



## Gastrointestinal parasitism and recursive movements in free-ranging mandrills



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Understanding animal movements is a key prerequisite for deciphering ecological processes such as population dynamics, community structure or biological invasions. Many animals restrict their movements to certain areas (home ranges) by alternating visits among several suitable sites. The dynamics of these recursive movements are assumed to be primarily driven by food availability and predation risk. In contrast, environmental parasite pressures have rarely been considered as possible drivers of animals' ranging patterns. In this article, we present evidence that environmentally transmitted gastrointestinal parasites may shape recursive movement patterns of a group of free-ranging mandrills, *Mandrillus sphinx*. These rainforest-dwelling primates returned less frequently and after longer time lags to sites, including sleeping sites, they had contaminated than to sites with low contamination levels. This pattern was especially pronounced during the dry season, when contamination risk was highest. In contrast, rainfall shortened the time between visits, consistent with the hypothesis that rainfall may wash away parasites, allowing a more rapid return to previously used sites. Although resource distribution and predator threat could not be ruled out in this study, we suggest that the risk of acquiring environmentally transmitted parasites is possibly another factor influencing animal ranging patterns as well as habitat selection or species distribution. Consequently, parasites and their distribution in the environment, as well as the possible antiparasite strategy we document here, should be targets for future research on animal movement.

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Animal movements and space use are at the core of ecological and evolutionary processes, including population dynamics, responses to climate change, spread of invasive species and disease dissemination (Börger, Dalziel, & Fryxell, 2008; Hastings, Petrovskii, & Morozov, 2011; Morales et al., 2010; Nathan, 2008). A common feature of space use in a range of species is repeated visits to profitable sites (Benhamou & Riotte-Lambert, 2012; Berger-Tal & Bar-David, 2015) leading to the emergence of home ranges (Riotte-Lambert, Benhamou, & Chamaillé-Jammes, 2015). The spatiotemporal dynamics of such recursive movements, defined as returns to previously visited sites (Bar-David et al., 2009), has been related to food availability (Bar-David et al.,

2009; English et al., 2014; Williams & Thomson, 1998; van Beest, Mysterud, Loe, & Milner, 2010) and predation risk (Courbin et al., 2015; Heithaus & Dill, 2002; Latombe, Fortin, & Parrott, 2014). Indeed, animals displaying home range behaviour tend to adjust the 'recursion time', i.e. the time elapsed between two successive visits of a site, as a function of food depletion and recovery rate as well as the presence of predators.

Parasites have been proposed as another influence on animal movement patterns (Hart, 1990). For example, feral horses, *Equus caballus*, use windy shelters to avoid flies (Keiper & Berger, 1992), caribou, *Rangifer tarandus*, move to higher altitudes during summer when mosquitoes pullulate at lower altitudes (Downes, Theberge, & Smith, 1986), cattle, *Bos taurus*, avoid tick-infested habitats (Sutherst, Floyd, Bourne, & Dallwitz, 1986), and the need to avoid high infection levels of warble fly larvae may drive postcalving migrations of wild reindeer (Folstad, Nilssen, Halvorsen, & Andersen, 1991). As parasite hosts, individuals may also

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contaminate their environment, for example with gastrointestinal parasites contained in their faeces. When individuals use an area for an extended period of time, the parasites that they excrete should accumulate in the environment. Foraging in such contaminated areas would thus increase the risk of parasite (re-)infection. In line with this notion, territorial and gregarious African bovid species harbour more parasites than nonterritorial species (Ezenwa, 2004a). Moreover, a meta-analysis of studies on primates revealed a positive relationship between helminth richness and territoriality (Nunn & Dokey, 2006), suggesting that the intensity of habitat use is related to the probability of getting infected.

Selective defecation behaviours, such as the use of specific defecation sites (Ezenwa, 2004b) associated with the avoidance of faecal material when foraging (Cooper, Gordon, & Pike, 2000; Ezenwa, 2004b; Fleurance et al., 2007; Garnick, Elgar, Beveridge, & Coulson, 2010) may decrease transmission risk of gastrointestinal parasites. Wild animals may have further evolved movement strategies to reduce the risk of encountering environmentally transmitted parasites. However, the impact of individuals' own parasites, transmitted through soiled environments, on fine-scale group movements has received little attention so far (but see Freeland, 1980; Hausfater & Meade, 1982), even though prophylactic measures in livestock management have long promoted the rotation of pastures to maintain low parasite infection levels (Cameron, 1939). Leaving contaminated areas and avoiding them for a period of time may, indeed, act as a fallowing period, allowing decontamination processes to occur through the death and/or the dilution of parasites in the environment (Bar-David et al., 2009). This strategy may explain why some species, such as African buffalos, *Syncerus caffer*, usually leave an area before completely depleting the resource (Bar-David et al., 2009). Indeed, in the absence of (appropriate) hosts, parasites survive in the environment for a limited time (Altizer, Bartel, & Han, 2011). Environmental factors may further reduce the presence and survival of these parasites, for example through desiccation in dry and hot climates or through dispersion following rainfall or active migration of mobile parasites.

In this study, we examined the relationship between environmentally transmitted gastrointestinal nematodes and recursive movement patterns of a free-ranging group of mandrills, *Mandrillus sphinx*, an Old World primate inhabiting equatorial rainforests of Central Africa. Mandrills are naturally infected with five gastrointestinal nematode taxa (Poirotte et al., 2016) with a direct life cycle (i.e. transmitted directly between hosts without the intervention of an intermediary host). However, these nematode eggs emitted in fresh faeces need to mature within the environment before becoming transmissible to other hosts through ingestion or skin penetration of the infective stage (Neveu-Lemaire, 1952). Ranging in contaminated environments should increase the risks of nematode transmission. Some primates exhibit behaviour that may help alleviate these risks. For example, red howler monkeys, *Alouatta seniculus*, avoid defecating on mid-canopy vegetation, where food resources are located (Gilbert, 1997). Mandrills do not exhibit such sanitary behaviours, and should therefore modify their ranging patterns according to the level of parasite contamination of their habitat.

We assumed that the mandrills we studied were the main source of environmental parasite contamination. Indeed, other primates that possibly share common parasites with these mandrills were only anecdotally reported in the study area (see Methods). In addition, although other mammals such as buffalos are present within the mandrills' home range, they are unlikely to be infected with the same species as most intestinal nematodes are host specific (Sloss, Kemp, & Zajac, 1994). For example, the two main taxa infecting the studied mandrills (*Necator americanus*/

*Oesophagostomum* complex and *Strongyloides* spp.) exclusively parasitize primate species (Sloss et al., 1994; Stewart & Gasbarre, 1989). As such, nematode infection of group members may influence space use, particularly recursive movement patterns. In particular, once the transmission risk is effective (i.e. parasites have reached infective stages), mandrills should avoid revisiting a contaminated site for periods long enough to allow a decline in the level of contamination of this site that will depend on the 'initial' level of contamination during a visit and the subsequent decontamination rate following this visit.

Specifically, we predicted that (1) the probability of returning to a site should decrease, and the recursion time should increase, when the level of nematode infection of the mandrills at the time of the previous visit and/or residence time during this visit increase, as these two factors should positively influence the initial level of contamination of a site; (2) the probability of returning to a site should increase, and the recursion time should decrease, when the amount of rainfall following the group's departure from the site increases. Indeed, rainfall is negatively correlated with the level of nematode infection of the study group (Poirotte et al., 2016). This relationship may be regarded as a 'washout mechanism', heavy rainfall washing away faecal material from the surrounding environment (Freeland, 1980).

## METHODS

### Study Area and Seasonality

We conducted a 41-month study (October 2012–February 2016) in a private park (Lékédi Park), near Bakoumba village in southern Gabon (570 m above sea level; 12°59'55.91"E, 1°46'49.21"S). The landscape is principally composed of closed canopy forest with some areas of forest-savannah mosaics. Our study area experiences a long dry season (June–September, average daily rainfall  $\pm$  SD = 0.6  $\pm$  2.2 mm with a maximum of 16.8 mm, average daily temperature  $\pm$  SD = 22.1  $\pm$  1.0 °C), while the rest of the year is extremely humid, with two rainy seasons (long rainy season in February–May: daily rainfall = 8.0  $\pm$  12.8 mm with a maximum of 61.7 mm, daily temperature = 23.9  $\pm$  1.0 °C; short rainy season in October–November: daily rainfall = 6.9  $\pm$  13.4 mm with a maximum of 67 mm, daily temperature = 23.7  $\pm$  1.1 °C) and a short dry season during which rainfall ceases at most only for a few days (December–January, daily rainfall = 5.0  $\pm$  9.8 mm with a maximum of 48.4 mm, daily temperature = 23.7  $\pm$  1.1 °C).

During the long dry season, food availability for mandrills is lower than for the rest of the year. As this shift in resource availability could impact ranging patterns, we analysed recursive movement patterns for periods of similar ecological conditions including resource availability, considering separately the long dry season (June–September, referred to as the 'dry season') from the rest of the year (October–May; referred to as the 'rainy season'); however, considering the long rainy season alone (February–May) did not change our results. For each year, we determined the exact dates of these seasons based on recorded patterns of rainfall instead of calendar dates. Patterns of rainfall were used as a proxy for the environmental 'decontamination rate' used in the analyses.

### Study Group

We studied a free-ranging group of mandrills, habituated to close and almost permanent human presence since January 2012. This group occupies a home range area of 866 ha, which extends beyond the park's boundaries (mandrills may spend weeks outside the park), and travels on average 2.42 km/day (Brockmeyer et al., 2015). The group originates from captive-born individuals housed

at the Centre International de Recherches Médicales de Franceville, southern Gabon, which were released into the park on two occasions in 2002 (36 individuals) and 2006 (29 individuals). Wild immigrant males joined the group and were seen copulating with captive-born females starting in 2003, i.e. about 18 months following the first release. In February 2016, the group consisted of about 130 individuals of both sexes and all ages and comprised more than 85% wild-born animals. The study group has never been observed to join other mandrill groups and, even though individuals from this group may be spread out during the day, we never witnessed any evidence of temporary fissioning between groupmates.

As a part of a long-term field project ([www.projetmandrillus.com](http://www.projetmandrillus.com)) that started in January 2012, the location of the group has been recorded routinely by human observers, using a handheld GPS device that automatically registered locations every 5 min from dawn to dusk (mandrills do not usually move at night). Because of field conditions, the location of field observers in relation to the group varied on a day-to-day basis. However, for all recorded GPS data points, field observers were in contact with the group which remained cohesive. Even though the location of the field observers did not correspond to the centroid of the group, the distance between their location and the group's centroid remained insignificant compared to the large distances covered by the group (2.42 km/day). We are therefore confident that the recorded observers' movements accurately represented actual movements of the group. We obtained daily movement data for a total of 898 days over the course of the study period. Additionally, sleeping site locations were unambiguously determined for 292 nights for which the last location obtained in the late afternoon was recorded after 1700 hours, and the first location obtained the following morning was recorded before 0700 hours. We noted that both locations were very close, indicating that mandrills generally stayed in the same area between 1700 and 0700 hours. The observed difference (mean distance  $\pm$  SEM =  $50 \pm 4$  m) was due to slight variations in the locations of the field observers with respect to the group. For these 292 nights, we kept the last location recorded in the late afternoon as the location of the sleeping site. For 313 additional nights, we recorded locations either in the late afternoon or in the early morning. Sleeping site locations were therefore extrapolated from the last location of the day if acquired after 1700 (174 nights with no location data the next morning), or from the first location in the next morning if acquired before 0700 (139 nights with no location data the preceding afternoon).

Since the beginning of the project, encounters with other mandrill groups have never been observed. Moreover, sympatric primate species such as gorillas, *Gorilla gorilla*, or guenons (*Cercopithecus cephus*, *Cercopithecus nictitans* and *Cercopithecus pogonias*) have only rarely been recorded within the home range of the group.

#### Parasitological Analyses

We opportunistically collected 1275 faecal samples following defecation from 103 identified individuals of both sexes and all ages. We systematically collected the whole faecal bolus. We performed qualitative analyses based on the presence/absence of nematode taxa using a protocol of sedimentation (described in [Poirotte et al., 2016](#)). We did not quantify nematode eggs in faecal samples for practical reasons: the protocol we used allows the detection of other gastrointestinal parasites, such as protozoa, but it is not appropriate for counting nematode eggs, and routinely performing two protocols on each faecal sample was not feasible in the field. Moreover, although information about parasite abundance would have been of interest for this study, quantifying nematodes from a limited number of faecal samples available per individual

often produces biased estimates of infection levels of individuals ([Neveu-Lemaire, 1952](#)). This motivated our choice to routinely perform qualitative analyses only, but on a large number of parasite species. Using this method, we identified five nematode gastrointestinal taxa infecting the group: *N. americanus/Oesophagostomum* complex (percentage of faecal samples collected containing this taxon: 61.5%), *Strongyloides* spp. (16.2%), *Trichostrongylus* spp. (12.2%), *Mammomonogamus* spp. (1.4%) and *Enterobius vermicularis* (1.7%).

To estimate the level of nematode infection of the group at the time of a visit of a site, we used nematode prevalence (i.e. the proportion of individuals infected, corresponding to the number of faecal samples containing at least one nematode taxon divided by the total number of faecal samples available, as defined in [Bush, Lafferty, Lotz, & Shostak, 1997](#)), and average nematode richness (i.e. the mean number of nematode taxa per faecal sample, as defined in [Bush et al., 1997](#)) as proxies, hereafter called 'nematode prevalence' and 'nematode richness', respectively. Finally, we evaluated the prevalence of each of the three main nematode taxa found in the group (i.e. the proportion of individuals infected with one given parasite taxon divided by the total number of faecal samples available, as defined in [Bush et al., 1997](#)). To obtain reliable parasite estimates, we considered all faecal samples collected for 2 weeks preceding a visit (as levels of infection vary little over such short periods), with a lower limit of five samples per week (mean number of samples collected for 2 weeks before a visit  $\pm$  SD =  $16.5 \pm 10.1$ ). In preliminary analyses, we investigated whether the number of faecal samples collected for these 2-week periods influenced nematode richness estimates. We found that these two variables were not correlated ( $r = 0.07$ ). These levels of nematode prevalence and nematode richness constituted one component of the 'initial level of contamination' in our analyses. The second component concerned residence time (defined below).

We evaluated the maturation time required for nematode eggs to reach the infective stage by performing cultures of these eggs retrieved from 10 faecal samples containing both *N. americanus/Oesophagostomum* complex and *Strongyloides* spp. These cultures allowed us to estimate the time window during which environmental transmission risk is expected to be maximal, following a visit of a site. Every day, faecal samples stored in nonhermetically sealed boxes were exposed to ambient air for 1–3 h. We used a Baermann apparatus to concentrate potential nematode larvae via their tendencies to migrate towards water ([Sloss et al., 1994](#)). We found that nematode eggs started maturing into infective-stage larvae the fifth day following faecal emission (cf. [Hausfater & Meade, 1982](#)). Additionally, we observed that faecal material persisted up to 2 weeks in the environment. However, nematode larvae are highly resistant and may persist for several days in the soil following faeces decomposition ([Sloss et al., 1994](#)). Even though specific characteristics of the habitat might have influenced the decontamination dynamic, given these parasitological parameters, we defined a conservative 'contamination time window' for a given site, ranging from day 5 to day 21 following the group's departure (in preliminary analyses, we found similar results based on contamination time windows ranging from day 7 to day 21 or day 5 to day 14).

#### Spatial Analyses

We determined recursive movement patterns for a number of sites located within the areas highly used by mandrills, i.e. those that were visited both frequently and intensively ([Benhamou & Riotte-Lambert, 2012](#)). For this purpose, we first determined the utilization distribution (UD) of the group each year for each dry and each rainy season separately, using the biased random bridge/

movement-based kernel density estimation method (Benhamou, 2011). Whereas the group occupies a home range (defined as the area within 95% cumulative UD isopleths) of 866 ha all year-long (Brockmeyer et al., 2015), we focused on the 20% core areas of the home range (for each season of each year), i.e. the areas encompassed within the 20% cumulative UD isopleths based on total (daily and sleeping) time. Within these 20% core areas, we set up nonoverlapping virtual circles of 150 m in diameter, hereafter referred to as 'sites' (dry season:  $N = 34$  sites; rainy season:  $N = 93$  sites; see Appendix Fig. A1). This 150m-diameter circle was chosen according to a rough estimation of the average area occupied by the group when resting or foraging. However, we obtained similar qualitative results considering for example 300 m diameter circles (see Appendix Tables A1, A2). We then computed residence times, number of visits and recursion times for each site based on established procedures (Barraquand & Benhamou, 2008; Benhamou & Riotte-Lambert, 2012). For a given visit to a site, residence time, which constituted the second component of the 'initial level of contamination' used in our analyses, was computed as the active time spent (in hours, excluding night time between 1730 and 0600 hours) within the site until the group left it. A new visit to this site was counted each time the group re-entered it after a time lag spent outside the site longer than 2 h and remained in that site for at least 15 min (to exclude cases in which mandrills went through a site without using it extensively for foraging or resting). By contrast, when the group re-entered the site after a time lag of less than 2 h the time spent within this site was counted as part of residence time of the current visit. This 2 h time threshold was set up to discriminate between cases where the group entered and left the site several consecutive times during the same visit to a given area and cases where the group moved far away before revisiting this area. The night time was excluded from residence time because we assumed, based on our field experience, that mandrills did not defecate at night, or at least defecated less while sleeping than during active periods of the day. Considering night times would have therefore led to higher times spent in some sites that did not correspond to higher levels of faecal contamination. Recursion time was computed as the total time (i.e. including night time, because both night and day times were assumed to be involved in the same way in possible decontamination processes) between the end of a visit of a site and the beginning of the next visit to this site. As previously mentioned, we analysed recursive movement patterns separately for the dry and the rainy seasons because patterns of nematode infection (Poirotte et al., 2016) and food availability are highly seasonal (nematode infection is highest and food resources are lowest during the dry season). Utilization distribution, residence and recursion time computations were performed using custom-written programs.

We also studied recursive movements to sleeping sites because mandrills spend several hours near such sites before and after the night. We considered that the group reused a sleeping site when animals returned to sleep within a given distance (set to different values: 150, 200, 250, 350 and 500 m because the group could spread out at night) of this site.

### Statistical Analyses

We fitted two sets of models, each focusing on a different but complementary response variable. First, using generalized linear models (GLM) with a binomial distribution and a logit link function, we tested the probability of returning to a visited site during the contamination time window (i.e. 5–21 days following the group's departure). Second, using general linear models (LM), we considered recursion times greater than 5 days without constraining the upper limit of the contamination time window to 21 days because

transmission risk may still exist, even if reduced. Recursion times were log-transformed to fit a normal distribution. We verified that all statistical analyses performed met model assumptions and we did not detect any multicollinearity issues in any of our models (variance inflation factors [VIFs] < 1.5). We performed each set of models on the two data sets (dry versus rainy seasons).

We designed our analyses based on the hypothesis that mandrills should adjust their recursive movement patterns according to the level of contamination of visited sites. This level depends on both the 'initial level of contamination' and the 'decontamination rate' of the sites (as defined above). We investigated the effects of the following variables on recursive movement patterns: (1) either nematode prevalence, nematode richness or prevalence of each of the three main nematode taxa at the time of a visit of a site, alternatively considered in five models, (2) residence time during this visit and (3) patterns of rainfall, considered in two ways: (a) as the daily average amount of rainfall following the group's departure from a site (for the 21 first days when studying the probability of returning to a site; for all days before a return when studying the recursion time; note that we did not discard the first 5 days in rainfall estimation because of possible washout effects on immature nematode stages during this period); (b) as the first heavy rainfall (>60 mm/h, corresponding to the 15% of maximum rain rates recorded in the entire climatic data set) following the group's departure in the models with recursion time as the response variable (during the rainy season only, as rainfall never reached this rate during the dry season).

In another set of models, we studied the probability of reusing a sleeping site during the contamination time window and during the time when contamination risk was highest, i.e. during the dry season. As previously, we investigated (1) either nematode prevalence, nematode richness or prevalence of each of the three main nematode taxa at the time of a visit of a site, alternatively considered in five models, and (2) the daily average amount of rainfall following the group's departure from a site for the first 21 days. We did not include residence time as a covariate because it varied little across nights.

## RESULTS

The number of recursions at a given site (mean  $\pm$  SD) was  $6.7 \pm 4.5$  during the dry season and  $11.8 \pm 8.8$  during the rainy season. The mean recursion time was  $25.4 \pm 22.4$  days during the dry season and  $22.0 \pm 20.9$  days during the rainy season.

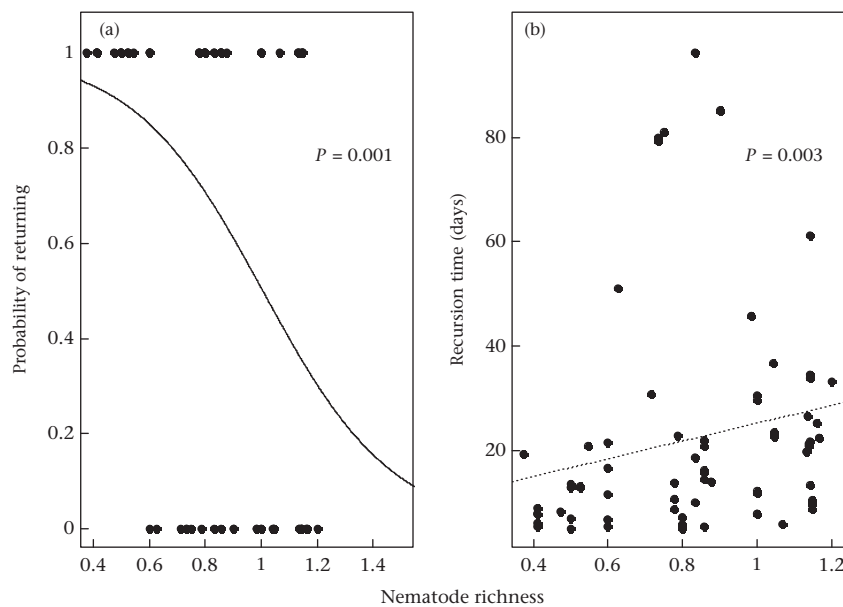
During the dry season, the probability of returning to a visited site during the contamination time window decreased significantly when nematode prevalence and richness at the time of the previous visit increased (GLM: Table 1, Fig. 1a). This probability also decreased significantly when the prevalence of both *N. americanus/Oesophagostomum* complex and *Trichostrongylus* spp. (Table 1), but not that of *Strongyloides* spp., increased (Table 1). We found similar, but less pronounced effects of nematode contamination on recursive movement patterns during the rainy season: this probability decreased significantly when both overall nematode prevalence and specific prevalence of *N. americanus/Oesophagostomum* complex increased (Table 1). Moreover, we found that this probability increased significantly with the daily average amount of rainfall for the first 21 days following a visit (Table 1, Fig. 2a). Contrary to our predictions, however, the probability that the group returned to a visited site during the contamination time window was not correlated with residence time during the previous visit, for both seasons (Table 1).

We also found that recursion time increased significantly with nematode prevalence in both seasons: the more mandrills were parasitized at the time of a visit to a site, the later they returned

**Table 1**  
Possible predictors of the probability of returning to a visited site during the dry and the rainy seasons

Season	Predictor	Estimate	SE	z	P	R <sup>2</sup>	OR
Dry	<b>Nematode prevalence</b>	-5.54	1.96	-2.83	0.005	0.09	0.57
	Rainfall	1.46	0.96	1.53	0.13		
	Residence time	-1.1e-03	8.1e-04	-1.30	0.19		
Dry	<b>Nematode richness</b>	-4.83	1.39	-3.48	0.001	0.15	0.62
	Rainfall	1.35	0.93	1.45	0.15		
	Residence time	-5.0e-04	8.4e-04	-0.60	0.55		
Dry	<b>Prevalence of taxa 1</b>	-5.69	2.06	-2.76	0.006	0.10	0.57
	Rainfall	1.48	0.96	1.55	0.12		
	Residence time	-9.2e-04	8.1e-04	-1.15	0.25		
Dry	<b>Prevalence of taxa 2</b>	-3.77	3.18	-1.20	0.23		
	Rainfall	-0.03	0.86	-0.03	0.97		
	Residence time	1.0e-03	8.1e-04	-1.28	0.20		
Dry	<b>Prevalence of taxa 3</b>	-8.85	3.11	-2.84	0.004	0.09	0.41
	Rainfall	0.55	-0.88	0.62	0.53		
	Residence time	-1.1e-03	8.3e-04	-1.29	0.20		
Rainy	<b>Nematode prevalence</b>	-1.12	0.56	-2.03	0.043	0.01	0.89
	<b>Rainfall</b>	0.15	0.04	3.72	<0.001		
	Residence time	1.1e-03	6.7e-04	1.68	0.09		
Rainy	<b>Nematode richness</b>	-0.48	0.43	-1.12	0.26	0.05	1.16
	<b>Rainfall</b>	0.15	0.04	3.79	<0.001		
	Residence time	1.1e-03	6.7e-04	1.73	0.09		
Rainy	<b>Prevalence of taxa 1</b>	-1.13	0.53	-2.15	0.032	0.01	0.89
	<b>Rainfall</b>	0.14	0.04	3.47	<0.001		
	Residence time	1.1e-03	6.7e-04	1.68	0.09		
Rainy	<b>Prevalence of taxa 2</b>	1.50	1.99	0.75	0.45	0.05	1.19
	<b>Rainfall</b>	0.17	0.04	4.09	<0.001		
	Residence time	1.0e-03	6.7e-04	1.50	0.13		
Rainy	<b>Prevalence of taxa 3</b>	2.20	1.48	1.48	0.14	0.05	1.16
	<b>Rainfall</b>	0.15	0.04	3.93	<0.001		
	Residence time	1.1e-03	6.6e-04	1.64	0.10		

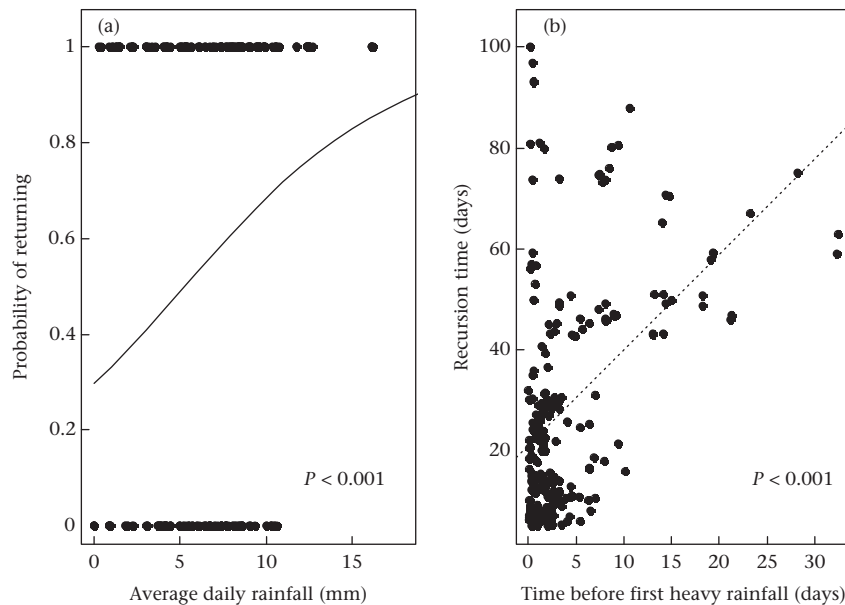
Taxa 1, 2 and 3 correspond, respectively, to *N. americanus/Oesophagostomum* complex, *Strongyloides* spp. and *Trichostrongylus* spp. Estimates, standard errors, z values and their associated P values are provided considering full models. Proportions of variance explained (R<sup>2</sup>) and odds ratios (OR) are given for predictors showing a significant effect (P < 0.05). Odds ratios give the multiplicative increase in the odds associated with each unit increase for rainfall and each 0.1 unit increase for nematode prevalence and richness.



**Figure 1.** Nematode richness at the time of a visit of a site during the dry season versus (a) probability of returning to this site during the contamination time window and (b) recursion time. Dotted and continuous lines represent the regression lines of the models (with the associated P values).

to this site (LM; Table 2). Again, we found that recursion time increased especially with the prevalence of *N. americanus/Oesophagostomum* complex (Table 2). Moreover, recursion time also increased with nematode richness during the dry season (Table 2, Fig. 1b) but not during the rainy season (Table 2). More importantly, during the rainy season, rainfall was strongly

associated with decreased recursion time (Table 2). Additionally, the earlier the first heavy rainfall (see Methods) following the group's departure from a site, the earlier the return to this site (Table 2, Fig. 2b). As in the previous analyses, recursion time was not correlated with residence time during the previous visit (Table 2).



**Figure 2.** Recursive movement patterns during the rainy season versus (a) average daily rainfall recorded for the first 21 days following group's departure from a site and (b) time elapsed between group's departure and the first heavy rainfall. Dotted and continuous lines represent the regression lines of the models (with the associated  $P$  values).

Finally, we found that the probability of returning to a sleeping site during the contamination time window was negatively correlated with nematode prevalence and richness: the more mandrills were parasitized during the occupation of a sleeping site, the less likely they were to sleep again within 350 m of that site (GLM: Table 3, Fig. 3). When we considered the three nematode taxa separately, the probability of returning to a used sleeping site decreased only when the prevalence of *N. americanus/Oesophagostomum* complex increased (Table 3).

## DISCUSSION

Parasites in the environment have been proposed to influence animal movements (Altizer et al., 2011; Hart, 1990), but the few empirical studies on this topic concerned almost exclusively ectoparasites (Downes et al., 1986; Keiper & Berger, 1992; Sutherst et al., 1986). Although theoretical studies recently proposed that avoiding previously used areas represents one strategy limiting infection with gastrointestinal parasites (Bar-David et al., 2009; Berger-Tal & Bar-David, 2015), there are few documented examples of a possible impact of gastrointestinal parasitism on recursive movements. Yellow baboons, *Papio cynocephalus*, and mangabeys, *Cercocebus albigena*, avoid using the same site for an extensive period of time and return to visited sites when parasite contamination of the environment is assumed to be low (Freeland, 1980; Hausfater & Meade, 1982). Neither study, however, controlled for variations in infection levels of the group.

In our study, we investigated whether recursive movement patterns varied with nematode prevalence and average nematode richness of the group at the time of a visit of a site. Indeed, nematode infection of the group should influence environmental contamination. Other factors might have further impacted this contamination level, such as the intensity of nematode infection or the type of vegetation and soil, but we were not able to take them into account because of field work constraints. Combining analyses of small-scale ranging patterns with long-term monitoring of climate data and parasitism, we showed that recursive movement patterns were significantly associated with the inferred initial level of contamination of a site. In agreement with our hypotheses,

mandrills returned less frequently (lower probability of returning) and after longer time lags (higher recursion times) to sites that were inferred to be previously highly contaminated than to those inferred to be lightly contaminated. This effect was particularly pronounced during the dry season, when contamination was expected to be maximal (based on nematode prevalence at this time of the year compared to other seasons: Poirotte et al., 2016). However, contrary to our hypotheses, residence time did not appear to influence recursive movement patterns, possibly because these sites were all highly used and therefore highly soiled by mandrills' faeces. In addition, the level of faecal contamination of a site following a visit should depend not only on the time spent but also on other factors such as the activity of the group during that visit, or factors related to larval development and survival.

Interestingly, we found that the prevalence of *N. americanus/Oesophagostomum* complex explained a similar proportion of variance in the probability of returning to a site and in recursion times than did overall nematode prevalence. Little is known about the effects of this parasite complex on the health of nonhuman primates. While often asymptomatic, severe clinical signs associated with nodular lesions have sometimes been reported in primate species (Krief et al., 2008; Terio et al., 2016). Moreover, it is a major concern for human health. Specifically, *N. americanus* is responsible for significant blood loss (a single larva consumes about 0.25 ml of host blood per day) and iron deficiency anaemia (Kucik, Martin, & Sortor, 2004). *Oesophagostomum* spp. can cause acute intestinal disease because of the presence of encapsulated larvae adhering to the abdominal wall (Gasser, De Grujter, & Polderman, 2006). Long-term data are now needed to assess the impact of these parasites on mandrills' health and fitness. In addition, nematode richness was highly correlated with recursive movement patterns during the dry season, explaining a larger proportion of variance in the probability of returning to a visited site and recursion times than the overall nematode prevalence. This latter finding suggests that the effect of several parasite infections could be higher than the sum of the effects caused by each parasite taxon, as observed in other host–parasite systems (Vaumourin, Vourc'h, Gasqui, & Vayssier-Taussat, 2015). Alternatively, our findings may just reflect the fact that the probability of

**Table 2**  
Possible predictors of the recursion times between two successive visits during the dry and the rainy seasons

Season	Predictor	Estimate	SE	<i>t</i>	<i>P</i>	<i>R</i> <sup>2</sup>
Dry	<b>Nematode prevalence</b>	1.34	0.54	2.47	0.016	0.07
	Rainfall	-0.29	0.48	-0.59	0.56	
	Residence time	1.3e-04	2.8e-04	0.46	0.65	
Dry	<b>Nematode richness</b>	1.14	0.38	3.03	0.003	0.11
	Rainfall	-0.31	0.46	-0.66	0.51	
	Residence time	-2.0e-05	2.9e-04	-0.07	0.94	
Dry	<b>Prevalence of taxa 1</b>	1.33	0.52	2.55	0.013	0.08
	Rainfall	-0.27	0.48	-0.56	0.58	
	Residence time	9.8e-05	2.9e-04	0.35	0.73	
Dry	Prevalence of taxa 2	1.82	1.14	1.60	0.11	
	Rainfall	0.19	0.45	0.43	0.67	
	Residence time	9.3e-05	3.0e-04	0.32	0.75	
Dry	Prevalence of taxa 3	1.25	0.98	1.27	0.21	
	Rainfall	5.9e-02	0.47	0.13	0.90	
	Residence time	1.6e-04	2.9e-04	0.55	0.59	
Rainy	<b>Nematode prevalence</b>	0.53	0.21	2.47	0.014	0.02
	<b>Rainfall</b>	-3.2e-02	1.2e-02	-2.73	0.007	
	Residence time	-2.8e-04	2.4e-04	-1.15	0.25	
Rainy	Nematode richness	0.29	0.17	1.73	0.085	0.04
	<b>Rainfall</b>	-3.4e-02	1.2e-02	-2.87	0.004	
	Residence time	-3.1e-04	2.5e-04	-1.26	0.21	
Rainy	<b>Prevalence of taxa 1</b>	0.50	0.20	2.47	0.014	0.02
	<b>Rainfall</b>	-3.1e-02	1.2e-02	-2.64	0.009	
	Residence time	2.8e-04	2.4e-04	-1.15	0.25	
Rainy	Prevalence of taxa 2	0.36	0.75	0.48	0.63	0.03
	<b>Rainfall</b>	-3.8e-02	1.2e-02	-3.21	0.002	
	Residence time	-3.1e-04	2.5e-04	-1.27	0.21	
Rainy	Prevalence of taxa 3	-0.62	0.56	-1.12	0.26	0.03
	<b>Rainfall</b>	-3.8e-02	1.2e-02	-3.29	0.001	
	Residence time	-2.9e-04	2.5e-04	-1.17	0.24	
Rainy	<b>Nematode prevalence</b>	0.50	0.21	2.46	0.015	0.02
	<b>Time before 1st heavy rain</b>	6.5e-02	9.2e-03	6.98	<0.001	
	Residence time	-1.2e-04	2.4e-04	-0.53	0.59	
Rainy	<b>Nematode richness</b>	0.33	0.16	1.98	0.049	0.01
	<b>Time before 1st heavy rain</b>	6.5e-02	9.3e-03	7.05	<0.001	
	Residence time	-1.6e-04	2.3e-04	-0.68	0.50	
Rainy	<b>Prevalence of taxa 1</b>	0.45	0.19	2.34	0.020	0.02
	<b>Time before 1st heavy rain</b>	6.4e-02	9.2e-03	6.93	<0.001	
	Residence time	-1.3e-04	2.4e-04	-0.57	0.57	
Rainy	Prevalence of taxa 2	1.41	0.74	1.92	0.056	0.19
	<b>Time before 1st heavy rain</b>	6.8e-02	9.0e-03	7.50	<0.001	
	Residence time	-2.2e-04	2.3e-04	-0.92	0.36	
Rainy	Prevalence of taxa 3	-0.77	0.58	-1.32	0.19	0.20
	<b>Time before 1st heavy rain</b>	7.0e-02	9.1e-03	7.64	<0.001	
	Residence time	-1.5e-04	2.4e-04	-0.63	0.53	

Taxa 1, 2 and 3 correspond, respectively, to *N. americanus/Oesophagostomum* complex, *Strongyloides* spp. and *Trichostrongylus* spp. Estimates, standard errors, *t* values and their associated *P* values are provided considering full models. Proportions of variance explained are given for predictors showing a significant effect ( $P < 0.05$ ).

carrying nematode species influencing ranging patterns increases with nematode richness.

During the rainy season, mandrills returned more rapidly to a site when significant rainfall occurred following the group's departure. We suggest that the initial level of contamination of the habitat may drive mandrills' movements and that heavy rainfall may accelerate decontamination processes. Indeed, in this study system, nematode richness is higher during the dry season than during the rainy season and decreases following significant rainfall (Poirotte et al., 2016). Humidity generally favours the maturation of nematode eggs into larvae and dry weather is often associated with a lower nematode prevalence and richness in primates in various study sites (Benavides et al., 2012; Gillespie et al., 2010). However, in equatorial rainforests humidity remains high throughout the year, even during the dry season. In these climatic conditions, humidity should not be a limiting factor for parasite development but significant rainfall may represent adverse environmental conditions for free-living stages of nematodes, explaining the negative impact of rainfall on nematode richness. In line with these findings, in Ugandan rainforests, day-to-day overlap in space use by mangabey social groups was higher during rainy than during dry

weather (Freeland, 1980). Although changes in food distribution associated with rainfall may explain this pattern, Freeland (1980) noted that experimental data show that the survival of gastrointestinal parasites within faecal material is reduced during rainy weather, suggesting that increased rainfall may allow mangabeys to use certain sites more intensively. Measurements of environmental nematode contamination following defecation on different substrates and under different climatic conditions are needed to confirm this washout hypothesis.

We also analysed the probability of reusing a sleeping site during the dry season, when environmental conditions seem to favour the survival of nematodes. Mandrills' sleeping sites are highly soiled with faecal material because, like other primates (Andresen, 2002), they generally defecate early in the morning before leaving the site. In agreement with our predictions, we found that, during the contamination time window, mandrills avoided reusing a sleeping site that they had previously highly contaminated with nematodes, especially with *N. americanus/Oesophagostomum* complex. In other taxa, parasites have also been proposed to drive shelter choice. For example, great tits, *Parus major*, avoid using contaminated nests (Oppliger, Richner, &

**Table 3**  
Possible predictors of the probability of reusing sleeping sites during the dry season

Distance considered (m)	Predictor	Estimate	SE	Z	P	R <sup>2</sup>	OR
150	Nematode prevalence	−4.40	2.33	−1.88	0.058	0.08	0.71
	Rainfall	−1.23	1.11	−1.11	0.26		
150	<b>Nematode richness</b>	−3.46	1.63	−2.12	0.034	0.06	0.45
	Rainfall	−1.17	1.10	−1.06	0.29		
150	<b>Prevalence of taxa 1</b>	−8.02	3.72	−2.16	0.031	0.07	0.57
	Rainfall	−1.99	1.09	−1.81	0.090		
150	Prevalence of taxa 2	−7.39	4.17	−1.18	0.077	0.07	0.70
	Rainfall	−1.13	1.12	−1.01	0.31		
150	Prevalence of taxa 3	−2.55	2.16	−1.18	0.24	0.07	0.40
	Rainfall	−1.28	1.13	−1.13	0.26		
200	<b>Nematode prevalence</b>	−5.59	2.20	−2.53	0.011	0.10	0.54
	Rainfall	−0.11	0.85	−0.12	0.90		
200	<b>Nematode richness</b>	−3.58	1.51	−2.38	0.017	0.10	0.68
	Rainfall	−0.16	0.84	−0.20	0.84		
200	<b>Prevalence of taxa 1</b>	−9.10	3.55	−2.57	0.010	0.09	0.35
	Rainfall	−1.09	0.82	−1.33	0.18		
200	Prevalence of taxa 2	−3.02	3.34	−0.90	0.37	0.05	0.70
	Rainfall	−0.54	0.82	−0.66	0.51		
200	Prevalence of taxa 3	−1.59	1.93	−0.83	0.41	0.04	0.49
	Rainfall	−0.44	0.88	−0.50	0.61		
250	<b>Nematode prevalence</b>	−6.16	2.07	−2.99	0.003	0.09	0.35
	Rainfall	−0.50	0.79	−0.64	0.52		
250	<b>Nematode richness</b>	−3.90	1.42	−2.74	0.006	0.05	0.70
	Rainfall	−0.52	0.77	−0.67	0.50		
250	<b>Prevalence of taxa 1</b>	−10.48	3.49	−3.00	0.003	0.04	0.49
	Rainfall	−1.53	0.78	−1.97	0.050		
250	Prevalence of taxa 2	−2.88	3.20	−0.90	0.37	0.04	0.49
	Rainfall	−0.58	0.77	−1.17	0.24		
250	Prevalence of taxa 3	−2.49	1.75	−1.42	0.155	0.04	0.49
	Rainfall	−0.58	0.82	−0.71	0.47		
350	<b>Nematode prevalence</b>	−3.87	1.81	−2.14	0.033	0.04	0.49
	Rainfall	−0.71	0.71	−0.99	0.31		
350	Nematode richness	−2.37	1.13	−1.92	0.059	0.04	0.49
	Rainfall	−0.78	0.71	−1.11	0.27		
350	<b>Prevalence of taxa 1</b>	−7.06	3.12	−2.26	0.024	0.04	0.49
	Rainfall	−0.82	0.73	−1.12	0.26		
350	Prevalence of taxa 2	−1.44	3.08	−0.47	0.64	0.04	0.49
	Rainfall	−1.10	0.70	−1.57	0.12		
350	Prevalence of taxa 3	−1.00	1.62	−0.62	0.54	0.04	0.49
	Rainfall	−0.96	0.76	−1.26	0.21		
500	Nematode prevalence	−2.10	1.68	−1.25	0.31	0.04	0.49
	Rainfall	0.04	0.65	0.07	0.94		
500	Nematode richness	−0.73	1.16	−0.63	0.52	0.04	0.49
	Rainfall	−0.11	0.64	−0.19	0.85		
500	Prevalence of taxa 1	−5.93	3.60	−1.65	0.10	0.04	0.49
	Rainfall	−0.58	0.64	−0.91	0.36		
500	Prevalence of taxa 2	0.22	2.96	0.08	0.94	0.04	0.49
	Rainfall	−0.27	0.62	−0.43	0.67		
500	Prevalence of taxa 3	0.82	1.53	0.53	0.59	0.04	0.49
	Rainfall	−0.44	0.70	−0.63	0.53		

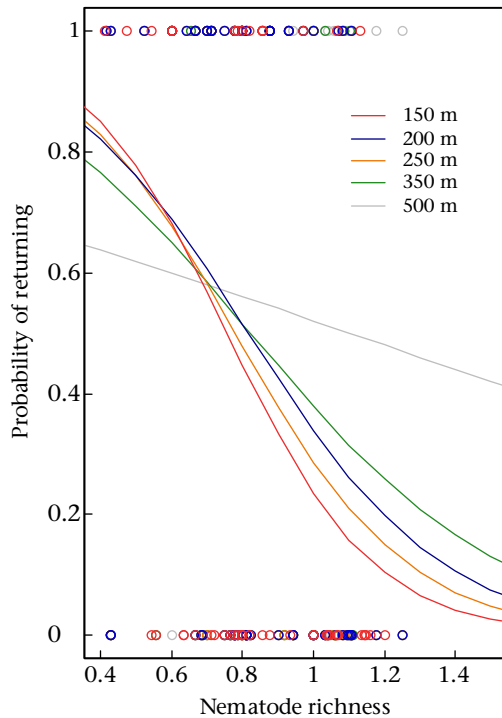
Taxa 1, 2 and 3 correspond, respectively, to *N. americanus/Oesophagostomum* complex, *Strongyloides* spp. and *Trichostrongylus* spp. Estimates, standard errors, z values and associated *P* values are provided considering full models. Proportions of variance explained (*R*<sup>2</sup>) and odds ratios (OR) are given for predictors showing a significant effect (*P* < 0.05). Odds ratios give the multiplicative increase in the odds associated with each unit increase for rainfall and each 0.1 unit increase for nematode prevalence and richness. We alternatively considered that the group was in a previously used sleeping site when individuals returned to sleep within 150, 200, 250, 350 and 500 m of that sleeping site.

Christe, 1993). Moreover, the re-occupancy rate of used roosts by Bechstein's bats, *Myotis bechsteinii*, is negatively correlated with the presence of infective stages of parasitic bat flies (Reckardt & Kerth, 2007). In yellow baboons, individuals alternate between several sleeping groves in relation to the life cycle of their gastrointestinal parasites (Hausfater & Meade, 1982).

Because of the correlational nature of our study, alternative hypotheses may also explain the relationships we found. First, in the study system, long recursion times are associated with long daily path lengths (Poirotte & Charpentier, 2016) that may, in turn, be positively correlated with the probability of encountering environmentally transmitted parasites (e.g. Benavides et al., 2012). However, daily path length of the study group was not correlated with nematode richness (Brockmeyer et al., 2015) and thus probably cannot

explain our findings. Second, both recursive movement patterns and the choice of sleeping sites have been repeatedly linked to the availability of (or the distance to) food resources (Bar-David et al., 2009; van Beest et al., 2010; English et al., 2014; Markham, Alberts, & Altmann, 2015; Williams & Thomson, 1998). In this study, we were unable to control for possible confounding effects of the distribution and abundance of food resources that may covary with both the initial contamination level and rainfall. In contrast to other studies (Freeland, 1980; Hausfater & Meade, 1982), we partly circumvented this issue by considering periods of the year that differed in resource availability in two different sets of analyses (dry versus rainy seasons). Food resources are, however, distributed heterogeneously in both time and space within each season, which may still have confounded our results. For example, rainfall may





**Figure 3.** Nematode richness at the time of a visit to a sleeping site versus probability of returning to sleep close to (within 150, 200, 250, 350 and 500 m) this sleeping site during the contamination time window.

have enhanced food recovery rates, especially for fruiting trees, which, in turn, may have impacted recursive movement patterns. Although mandrills are eclectic omnivores that feed on about 150 plant species, during the rainy season, only six plant species constitute about 45% of their total frequency of food intake (Nsi Akoué et al., 2017). The phenology of these key food resources during the rainy season may have therefore largely influenced recursive group movements and the choice of sleeping sites. Indeed, although mandrills have been repeatedly observed sleeping in high trees on the edge of forest patches (M.J.E. Charpentier, personal observation), probably to reduce predation risk, the distance to food resources may have also influenced the choice of sleeping sites, as reported elsewhere (Janmaat, Polansky, Dagui Ban, & Boesch, 2014).

Further studies assessing parasite contamination of the habitat and spatiotemporal distribution of food resources are needed to disentangle the effects of parasitism versus those of food resources on movement patterns. Interestingly, and in line with our hypotheses, helminth richness is higher in territorial primates, which intensively use some areas, than in nonterritorial primates, suggesting that patterns of space use influence parasite infection levels (Nunn & Dokey, 2006). Moreover, while parasite infection increases with group size for sedentary hosts, such a positive correlation does not hold true for mobile hosts, suggesting that animal movements may further alleviate contamination risk from environmentally transmitted parasites (Patterson & Ruckstuhl, 2013). Our study supports the idea that environmentally transmitted parasites may represent a selective force, in addition to food resources or predation risk, constraining animal space use. Notably in relation to this point, the magnitude of antiparasite and antipredator responses were found to be qualitatively equivalent in American toad, *Anaxyrus americanus*, tadpoles, suggesting that the avoidance of disease is comparable to that of predation in this species (Rohr, Swan, Raffel, & Hudson, 2009). Finally, our study supports the idea that a parasite contamination/decontamination system is

somehow similar to a food depletion/recovery scheme because the 'parasite-free' property of a site may be viewed as a renewable resource (Berger-Tal & Bar-David, 2015). In conclusion, the avoidance of contaminated habitats in our study species may act as a sanitary strategy to reduce contamination with environmentally transmitted parasites. Our study should motivate further analyses evaluating the influence of parasite contamination on small-scale animal movements. Such studies should improve our understanding of animal space use.

## AUTHORSHIP

CP, SB and MJEC designed the study and analysed the data, and with PMK wrote the article. CP and AM collected data. MJEC and EW contributed to data collection and MJEC acquired and managed the databases used in this study.

## COMPETING INTERESTS

The authors declare no competing financial interests.

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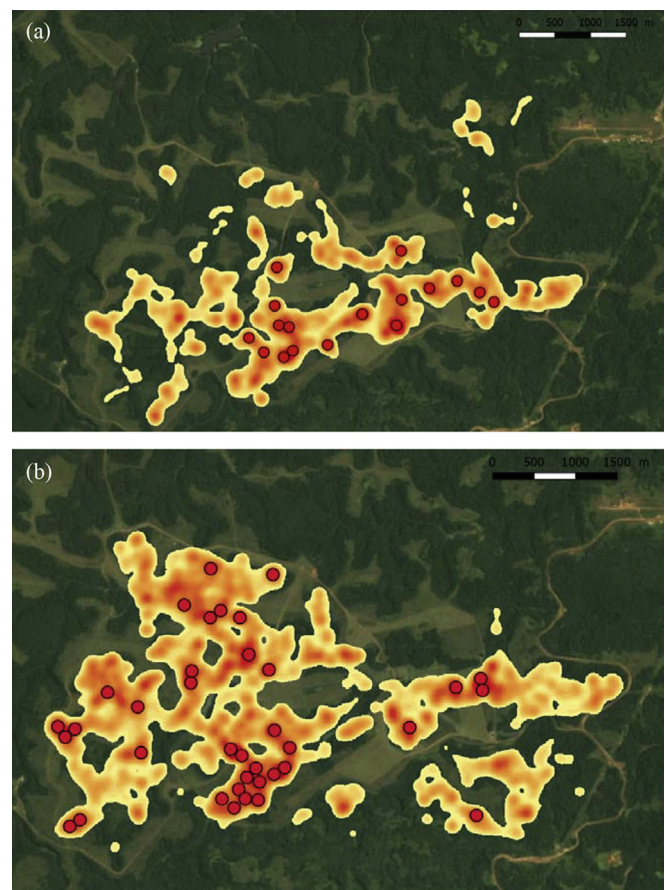
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## Appendix



**Figure A1.** Mandrills' home range and recursion sites during (a) one dry season (2013) and (b) one rainy season (2013–2014). Utilization distribution (variations in yellow and red colours) is drawn up to 95% cumulative frequencies, based on the GPS data points. Red indicates higher utilization density. Delineated circles materialize recursion sites localized on the very core areas of the home range, defined as the areas encompassed within the 20% cumulative UD isopleths based on total (daily and sleeping) time.

**Table A1**  
Possible predictors of the probability of returning to a visited site during the dry and the rainy seasons

Season	Predictor	Estimate	SE	z	P	R <sup>2</sup>	OR
Dry	<b>Nematode prevalence</b>	-6.11	2.39	-2.55	0.010	0.11	0.54
	Rainfall	0.91	1.09	0.84	0.40		
	Residence time	-1.7e-03	1.1-03	-1.56	0.12		
Dry	<b>Nematode richness</b>	-4.05	1.44	-2.83	0.005	0.12	0.66
	Rainfall	0.48	0.98	0.50	0.62		
	Residence time	-1.6e-03	1.1-03	-1.47	0.14		
Dry	<b>Prevalence of taxa 1</b>	-7.26	2.81	-2.58	0.010	0.13	0.48
	Rainfall	1.04	1.09	0.95	0.34		
	Residence time	-2.0e-03	1.1e-03	-1.78	0.075		
Dry	<b>Prevalence of taxa 2</b>	-5.41	3.11	-1.74	0.082	0.13	0.36
	Rainfall	-0.77	0.93	-0.83	0.41		
	Residence time	1.5e-03	1.0-03	-1.48	0.14		
Dry	<b>Prevalence of taxa 3</b>	-10.33	3.36	-3.07	0.002	0.13	0.36
	Rainfall	-0.22	0.96	-0.22	0.82		
	Residence time	-2.1e-03	1.1e-03	-1.90	0.057		
Rainy	<b>Nematode prevalence</b>	-1.03	0.54	-1.92	0.055	0.05	1.15
	<b>Rainfall</b>	0.13	0.04	3.50	<0.001		
	Residence time	1.0e-04	4.6e-04	0.23	0.82		
Rainy	<b>Nematode richness</b>	-0.37	0.39	-0.95	0.34	0.05	1.14
	<b>Rainfall</b>	0.14	0.04	3.79	<0.001		
	Residence time	1.4e-04	4.5e-04	0.33	0.74		
Rainy	<b>Prevalence of taxa 1</b>	-1.39	0.54	-2.59	0.010	0.05	0.97
	<b>Rainfall</b>	0.12	0.04	3.22	0.001		
	Residence time	8.5e-05	4.6e-04	0.11	0.91		
Rainy	<b>Prevalence of taxa 2</b>	1.50	1.78	0.84	0.40	0.05	1.18
	<b>Rainfall</b>	0.16	0.04	4.18	<0.001		
	Residence time	1.2e-04	4.3e-04	0.29	0.77		
Rainy	<b>Prevalence of taxa 3</b>	1.09	1.97	0.55	0.58	0.05	1.16
	<b>Rainfall</b>	0.15	0.04	4.12	<0.001		
	Residence time	1.6e-04	4.4e-04	0.38	0.70		

Recursion sites considered in these analyses are 300 m diameter circles. Taxa 1, 2 and 3 correspond, respectively, to *N. americanus/Oesophagostomum* complex, *Strongyloides* spp. and *Trichostrongylus* spp. Estimates, standard errors, z values (for binary response variables) or t values (for linear response variables) and their associated P values are provided considering full models. Proportions of variance explained (R<sup>2</sup>) and odds ratios (OR) are given for predictors showing a significant effect (P < 0.05). Odds ratios give the multiplicative increase in the odds associated with each unit increase for rainfall and each 0.1 unit increase for nematode prevalence and richness.

**Table A2**  
Possible predictors of the recursion times between two successive visits during the dry and the rainy seasons

Season	Predictor	Estimate	SE	t	P	R <sup>2</sup>
Dry	<b>Nematode prevalence</b>	1.42	0.47	3.02	0.004	0.10
	Rainfall	0.09	0.21	0.44	0.66	
	Residence time	6.5e-04	3.3e-04	1.96	0.054	
Dry	<b>Nematode richness</b>	0.88	0.39	2.28	0.026	0.11
	Rainfall	-0.14	0.23	-0.63	0.53	
	Residence time	-5.4-04	3.4e-04	1.60	0.11	
Dry	<b>Prevalence of taxa 1</b>	1.45	0.46	3.19	0.002	0.12
	Rainfall	0.16	0.21	0.78	0.44	
	<b>Residence time</b>	7.0e-04	3.3e-04	2.12	0.038	
Dry	<b>Prevalence of taxa 2</b>	1.80	0.99	1.81	0.075	0.05
	Rainfall	0.03	0.21	0.13	0.89	
	Residence time	5.0e-04	3.5e-04	1.46	0.15	
Dry	<b>Prevalence of taxa 3</b>	2.31	0.99	1.27	0.024	0.06
	Rainfall	-0.11	0.22	-0.47	0.63	
	Residence time	5.9e-04	3.4e-04	1.76	0.08	
Rainy	<b>Nematode prevalence</b>	0.58	0.19	2.29	0.004	0.02
	<b>Rainfall</b>	-0.03	9.6e-03	-2.67	0.008	
	Residence time	-1.1e-04	1.6e-04	-0.69	0.49	
Rainy	<b>Nematode richness</b>	0.27	0.15	1.77	0.08	0.04
	<b>Rainfall</b>	-0.03	9.8e-03	-2.93	0.004	
	Residence time	-1.4e-04	1.6e-04	-0.90	0.37	
Rainy	<b>Prevalence of taxa 1</b>	0.69	0.19	3.52	0.005	0.02
	<b>Rainfall</b>	-0.02	9.7e-03	-2.36	0.019	
	Residence time	-9.4e-05	1.6e-04	-0.60	0.55	
Rainy	<b>Prevalence of taxa 2</b>	0.54	0.64	0.84	0.40	0.04
	<b>Rainfall</b>	-0.03	9.4e-03	-3.46	<0.001	
	Residence time	-1.7e-04	1.5e-04	-1.09	0.28	
Rainy	<b>Prevalence of taxa 3</b>	-0.97	0.74	-1.31	0.19	0.02
	<b>Rainfall</b>	-0.03	9.3e-03	-3.64	<0.001	
	Residence time	-1.8e-04	1.6e-04	-1.12	0.26	

(continued on next page)

**Table A2** (continued)

Season	Predictor	Estimate	SE	<i>t</i>	<i>P</i>	<i>R</i> <sup>2</sup>
Rainy	<b>Nematode prevalence</b>	0.70	0.19	3.72	<0.001	0.03
	<b>Time before 1st heavy rain</b>	0.07	9.1e–03	7.82	<0.001	0.18
	Residence time	–3.6e–05	1.5e–04	–0.25	0.81	
Rainy	<b>Nematode richness</b>	0.40	0.14	2.77	0.006	0.02
	<b>Time before 1st heavy rain</b>	0.07	9.2e–03	7.94	<0.001	0.19
	Residence time	–6.6e–05	1.5e–04	–0.45	0.65	
Rainy	<b>Prevalence of taxa 1</b>	0.74	0.18	4.08	<0.001	0.03
	<b>Time before 1st heavy rain</b>	0.07	9.1e–03	7.63	<0.001	0.18
	Residence time	–3.0e–05	1.5e–04	–0.21	0.84	
Rainy	Prevalence of taxa 2	0.87	0.66	1.32	0.19	
	<b>Time before 1st heavy rain</b>	0.08	9.2e–03	8.27	<0.001	0.20
	Residence time	–1.0e–04	1.5e–04	–0.69	0.49	
Rainy	Prevalence of taxa 3	–0.90	0.73	–1.23	0.22	
	<b>Time before 1st heavy rain</b>	0.08	9.1e–03	8.53	<0.001	0.21
	Residence time	–1.0e–04	1.5e–04	–0.68	0.49	

Recursion sites considered in these analyses are 300 m diameter circles. Taxa 1, 2 and 3 correspond, respectively, to *N. americanus/Oesophagostomum* complex, *Strongyloides* spp. and *Trichostrongylus* spp. Estimates, standard errors, *z* values (for binary response variables) or *t* values (for linear response variables) and their associated *P* values are provided considering full models. Proportions of variance explained are given for predictors showing a significant effect (*P* < 0.05).