

## Searching in heterogeneous and limiting environments: foraging strategies of white-lipped peccaries (*Tayassu pecari*)

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Searching for patchily distributed, highly localized, and seasonally variable resources in heterogeneous environments poses significant challenges for social species living in cohesive groups. Here, we studied the searching strategies of a highly social mammal, the white-lipped peccary (*Tayassu pecari*), in Calakmul Biosphere Reserve, Mexico. Calakmul Biosphere Reserve is a seasonal tropical forest where important resources, such as water and food, are patchy distributed and temporarily scarce. We attempted to determine what theoretical searching model best explained the movement patterns of groups of white-lipped peccaries, including short-tailed, long-tailed, and scale-free distributions. We found that the only distribution that was well supported by the data was a zero-inflated lognormal distribution; this implies a general pattern of normally short-range intensive searching with occasional long-distance directed movements taking the animals away from previously searched areas. We also found that groups concentrated foraging activities around sources of water during the dry season, behaving as central-place foragers while occasionally searching distant areas. We discuss the potential adaptive values of such behavioral strategies for social species living in highly heterogeneous environments.

Key words: central-place foraging, Lévy walk, lognormal distribution, searching strategies, *Tayassu pecari*, white-lipped peccary

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DOI: 10.1644/10-MAMM-A-384.1

Species that depend on resources that are patchily distributed across the landscape and whose availability is difficult to predict, such as a number of tropical fruits, seeds, or water reservoirs (Chapman et al. 1999; Terborgh 1986), need to develop searching strategies to find and exploit the resources. These strategies can involve choices about movement distance and speed, changes in direction, and how these choices change with the environment (Turchin 1998).

Debates about foraging distances have generally focused on whether movement distances follow a normal distribution or a heavy-tailed distribution such as a Lévy walk. The Lévy walk, originally used in physics to describe the movement of particles in turbulence, has been suggested as a model of optimal animal foraging in patchy habitats (Shlesinger and Klafter 1986; Viswanathan et al. 1996, 1999). A Lévy walk is a random walk where the probability of taking a step of length  $x$  is proportional to some power of  $x$ :  $p(x) \sim x^{-\alpha}$ ; this type of random walk is characterized by a high frequency of short-distance movements,

interspersed with rarer movements at much greater distance. Such movement patterns give the animal the ability to search at different spatial scales (Viswanathan et al. 2008). Lévy walks are viewed as having an adaptive value for animals facing uncertainty in the distribution of their resources (Bartumeus et al. 2005; Humphries et al. 2010). However, it has been shown that a mixture of Brownian random walks can outperform a Lévy walk when resource distributions are patchy, and may be confused with a Lévy walk due to similar empirical patterns (Benhamou 2007). Further, the statistical validity of typical methods for fitting and testing the goodness-of-fit of Lévy-walk exponents from empirical data has been brought into question (Clauset et al. 2009; Sims et al. 2007). Edwards et al. (2007) revisited the topic and questioned the empirical evidence of the



pioneer studies, challenging the idea that Lévy walks are common in nature and encouraging the use of maximum-likelihood methods to test alternative distributions that fit observed animal movement patterns.

A 2nd major component of movement strategy is the choice of region in which to confine foraging. The central-place foraging model (Orians and Pearson 1979) was devised to explain foraging activity around a single key immobile resource or site. In this model, foraging is concentrated in proximity to a central place (e.g., a burrow or sleeping site), and foraging activities, such as prey type captured, time spent searching for it, and distance travelled, are affected by the distribution and proximity of resources around this central place (Orians and Pearson 1979). This model has received considerable qualitative and quantitative support from laboratory and field studies (Kramer and Nowell 1980; Olsson et al. 2008; Stephens and Krebs 1986). It has also been suggested that animals behave like central-place foragers when they returned periodically to a burrow, sleeping site, or water body (e.g., *Hippopotamus*—Lewison and Carter 2004), or even that they can have multiple central sites (e.g., *Ateles geoffroyi*—Chapman et al. 1989).

The white-lipped peccary (WLP; *Tayassu pecari*) is unique among tropical forest ungulates in the size of persistent groups it forms (typically from 10 to 300 but there are reports of 700 individuals in a single group—Mayer and Wetzel 1987); the bearded pig of Borneo (*Sus barbatus*) also forms large aggregations, but these are only temporary, and divide into subgroups for some parts of the year (Caldecott et al. 1993). WLP groups perform long, straight-line movements thought to allow the groups to find sufficient food while still maintaining group cohesion (Fragoso 1998; Reyna-Hurtado et al. 2009). WLPs feed on high-energy food such as fallen fruits and seeds (Altrichter et al. 2001; Beck 2006; Pérez-Cortéz and Reyna-Hurtado 2008; Sowsls 1997) that are generally distributed patchily in space and time (Terborgh 1986). Furthermore, WLP groups typically visit water bodies daily; such water bodies also are patchily distributed (Altrichter et al. 2001; Fragoso 1994; Reyna-Hurtado et al. 2009). WLPs have the largest home ranges of any ungulate species living in tropical forests, with home ranges of up to 200 km<sup>2</sup> (Fragoso 2004). However, it is not known what foraging strategies WLPs employ to cope with seasonality and spatiotemporal unpredictability of most resources.

Calakmul Biosphere Reserve in southern Mexico is an ideal place to study how WLP groups search for resources in a heterogeneous landscape. This area is a protected, seasonal semidry forest where water and food resources are seasonally scarce and highly localized. Evidence suggests that Calakmul Biosphere Reserve has been sparsely populated for more than 1,000 years after the Mayans abandoned the area (Folan et al. 1999) and it has been legally protected since 1989. Compared with previous studies, Calakmul Biosphere Reserve represents very different conditions from where the WLP has been studied in the past because of the climate and water availability that characterize this seasonal region (Altrichter



FIG. 1.—Map of the study site and Calakmul Biosphere Reserve in Campeche State, Mexico.

2005; Altrichter et al. 2001; Carrillo et al. 2002; Fragoso 1994; Keuroghlian et al. 2004, 2009; Kiltie and Terborgh 1983).

We used a combination of radiotelemetry and direct observations to explore the searching strategies of 4 WLP groups in Calakmul Biosphere Reserve. We documented how this social ungulate combines different searching strategies to access seasonally scarce resources in a semidry tropical forest. First, we described the distribution of important resources for WLPs, and then we described the spatial and temporal scales of movements in 4 groups by comparing strategies and movements in the rainy and the dry season. We tested ranging patterns of WLPs against multiple theoretical distributions, including 2 light-tailed distributions—the half-normal and exponential—and 2 heavy-tailed distributions—the lognormal and Lévy walk. We further tested if average movement distances changed with forest habitat. The dry season of 2005 was more intense than the average year (Comisión Nacional del Agua 2010) and we observed that groups of WLPs were highly dependent on a few ponds that retained water. Therefore, we explored whether WLP group movements and foraging activities occurring around water sources resembled the central-place foraging model (Orians and Pearson 1979).

## MATERIALS AND METHODS

**Study area.**—This study was conducted in the southern area of Calakmul Biosphere Reserve in the Mexican state of Campeche (18°07'21"N, 89°48'56"W; Fig. 1). Calakmul Biosphere Reserve was decreed a protected area in 1989 and is the largest protected tropical forest in Mexico (7,238 km<sup>2</sup>). The area is effectively protected against hunting and other human activities by 2 checkpoints along the only existing

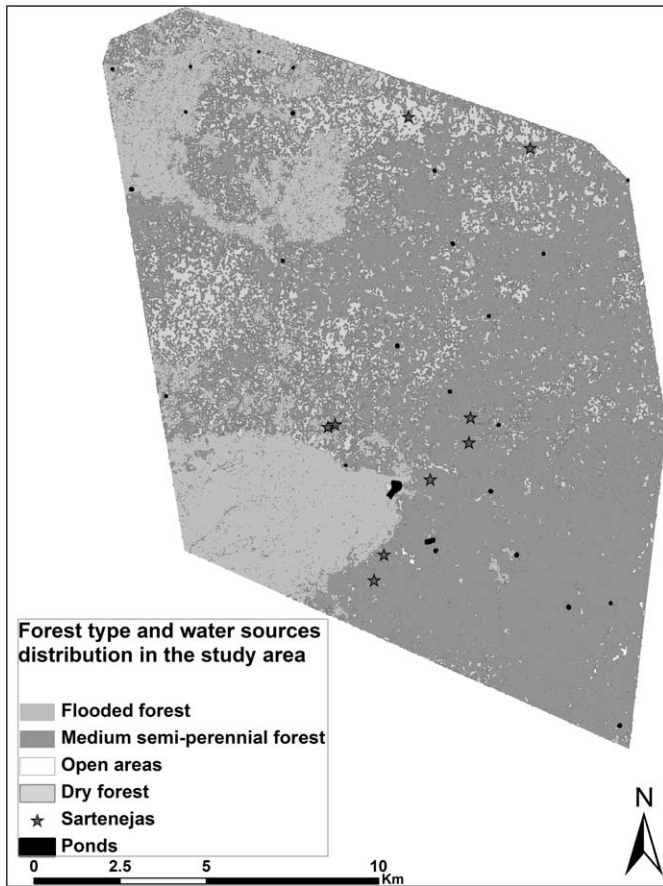


FIG. 2.—Forest types and pond locations within the 100% minimum convex polygon (242.3 km<sup>2</sup>) that encompasses all radio-tracking locations of 4 different white-lipped peccary (*Tayassu pecari*) groups within Calakmul Biosphere Reserve, Campeche, Mexico.

narrow road. Human activity is only present at an archeological site and on the road leading to it, and is limited to tourism and archeological research (Folan et al. 1999).

Based on a radiotelemetry study, we defined the study area as the 236.7-km<sup>2</sup> 100% minimum convex polygon that encompasses all the locations where individuals from the 4 WLP groups were located (Fig. 2). This minimum convex polygon was defined in ArcView 3.3 (ESRI, Redlands, California) using the animal movement analyst extension (Hooge and Eichenlaub 1997). The mean annual temperature is 24.6°C with a range of 8–40°C (García 1988). Rainfall occurs primarily from mid-May to September, with an annual average of 1,076 mm. The dry season normally occurs from January to mid-May, with an average rainfall of 50 mm.

According to Pennington and Sarukhán (1998), 4 different forest communities dominate the study site: Medium Sub-Perennial Forest (Medium forest), the most humid habitat, where canopy trees are between 15 and 25 m tall; Low-Flooded Forest (Flooded forest), which is seasonally inundated after 2–3 months of heavy rains, and where canopy trees are between 5 and 15 m tall; and the Medium and Low Semi-Deciduous Forests, which both can be classified as dry forest

(Dry forest), where trees range from 10 to 25 m high, but species composition and abundance differs from the Medium Sub-Perennial Forest (Pennington and Sarukhán 1998). These 4 types of forest are highly intermingled, although a humidity gradient that increases from north (driest) to south (wettest) impacts the proportion of the different forest types.

Because there is no permanent river system, water is only available after precipitation. Most of the rainfall percolates through the limestone, but some drains superficially and collects in ponds. These ponds, which are natural depressions, can range in size from 10 m<sup>2</sup> to 3–4 ha (although the majority of ponds are <0.5 ha in size); such depressions are the only water source for WLPs and other terrestrial wildlife throughout the dry season.

*Data collection.*—We captured 17 WLPs from 4 groups (named Red, Blue, Green, and Yellow, which have 31, 25, 20, and 25 individuals, respectively) during the 2005 dry season and fitted them with radiotransmitters (Reyna-Hurtado et al. 2009). We followed the guidelines of the American Society of Mammalogists (Sikes et al. 2011) and University of Florida Institutional Animal Care and Use Committee permit D594. These 4 groups were living sympatrically around Calakmul pond, one of the largest ponds in the study area at 1 ha. Given the cohesiveness of WLP groups (Fragoso 1998; Reyna-Hurtado et al. 2009), we found it necessary to only radiocollared 2 or 3 individuals per group. During the 18-month study we monitored the WLP groups (with encounters with 1 or more groups taking place in 203 of those days); during this period the radiocollared animals always remained in their respective groups, despite times when the 4 groups were within 10 m of each other. We did not observe mixing of individuals among groups and there were only 2 occasions when we sighted solitary individuals that could not be unambiguously assigned to a group. Consequently, we used the radiomarked animals as an indicator of the movements and habitat preferences of each group.

Groups were monitored using the homing method (White and Garrot 1990), which consisted of securing bearings of the collared animals from the only existing high points, 2 Mayan temples of Calakmul Archeological City, and then walking toward the groups. Once groups were contacted, initial and subsequent locations were recorded when possible, sometimes as frequently as every 15 min; we used a global positioning system device (Garmin eTrex; Garmin Ltd., Olathe, Kansas) that is accurate to within 5–20 m while contact lasted typically 2–3 h (range 1–6 h). The 4 groups were monitored for different periods during the 18 months, ranging from 7 months for the Yellow group to 17 months for the Blue group, and 13 and 12 months for the Red and Green groups, respectively. WLP groups have some of the largest home ranges for ungulate species: 109–200 km<sup>2</sup> for groups living in Maraca Island, Brazil (Fragoso 1998, 2004), and 77–121 km<sup>2</sup> for the groups in this study (Reyna-Hurtado et al. 2009). Consequently, it was very difficult to locate and follow groups on a regular basis and continuous movement data were not always available for all groups and all months.

*Distribution of resources.*—A previous study at the same study site has shown that WLPs selectively use 3 main landscape features: ponds, Medium forest, and Flooded forest, while avoiding the 2 types of Dry forest (Reyna-Hurtado et al. 2009). The selection of Medium forest appeared to be related to ramon fruit (*Brosimum alicastrum*), which has been found in up to 90% of 9 analyzed WLP stomach contents (Pérez-Cortéz and Reyna-Hurtado 2008). *B. alicastrum* accounted for almost one-half (48.15%) of the fruit available for WLPs produced mainly in the Medium forest (83%—Reyna-Hurtado et al. 2009). Reyna-Hurtado et al (2009) indicated that WLPs visited the Flooded forest primarily in the wet season to forage on earthworms and other invertebrates present at that time, and to wallow in muddy areas.

To determine the spatial distribution of these 3 key habitats (ponds, Medium forests, and Flooded forests), we used a detailed map of the reserve compiled using aerial photographs (García-Gil et al. 2002). To measure the availability and spatial distribution of water sources in the landscape, we estimated the density of ponds within the study area and the mean distances to the nearest pond by using ArcView 3.3. Additionally, we closely monitored the water availability of 10 ponds that we visited regularly during 2005 and 2006.

We also found that WLPs visited some stony outcrops that act as temporary water storages sites. These stony outcrops, which are locally called “sartenejas” are typically natural depressions on a stone less than 1 m<sup>2</sup> in size and not deeper than 50 cm. These sartenejas are important because they can be filled by a small amount of precipitation, whereas ponds need large amounts of rain to start filling. We documented and georeferenced sartenejas used by WLPs as determined by radiotracking and estimated the mean distances to the nearest sarteneja (Fig. 2).

We used ERDAS (Intergraph, Norcross, Georgia) and ArcView 3.3 to perform a supervised classification of a satellite image to portray the spatial distribution of the forest types (Fig. 2) and used this distribution as a proxy for food distribution. Habitat classification was ground-truthed in the field. We measured the contagion index per forest type by using FRAGSTATS 3.3 (McGarigal and Marks 1994). The contagion index measures the degree of aggregation and distribution of forest patches on the landscape (Cardille and Turner 2002; McGarigal and Marks 1994). Contagion indexes have values from 0 to 1; lower values indicate that patches are dispersed uniformly over the landscape, whereas higher values result from patches with a high degree of aggregation (clumped).

*Ranging patterns of groups.*—Global positioning system position data were transformed into hourly movement rates for statistical analyses. We selected all the consecutive locations from the groups from which we knew the position before and after 1 h and estimated the straight-line distances between these locations using ArcView 3.3. These data were gathered between 0800 and 1700 h because the WLP is a diurnal species (Sowls 1997) and also this period encompasses when we were able to follow the groups, given the remote locations where they usually foraged. Because the global positioning

**TABLE 1.**—Probability density functions, parameters, and maximum-likelihood estimators for all tested movement distributions. Note: the half-normal distribution is the distribution of absolute values of a normal distribution with mean of zero and standard deviation  $\sigma$ . Half-normal estimators are from Pewsey (2004).

Distribution	Density function	Parameter	Maximum-likelihood estimate
Exponential	$\lambda \exp(-\lambda x)$	$\lambda$	$1/\bar{X}(x)$
Half-normal	$\frac{2}{\sigma\sqrt{2\pi}} \exp\left(-\frac{x^2}{2\sigma^2}\right)$ , ( $x > 0$ )	$\sigma$	$\left(\frac{1}{n-1} \sum_{i=1}^n x_i^2\right)^{\frac{1}{2}}$
Lognormal	$\frac{2}{x\sigma\sqrt{2\pi}} \exp\left(-\frac{(\ln x - \mu)^2}{2\sigma^2}\right)$	$\mu$ $\sigma$	$\bar{X}(\ln(x))$ $SD(\ln(x))$
Lévy walk	$\frac{\alpha - 1}{x_{\min}} \left(\frac{x}{x_{\min}}\right)^{-\alpha}$	$\alpha$ $x_{\min}$	$1 + n \left(\sum_{i=1}^n \ln \frac{x_i}{x_{\min}}\right)^{-1}$ See Clauset et al. (2009)

system units were only accurate up to 20 m, and the WLP groups were generally spread out over more than 20 m, movements of the collared individual shorter than this were coded as zeros. The results in subsequent analyses were not sensitive to what value we assigned these short movements.

*Statistical analyses of movement data.*—We fitted 2 sets of distributions to all the movement distance data ( $n = 173$ ): short-tailed (Gaussian and exponential) and long-tailed (Lévy walk, Lévy walk with an exponential cutoff, and lognormal), where we define a long-tailed distribution as any distribution for which the probability density drops off at a rate slower than exponentially with distance (Asmussen 2000). All distance values had 1 m added to them, because zero was not a valid value for several of the distributions tested. The parameters for all distributions were estimated using maximum-likelihood estimators (Table 1), except  $x_{\min}$  for the Lévy walk, for which we used the goodness-of-fit–based method recommended in Clauset et al. (2009). We also fitted the same set of distributions (zero-inflated) to only the movement data recorded as greater than zero ( $n = 143$ ), treating the zero and positive step lengths as potentially separate classes of movements.

We tested the absolute goodness-of-fit of each fitted distribution to the data using a simulation-based Kolmogorov–Smirnov test (Clauset et al. 2009). For each distribution, we found the maximum difference between model and empirical cumulative distribution functions (the Kolmogorov–Smirnov statistic). We then generated the theoretical distribution of the Kolmogorov–Smirnov statistic for that model by randomly drawing 2,000 new samples from the model distribution, each with as many points as the empirical data, estimated model parameters for the synthetic data, and then found the Kolmogorov–Smirnov statistic for each sample. The *P*-value for the observed statistic was calculated as the fraction of simulated Kolmogorov–Smirnov statistics as large as, or larger than the observed value.

We compared the relative goodness-of-fits between the fitted models using simulation-based unnested likelihood tests for within-group (uninflated or zero-inflated) comparisons, and nested tests for between-group comparisons (Clauset et al.

2009). When testing the goodness-of-fit of the Lévy walk against the data and other distributions, we only used data greater than the estimated  $x_{\min}$  ( $n = 53$ ), because the Lévy walk is only valid for values above  $x_{\min}$ .

We used a 2-stage modeling procedure to determine if groups were changing their foraging behavior due to season or habitat; 1st fitting a logistic regression to zero versus positive step lengths against season and habitat the move started in ( $n = 161$ , due to some cases where the starting habitat was not recorded) and linear regression of the log-transformed positive values against the same variables ( $n = 132$ ). Season was removed as a predictor from both analyses, due to strong collinearity between starting habitat and season. All these tests were performed in R 2.12 (R Development Core Team 2010), except the Lévy-walk fitting code, which was performed in Matlab 7.9.0 (MathWorks, Natick, Massachusetts) with code from Clauzet et al. (2009).

*Central-place foraging behavior.*—We tested if the groups visited the ponds more often in the dry season than in the wet season, and how far from the ponds they foraged during the dry season. For each group, we constructed a  $2 \times 2$  contingency table of the total days that we contacted the group in any location during the dry and wet season and the number of times the group visited Calakmul pond and other ponds during these seasons (we consider the group to be at a pond when the group was located within 20 m of it). We then performed a chi-square analysis to test for the higher use of ponds during one season over the other. To test if the foraging activities in the dry season occurred around Calakmul pond, we performed a repeated-measures analysis of variance (ANOVA) on the mean distances between Calakmul pond and the locations where each of the 4 groups foraged for the dry season ( $n = 181$  locations) and the wet season ( $n = 316$  locations).

## RESULTS

*Distribution of resources.*—We found a total of 23 ponds with a density of 1 pond/10.5 km<sup>2</sup> within the combined 100% minimum convex polygon home range (242.3 km<sup>2</sup>) of the 4 WLP groups; the ponds ranged from a few meters to 1 ha in size (accounting for less than 1% of the study area). The mean nearest-neighbor distance between ponds was 2,181 m ( $\pm 234$  m SE; range 374–5,210 m). We found that not all the ponds stored water year-round, and not in every year. For instance, Calakmul pond stored water during the 2005 dry season, but dried completely during the 2006 dry season. This was the 1st time this pond dried in at least 18 years (L. Sosa, Calakmul Archeological City Guards, pers. comm.). We detected the same seemingly unpredictable pattern in at least 10 other ponds that we visited regularly, some of which dried up, whereas others stored water in 2005; however, all ponds were dry in the 2006 dry season.

We documented and georeferenced 8 sartenejas that were regularly visited by WLP groups, especially during the 2006 dry season. We detected these sartenejas by following the WLP groups; thus, it is possible that others exist and were visited but remained undetected. The 8 known sartenejas were

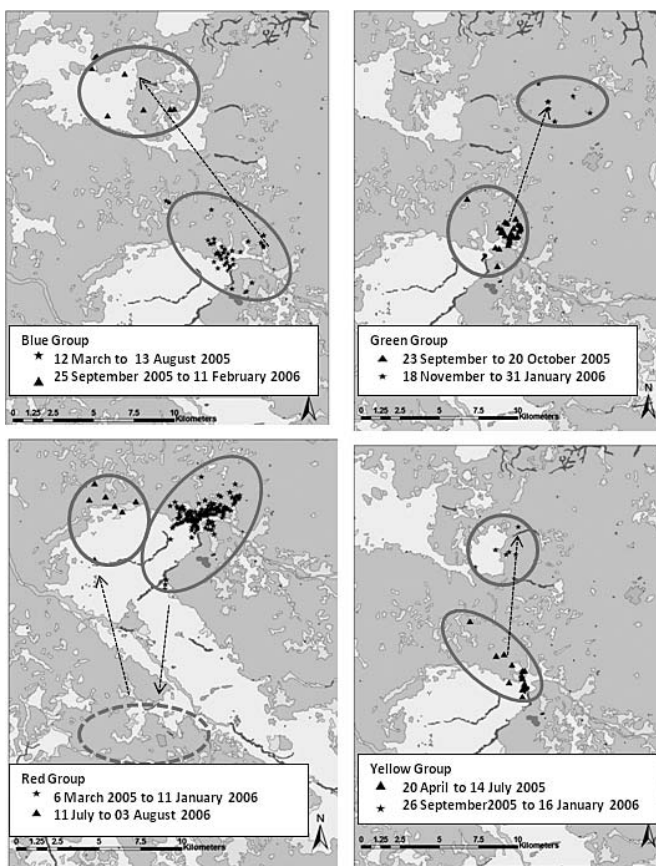


FIG. 3.—Spatiotemporal scale of movements in 4 different groups of white-lipped peccaries (*Tayassu pecari*) in Calakmul Biosphere Reserve. Dotted circle for Red group indicates a possible area where the group traveled for 5 months when radiotelemetry contact was lost given their last known heading and their heading when they returned. The dotted line indicates the last and 1st localization in each area.

dispersed over the landscape with a mean distance to nearest sarteneja of 1,462 m  $\pm$  456 SE (range 400–3,811 m). These reservoirs of water were typically short-lived (few weeks into the dry season), but some of them stored water even after the large Calakmul pond dried up.

Medium and Flooded forests, and consequently the food resources that they provided, were spatially clumped across the landscape (contagion index values of 0.70 and 0.74, respectively). Medium forest represented 47%, and Flooded forest only 23%, of the minimum convex polygon; the rest was Dry forest and some small open areas not larger than 1 ha, mainly around the archeological site.

*Ranging patterns of groups.*—The 4 groups of WLPs alternated between 2 movement patterns at different spatial and temporal scales. At the smaller scale, WLP groups moved over distances shorter than 3 km, characterized by WLPs searching intensively in one area by performing several movements of similar length every day; this movement pattern usually lasted for several weeks. The larger scale pattern occurred occasionally when WLPs performed long-distance movements (9 to >16 km) usually in a single direction that took them out of the previously searched area (Fig. 3). These long-distance movements occurred over a relatively short



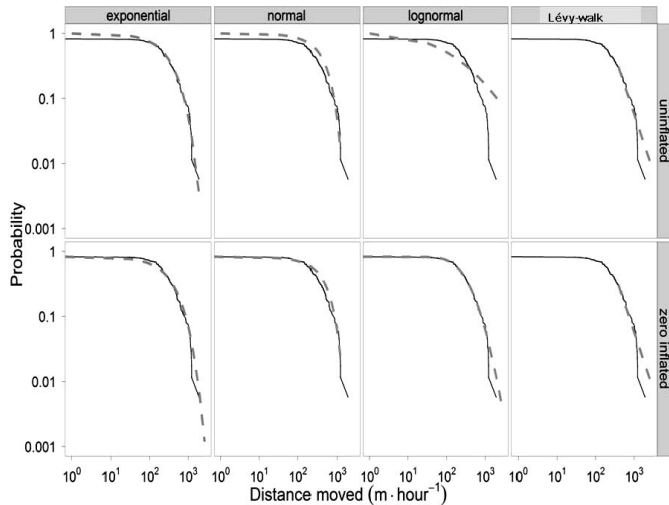


FIG. 5.—The empirical complementary cumulative distribution function of the hourly movement data, plotted with the predicted complementary cumulative distribution functions for all distributions fit to the hourly movement data. The complementary cumulative distribution function at  $x$  gives the probability of finding a given random draw from that distribution being equal to or higher than  $x$ . The plots have been log-log transformed to increase resolution of the distribution tails.

not indicate significant differences in fit between models (Table 2; Fig. 5). However, the lognormal distribution was the only one to pass the simulated Kolmogorov–Smirnov absolute goodness-of-fit test ( $P = 0.82$ ).

*Factors affecting movement distance.*—Both the probability of moving at all and the mean log-distance individuals moved varied by the habitat in which the groups started at in a given hour. Groups moved on average 4.5 times more often (95%  $CI = 0.95$ –22) in Dry or Medium forest than in Flooded forest and ponds, and moved 1.6 times longer distances (95%  $CI = 1.1$ –2.5) in Dry forest than in wet habitats (Flooded forest and ponds) and Medium forests (Table 4; Fig. 6).

*Behaving as central-place foragers.*—During 2005 the WLP groups foraged within a 6-km radius of Calakmul pond (mostly toward the northwest from this pond) and returned to it several times during the dry season (Fig. 7). The Red group returned 13 times, the Blue group 16, the Green group 14, and the Yellow group 11 times during the dry season. A chi-square analysis showed that they visited ponds disproportionately more during the dry season than the wet season (Red group:  $\chi^2_1 = 12.82$ ,  $P = 0.001$ ,  $n = 63$ ; Blue group:  $\chi^2_1 = 13.81$ ,  $P = 0.001$ ,  $n = 65$ ; Green group:  $\chi^2_1 = 18.19$ ,  $P = 0.001$ ,  $n = 59$ ; Yellow group:  $\chi^2_1 = 11.25$ ,  $P = 0.001$ ,  $n = 28$ ). Calakmul was by far the most visited pond (>90%) by all groups. Also, we found that during 2005 the mean distances between Calakmul pond and the sites where the WLP groups foraged were smaller for the dry season ( $\bar{X} = 595 \text{ m} \pm 59 \text{ SE}$ ,  $n = 181$ ) than for the wet season ( $\bar{X} = 2,560 \pm 170 \text{ m}$ ,  $n = 316$ ). Although the difference was only marginally significant when using a repeated-measure ANOVA ( $F_1 = 7.52$ ,  $P = 0.07$ ), it showed that during the dry season WLPs foraged mostly around Calakmul pond and that travel was affected by the distances to this water source.

TABLE 3.—Coefficient estimates and 95% confidence intervals (95%  $CI$ s) for distributions fitted to movement distances.

Model	Parameter	Estimate	95% $CI$
Exponential	$1/\lambda$	340	290–330
Half-normal	$\eta$	500	460–570
Lognormal	$\mu$	4.7	4.3–5
	$\sigma$	5.2	4.3–6.5
Zero-inflated exponential	$1/\lambda$	410	350–480
Zero-inflated half-normal	$\eta$	550	500–630
Zero-inflated lognormal	$\mu$	5.7	5.5–5.8
	$\sigma^2$	0.76	0.61–0.97
Lévy walk	$x_{\min}$	390	180–590
	$\alpha$	2.8	2–3.5
Zero	Weight	0.17	0.12–0.23

## DISCUSSION

We demonstrated that critical habitat and water resources for WLPs were found in low densities, dispersed, and temporally scarce in Calakmul Biosphere Reserve. Therefore, to access water during the dry season, WLPs must travel long distances or stay close to the few existing water bodies. Available forest habitat, hosting the majority of patches of selected food such as fruits (Medium forest: *B. alicastrum*, *Talisia olivaeformis*, and *Manilkara zapota*) or invertebrates such as earthworms (Flooded forest) were clumped and nonuniformly dispersed over the landscape and intermingled with other less-preferred forest patches, such as Dry forest. Food resources also were seasonally scarce (Reyna-Hurtado et al. 2009). In addition to these constraints, it has been demonstrated that WLPs live in some places in highly cohesive groups that feed, travel, and rest together throughout the year (Fragoso 1998; Reyna-Hurtado et al. 2009). So, how do WLP groups survive in a place such as Calakmul Biosphere Reserve where resources are temporarily scarce and spatially dispersed, while keeping group cohesiveness?

We found that movement patterns of WLPs were consistent with a foraging strategy based around patchy and unpredictable food resources. WLP groups ranged over large areas. Researchers have found that size of home range varies between 77 and 121  $\text{km}^2$  for the Blue and Green groups, respectively, using the 100% minimum convex polygon method (Reyna-Hurtado et al. 2009). This estimate includes occasional straight-line movements of >16 km in 2–3 days (Fig. 3). Performing these long-distance movements, WLPs can reach patches of preferred forest or water bodies on a landscape scale of tens of kilometers. At the same time, it has been hypothesized that by living in cohesive groups, WLPs make an efficient use of resources by visiting relatively “new,” distant patches that have less probability of visitation by other individuals (Kiltie and Terborgh 1983).

Our findings regarding the statistical distribution of movement rates imply that these long-distance movements may be due primarily to rare long steps, with most movements taking place over short distances. However, although long-tailed, there is no evidence that WLP movements are scale-free (following a Lévy-walk distribution); although lognormal

**TABLE 4.**—Coefficients and standard errors ( $\pm 1 SE$ ) for regression of probability of movement and  $\log^{10}$ -distance moved in a given hour. Wet forest included Flooded forest and ponds.

Parameter	Logistic regression of positive moves			Log-linear regression		
	Estimate	$\pm SE$	<i>P</i>	Estimate	$\pm SE$	<i>P</i>
Intercept	2.53	0.73	<0.001	6.00	0.17	<0.001
Beginning move in Medium forest <sup>a</sup>	−0.60	0.83	0.47	−0.48	0.21	0.02
Beginning move in wet forest <sup>b</sup>	−1.52	0.78	0.05	−0.47	0.21	0.03

<sup>a</sup> Medium Sub-Perennial Forest, the most humid habitat, where canopy trees are between 15 and 25 m tall.

<sup>b</sup> Wet forest included ponds and Low-Flooded Forest (Flooded) that is seasonally inundated after 2–3 months of heavy rains, and where canopy trees are between 5 and 15 m tall.

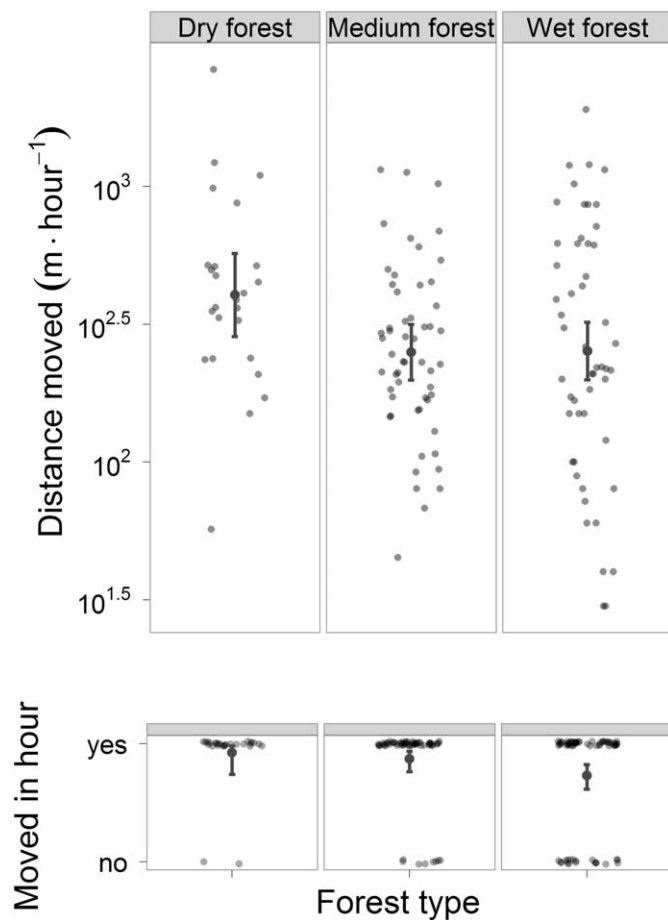
distributions are heavy-tailed, they still have finite variance, which means over long timescales WLP movements should appear to represent Brownian (random) motion. This lognormal movement pattern (with resource-dependent movement scales) has been seen in at least 1 other species foraging in patchy habitats, the bog fritillary butterfly (Schtickzelle et al. 2007). Furthermore, we show that the scale of movements in WLPs decreases and the frequency of stops increases in wet habitats (Flooded forest and pond) and Medium forest; this pattern was noted in a prior study of the habitat preferences of WLP groups in these areas (Reyna-Hurtado et al. 2009).

Groups of WLPs at Calakmul Biosphere Reserve move across the landscape at different spatial scales, as was suggested by Fragoso (1999). Long-distance movements also are common in Corcovado National Park (Costa Rica), where some WLP groups leave the park during parts of the year, apparently when fruit is scarce (Altrichter and Almeida 2002). The fact that WLP groups follow lognormal distribution movement rates does not tell which behavioral mechanisms are driving the movement. However, long-distance movements are expected for species that live in large groups and feed on patchy distributed food, as predicted by the ecological constraint model (Chapman and Chapman 2000).

Determining how individuals coordinate actions to generate the aggregate distribution of moves is an area of potentially fruitful future research. We also suggest that more theoretical work needs to be done to determine not only when long-tailed movements lead to superior foraging outcomes over Brownian motion but also what types of long-tailed distributions maximize foraging success, and what this implies about the scale of resource patchiness and behavioral cost. Further, our results reinforce Clauset et al. (2009) and Edwards et al. (2007) and the argument that it is essential to not only test relative goodness-of-fit of distributions, but also the absolute fit of each model when testing long-tailed distributions.

We demonstrated that at least for the 2005 dry season the 4 WLP groups concentrated their foraging activities around the northwestern areas of Calakmul pond, in a pattern resembling the central-place foraging model. Observations allowed us to confirm that water availability was the driving pattern, because when it started to rain the groups performed occasional long trips (~6 km) in search of resources, but always returned to this pond when the rain stopped, a pattern that was repeated several times until the rainfall was sufficient to fill the Flooded forest and other ponds (Fig. 7). When they were constrained around the ponds WLPs were seen eating food thought to be of low quality, such as herbs at the pond edge, indicating that water shortage may play a stronger role in driving behavior than food searching.

The combination of long-tailed movement and central-place foraging as searching and foraging strategies appears to be efficient for WLPs living in Calakmul Biosphere Reserve. The latter allows them to secure access to spatially and temporarily limited resources (such as water), whereas using the former they can also occasionally explore farther areas and monitor resources availability. The use of ponds and sartenejas also suggests multiple, central-place foraging behavior around



**FIG. 6.**—Hourly movement of white-lipped peccary groups by starting forest type. Bottom) frequency of movement; top) distance moved. Points are the original data, with lines indicating model estimates from the (bottom) logistic regression and (top) log-linear regressions, with  $\pm 2 SE$ .



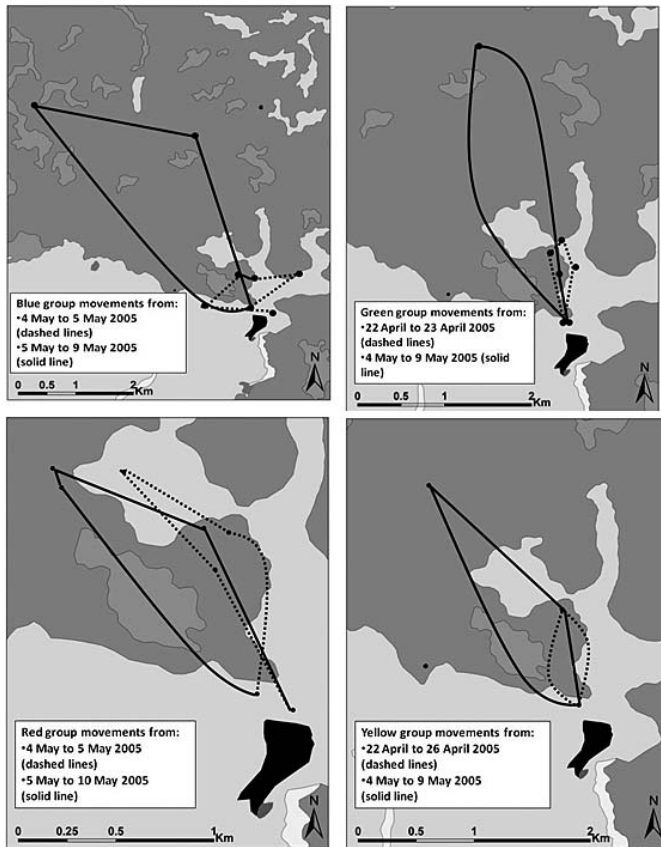


FIG. 7.—Typical foraging movements from Calakmul pond of the 4 groups in the dry season of 2005 in Calakmul Biosphere Reserve, Campeche, Mexico.

these water sources. Multiple, central-place foraging was demonstrated for spider monkeys where they selected different sleeping sites around which they temporarily behaved like central-place foragers, moving after some time to a new site (Chapman et al. 1989). This multiple, central-place model remains to be tested for WLPs.

The searching strategies demonstrated by WLPs in Calakmul Biosphere Reserve may be a complementary strategy to the fact that WLPs live in smaller groups and range over larger areas (Reyna-Hurtado et al. 2009) in comparison with much larger groups of the same species inhabiting other less-seasonal forests and less water-limited areas (Carrillo et al. 2002; Fragoso 1998; Keuroghlian et al. 2004; Kiltie and Terborgh 1983). A better understanding of the possible role of memory and spatial knowledge related to detailed group movements would be very interesting ecological research areas on this species because such research would shed light on the decision rules underlying those movements.

#### ACKNOWLEDGMENTS

We thank E. Rojas-Flores, N. Arias, S. Pérez-Cortéz, G. Arias, E. Gutiérrez, H. Ramírez, and S. Velázquez for field support. The authorities of Calakmul Biosphere Reserve provided permits and logistic support to work in Calakmul Biosphere Reserve, and the Dirección General de Vida Silvestre provided research permits. The

Instituto Nacional de Antropología e Historia gave permission to stay at Calakmul Archeological City. Special thanks to G. W. Tanner, L. Branch, M. Chrisman, E. Naranjo, M. Irwin, and A. Jacob, who improved the manuscript. M. Weber kindly provided radiotelemetry equipment. Funds to RR-H were provided by the Mexican Council for Science and Technology (grant 150332), the Tropical Conservation and Development Fund (University of Florida), and the Department of Wildlife Ecology and Conservation (University of Florida). The Wildlife Conservation Society provided funds for fieldwork and equipment through a Research Fellowship Program. Light-Hawk provided a flight. IDEAWILD provided field equipment. The Department of Anthropology of McGill University and Natural Sciences and Engineering Research Council and Canada Research Chair (CRC) grants to CAC provided time and space for writing to RR-H.

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Submitted 15 November 2010. Accepted 11 July 2011.

Associate Editor was Harald Beck.