks and Brownian motion are memory-less processes, arising due to the current distribution of resources (Gautestad and Mysterud 2005; Gautestad 2011). However, longer-tailed distributions of step lengths may also arise when animals remember food locations and make long-distance returns to known resources (Gautestad 2011). The relatively larger home ranges of frugivorous primates compared to folivores (Milton and May 1976) requires the memorization of many food sites that are out of sight of a moving animal or group and storing this type of spatial information was likely important in selecting for larger brain size (Harvey and Krebs 1990; Zuberbühler and Janmaat 2010).

In conclusion, we found that at least 3 but up to 5 primate species, 2 primarily frugivorous and 3 primarily folivorous monkeys, used search strategies that were predicted by their diet. Search strategies were found to change in 4 of 5 species with seasonal variation, indicating that these species modify their search strategy with food availability. With our large sample of primates with different dietary specialization we have confirmed that primates, similar to other animals modify their searching strategy according to food availability and distribution. Future studies on the use of spatial memory versus random searching of food items would be interesting to fully understand group movements in primates.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Reyna-Hurtado *et al.* (2017).

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