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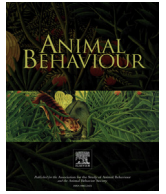
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Disentangling the importance of social and ecological information in goal-directed movements in a wild primate

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Memories linked to specific locations provide information for animals to plan future actions and anticipate the occurrence of events. Here, we examined goal-directed travel towards locations where biologically meaningful events had previously taken place to elucidate the relative importance of past social and ecological information for route planning. We inferred goal-directed travelling by detecting long sections of straight-line travel, followed by significant directional changes along travel trajectories of five neighbouring groups of black howler monkeys, *Alouatta pigra*, at Palenque National Park, Mexico. Post hoc, we determined at the approached locations: (1) the behaviour of the group; (2) the occurrence of previous intergroup interactions; and (3) the ecological properties of the feeding tree (i.e. importance in diet, level of phenological synchrony). The likelihood of goal-directed travel towards a location to engage in loud calling increased after having experienced an encounter with a neighbouring group at that same location in the past. Additionally, the likelihood of goal-directed travel towards a location to forage on fruits increased when the approached tree was considered important in the diet with highly synchronous phenological cycles. Our results indicate that route planning in wild animals involves an integration of both social and ecological variables.

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'It's a poor sort of memory that only works backwards,' says the White Queen to Alice' (Carroll, 1872, chapter 5). Memories provide information for animals to plan future actions and anticipate the occurrence of events (Gardner & Moser, 2017). By interacting with the environment, animals construct mental representations of the space wherein they live, such as cognitive maps (Tolman, 1948; Warren, 2019). In these maps, information related to personal, unique experiences is coded at specific locations (Clayton, Bussey, & Dickinson, 2003; Templer & Hampton, 2013). The contextual information associated with these experiences enables a wide range of animals to plan future actions (western scrub jays, *Aphe-locoma coerulescens*, Clayton & Dickinson, 1998; brown rats, *Rattus norvegicus*, Crystal, 2016; common squirrel monkeys, *Saimiri sciureus*, Naqshbandi & Roberts, 2006; chimpanzees, *Pan*

troglodytes, Martin-Ordas, Haun, Colmenares, & Call, 2010). Yet, there is a lack of understanding of which kind of contextual information is used among species to support planning skills in wild populations (Grodzinski & Clayton, 2010; Janmaat, 2019).

Social interactions among conspecifics have been shown to provide information that influence animals' movement decisions at the moment of travelling (e.g. avoidance of encounters with groups of conspecifics in baboons, *Papio ursinus*, Noser & Byrne, 2007; migratory departure time in sockeye salmon, *Oncorhynchus nerka*, Berdahl, Westley, & Quinn, 2017; migratory route's trajectory in caribou, *Rangifer tarandus*, Torney et al., 2018). Similarly, social events that took place in the past at given locations have been proposed to influence animals' movement decisions (Templer & Hampton, 2013). Remembering the occurrence of intergroup encounters, fission events among subgroups or loud vocal communication at given locations have been suggested to benefit wild populations' ability to adjust their trajectories by anticipating the

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potential recurrence of such events at that same location (Asensio, Brockelman, Malaivijitnond, & Reichard, 2011; Di Fiore & Suarez, 2007; Grodzinski & Clayton, 2010). However, to the best of our knowledge, there is no empirical evidence of movement planning skills associated with past social events in wild populations (Janmaat, 2019).

In addition to the social complexity, the complexity of the temporal and spatial patterns of food items is also likely to influence an animal's memory processing (Davies & Houston, 1981; Morand-Ferron, Hermer, Jones, & Thompson, 2019; Riotte-Lambert & Matthiopoulos, 2020). Free-living hummingbirds, the green-backed firecrown, *Sephanoides sephaniodes*, memorized the location and renewal rate of nectar in specific flowers and matched revisiting events to these flowers accordingly (González-Gómez, Bozinovic, & Vásquez, 2011; also rufous hummingbirds, *Selasphorus rufus*; Jelbert, Hurlly, Marshall, & Healy, 2014). Similarly, other species that rely on energetically valuable, yet ephemeral food items have been shown to plan revisits to foraging sites according to the renewal and expiration rates of these items in both the wild and captive settings (western scrub jays, Clayton & Dickinson, 1998; black-capped chickadees, *Poecile atricapillus*, Feeney, Roberts, & Sherry, 2009; savannah elephants, *Loxodonta africana*, Polansky, Kilian, & Wittmyer, 2015; black-horned capuchins, *Sapajus nigritus*, Janson, 2016). However, the high spatiotemporal complexity of fruits in rainforests can be especially challenging for animals' foraging success (Janmaat et al., 2016; Levey, 1988; van Schaik, Terborgh, & Wright, 1993). Tree species' phenological cycles vary in the degree of synchrony, from all individual trees producing fruit within the same temporal window annually to each individual producing fruits at irregular time intervals independently from one another (Adamescu et al., 2018; Rathcke & Lacey, 1985). While correctly predicting the presence of fruits at highly synchronous tree species requires memorizing phenological cycles at the species level, asynchronous species require memorization at the individual level (Janmaat, Chapman, Meijer, & Zuberbühler, 2012; Riotte-Lambert & Matthiopoulos, 2020). The amount of information that animal species integrate is dictated by their cognitive capacity (Tello-Ramos, Branch, Kozlovsky, Pitera, & Pravosudov, 2019; Tolman, 1948). Hence, a strategy that remembers both the phenological patterns of a small subset of feeding locations that show asynchronous patterns and a large number of feeding locations with synchronous cycles at the species level is likely to favour anticipating the availability of fruits while reducing the cognitive load of the animal (Delgado & Jacobs, 2017; Janmaat et al., 2012).

While animals probably value retaining information associated with social and ecological contexts, little is known about the relative importance of each kind of information across species (Burkart, Schubiger, & van Schaik, 2017; Spiegel & Crofoot, 2016). An examination of animals' movement trajectories to reach specific, revisited locations where different social and ecological events took place has the potential to shed light on the importance of these different events for the planning skills of individuals or groups (Berger-Tal & Bar-David, 2015; Bracis, Bildstein, & Mueller, 2018; Janson, 2019). Detecting directional changes in trajectories is a first step towards examining whether, and for how long, an individual has been heading in the direction of a target (Byrne, Noser, Bates, & Jupp, 2009; Potts et al., 2018). If a directional change preceded by a long straight line occurs at a location where biologically meaningful events took place, the observed individual or group could have been purposefully heading towards this location (Byrne et al., 2009; Noser & Byrne, 2014). For instance, Asensio et al. (2011) examined the relationship between directional changes in white-handed

gibbons, *Hylobates lar*, and biologically meaningful events that happened at such locations. While gibbons approached preferred feeding trees in a goal-directed manner when fruits were present, they did not engage in goal-directed travel towards locations where intergroup encounters or duets took place (Asensio et al., 2011). Thus, examining which biologically meaningful event had taken place at locations where directional changes happened in combination with the observed behaviour at the moment of changing direction may shed light on the importance of different types of information that aid in generating memories (Noser & Byrne, 2014).

The movement ecology of black howler monkeys, *Alouatta pigra*, hereafter black howlers, provides an ideal model to explore the influence of socioecological information in the process of movement decision making (Milton, 1981; Van Belle, Estrada, & Garber, 2013a). Black howlers interact vocally with neighbouring groups daily and regularly engage in intergroup encounters (Van Belle & Estrada, 2020; Van Belle, Estrada, & Garber, 2013b). These encounters are characterized by loud calling bouts (Van Belle et al., 2013b) and are associated with important costs such as potentially losing access to key food resources (Van Belle, Garber, Estrada, & Di Fiore, 2014). We predicted that black howlers would remember locations where previous intergroup encounters had taken place, which would allow them to plan future travel bouts towards these locations. In addition to intergroup encounters, loud calling also occurs in the absence of visual contact with neighbouring groups. Van Belle and Estrada (2020) suggested that spontaneous loud calling events inform conspecifics about the spatial position of the caller. While the low frequency of black howlers' calls favours the propagation of sound through rainforests (Naguib & Wiley, 2001; da Cunha, de Oliveira, Holzmann, & Kitchen, 2015), specific locations in their home ranges might be more conducive to long-distance calls than others (e.g. reduced physical barriers or foliage; Ramsier, Cunningham, Patiño, Glander, & Dominy, 2019). Therefore, we predicted that black howlers would purposefully return to locations where they had called before, which may help improve communication with neighbouring groups.

Black howlers' movement patterns have been shown to be mediated by the availability of fruits in rainforests (Plante, Colchero, & Calmé, 2014; Van Belle & Estrada, 2020), which comprise a large percentage of their diets (ca. 41%, Van Belle & Estrada, 2020). Anticipating the emergence of fruits at feeding trees is likely to increase black howlers' access to food resources and facilitate the nutrient balance of their diets (Hopkins, 2016; Righini, Garber, & Rothman, 2017). Owing to the high spatiotemporal complexity of fruits in rainforests, we predicted that black howlers would memorize a subset of feeding trees' locations (i.e. spatial elements) with synchronous phenological cycles (i.e. temporal elements), to minimize the complexity of the cognitive process associated with movement decision making and engage in efficient foraging patterns.

Here, we explored goal-directed behaviour in black howlers in relation to social and ecological events. We predicted that black howlers would be more likely to approach locations in a goal-directed manner at which intergroup encounters and loud calling bouts had taken place previously. Second, we predicted that black howlers would anticipate the availability of fruits and young leaves, and plan foraging movements accordingly. More specifically, we expected that the importance of individual feeding trees within their diet and their level of phenological synchrony would influence black howlers' goal-directed movement. By combining these data, we will shed light on the relative value that a wild primate

attaches to different social and ecological information to make efficient movement decisions.

METHODS

Study Site and Groups

We conducted this study at Palenque National Park (17°27'52"–17°30'10"N, 92°01'48"–92°01'48"W), southeastern Mexico, which covers a total of 1171 ha (Figueroa & Sánchez-Cordero, 2008). The vegetation within the park is predominantly primary tall, evergreen tropical rainforest (Díaz-Gallegos, 1996) and its terrain is rugged and varied (de Guinea, Estrada, Nekaris, & Van Belle, 2019). We selected five neighbouring groups of black howlers comprising 4–11 individuals with home ranges of 7.1–15.3 ha (de Guinea et al., 2019; Van Belle & Estrada, 2020).

Data Collection

We collected behavioural data from September 2016 through August 2017, 4 days a week for an average of 10.4 h per day per group. When two or more group members moved into a neighbouring tree, we started collecting GPS locations every 20 m behind the estimated centre of the group. Since black howlers travel mostly in a line formation in which individuals arrive sequentially to their travelling goal, we estimated the centre of the group while travelling as the mid location in between the front and last individual in line (Van Belle et al., 2013a). We collected GPS locations until at least two members of the group engaged in an activity other than travelling for more than 10 min (see Van Belle et al., 2013a for details).

We recorded the start and end times of all loud calling bouts of the focal group together with its geographical locations. Following Van Belle et al. (2013b), we determined whether loud calling took place in the context of an intergroup encounter (i.e. whenever a neighbouring group was within visual contact of the focal group during the loud calling bout). In addition, we recorded a feeding bout whenever one or more individuals fed on a plant for a minimum of 5 min accumulated among feeding individuals. We marked all feeding trees with a diameter at breast height larger than 10 cm in which at least one feeding bout took place to keep track of future revisits at that specific location. In addition, for each feeding bout, we recorded the item fed on, the plant species and, at 3 min intervals, the number of individuals feeding.

We estimated the phenological pattern of fruits and young leaves across trees of the same species within the study area by establishing a phenological trail (ca. 10 km) that crossed the entire area used by the five study groups between May 2016 and October 2019. We monitored all selected trees ($N = 968$ trees; $N = 60$ species) estimating the abundance of the main feeding items (i.e. mature fruits, young fruits, mature leaves, young leaves and flowers) every 3 weeks over a 4-day period. The estimations of abundance indicated the observed quantity of each item in the crown of the tree as follows: 0 = absent, 1 = 1–25%, 2 = 26–50%, 3 = 51–75% and 4 = 76–100% (Van Belle & Estrada, 2020).

Data Analyses

We identified directional changes preceding straight-line travelling (hereafter 'change points' or 'CPs') by applying the change point test (CPT; Byrne et al., 2009) to 396 daily paths. The CPT evaluates for each given waypoint along a path the collinearity (i.e. alignment) between a predetermined number (q) of vectors before and after the location of this waypoint. If the sum of the length of the vectors is significantly longer than the length of the vector

between the start and end locations of these vectors, a significant CP is detected and the CPT starts again with the next waypoint (Byrne et al., 2009; Noser & Byrne, 2014). Since the CPT is sensitive to the selected number of vectors (q), we followed Byrne et al. (2009) and applied the CPT on all daily paths using q values between 2 and 7. We selected $q = 5$ because it identified the greatest number of CPs and set the alpha level at $P < 0.05$ ($N = 1000$, tolerance = 0.00002; Noser & Byrne, 2014). Post hoc, we determined the behaviour (i.e. travelling, feeding, loud calling) of the respective study group at the exact location and time where each CP was detected (Asensio et al., 2011; Noser & Byrne, 2014).

We identified all CPs that occurred at locations where the group stopped for more than 10 min to engage in an activity other than travelling (i.e. loud calling, resting or foraging; Van Belle et al., 2013a) and defined them as locations that were approached in a goal-directed manner (Asensio et al., 2011; Ban et al., 2016; Byrne et al., 2009; Janmaat, Ban, & Boesch, 2013). If CPs occurred at locations where the group did not stop for more than 10 min (i.e. the group continued travelling), CPs seemingly represented locations where travel decisions were made and acted as an intermediate travel goal (Byrne et al., 2009). Both types of CPs were included in the statistical analyses to maximize the sample size and increase the power of the analyses (Ban et al., 2016). For CPs that occurred at goals, we identified whether the group engaged in loud calling or feeding. For CPs that occurred along travel bouts, we identified whether the behaviour at the end of its corresponding travel bout was loud calling or feeding.

We determined whether loud calling bouts occurred within intergroup overlap areas by estimating the home ranges of the study groups using kernel density estimations (KDE; R package *adehabitatHR* 0.4.15, Calenge, 2006). Thus, if black howlers engaged in loud calling bouts at locations intersected by the 95% KDE of at least two groups, we considered that these bouts occurred within intergroup overlap areas (Van Belle et al., 2013b). Similarly, we assessed whether a group had already experienced an intergroup encounter at the CP location associated with loud calling behaviour by mapping the locations where all previous intergroup encounters had occurred onto the CP locations. If at least one previous intergroup encounter fell within a 15 m radius from the location of these CPs, we determined that the group had previously experienced an intergroup encounter at that CP location (Appendix Fig. A1). We selected a 15 m radius taking into account: (1) the estimated crown radius for a tree in Palenque National Park, which was ca. 5 m (based on field estimations); therefore a 15 m radius would include not only the tree where black howlers were observed engaging in loud calls but also the first line of trees around the focal tree; (2) the estimated GPS error of our tracking devices (mean \pm SD = 6.6 \pm 2.3 m) to minimize the potential inaccuracy of our GPS device; (3) the average length of a travel bout, which was a mean \pm SD = 65.3 \pm 57.5 m; previous research has suggested using a quarter of the daily travel bout of wild animals as a realistic metric in spatial analysis (Bebko, 2018); and (4) the estimated distance between the two most distant members of the same group, which was ca. 15 m (Van Belle & Estrada, 2020). While the group is more dispersed during travelling bouts than during foraging or resting, when intergroup encounters happened all the members of the group tended to stay within the same tree either participating or observing the event (Van Belle et al., 2014).

If CPs were associated with feeding bouts, we determined the main item eaten by the group (i.e. fruits, young leaves or mature leaves). We combined mature and young fruits in the same category because black howlers rarely feed on young fruits (9–13% of the cumulative foraging time, Van Belle & Estrada, 2020). In addition, we estimated phenological synchrony of fruits and young leaves separately by calculating the Spearman rank correlation

coefficients between pairs of individual trees of the species included in the phenological trail. Finally, we calculated per species the mean of these pairwise correlation coefficients for young leaves and fruits separately (Bjørnstad, Ims, & Lambin, 1999; Fawcett, Marshall, & Higginson, 2015). Low mean correlation values indicate that individual trees of the same species do not synchronize the production of that specific item (i.e. young leaves, fruits) during the study period and high mean correlation values tree species that synchronize the production of either of these items. We standardized the synchrony values using a z transformation to facilitate the interpretation of the statistical models (Schielzeth, 2010). Additionally, following the definitions of Asensio et al. (2011) we classified feeding trees as important if the accumulated feeding time at that location made up at least 1% of the overall time spent feeding by that group during the study period.

We controlled for the potential influence of the structure of the route network and the landscape in detecting CPs by incorporating the following control variables in the models (see below). First, we calculated whether each observed feeding and loud calling bout fell within a 15 m diameter of an intersection ($N = 113$) between at least two habitual route segments to control for an overestimation of CPs at nodes (Presotto et al., 2018). Second, to control for the potential influence of the habitual route's curvature, we determined whether CPs located along habitual route segments occurred within 15 m of at least another CP. Black howlers often navigate using habitual route segments (de Guinea et al., 2019), which can impose significant directional changes as a by-product of the shape of the route rather than movement decisions. Third, we calculated the maximum rate of change in elevation for each quadrat relative to its adjacent quadrats to include a metric control for slope in our model (de Guinea et al., 2019; Presotto et al., 2018). Finally, we also controlled for the influence of sensory cues (i.e. olfaction, vision), which could influence the movement decisions of black howlers when travelling to feed at specific locations, by calculating the straight-line distance between the start and end points of each travelling bout. The larger the distance, the lower the potential influence of sensory cues on the decisions of black howlers when approaching specific locations in a goal-directed manner to feed.

Statistical Analyses

We conducted all statistical models in R 3.5.2 (R Core Team, 2018) using the functions lmer and glmer of the lme4 package 1.1–21 (Bates, Maechler, Bolker, & Walker, 2014). We used presence/absence of CPs before and at locations where black howlers travelled to engage in loud calling bouts (social model) and feeding bouts (ecological models) as the response variables. Because we were interested in the trajectory that led to the location where loud calling and feeding bouts happened, if two or more loud calling or feeding bouts occurred consecutively at the same site with no travelling in between, we considered only the first bout in the analyses. We fitted these GLMMs using a binomial error structure and a logit link function. In addition, we included group ID and tree ID as random effect variables (random intercept) to account for repeated measures, and random slopes for all predictor variables to keep type I error rates at a nominal level of 5% (Barr, Levy, Scheepers, & Tily, 2013; Schielzeth & Forstmeier, 2009).

In the social model, the predictor variables were loud calling context (i.e. occurrence or absence of intergroup encounters at the moment of engaging in loud calls), home range overlap area, occurrence of previous intergroup encounters at the CP's location and the accumulated previous number of visits to that location to

Table 1

Structure of the GLMMs designed to test the influence of different social and ecological variables in the goal-directed travelling behaviour of black howler monkeys

Social model	CP_{loud calling} ~ loud calling context * overlap area + previous intergroup encounters + accumulated visits to call location + loud calling duration ^a + intersection ^a + route's curvature ^a + slope ^a + (1 + loud calling context + overlap area + previous intergroup encounters + accumulated visits to call location + loud calling duration + intersection + route's curvature + slope + loud calling context : overlap area group ID ^b)
Ecological model 1	CP_{feeding} ~ item fed on + intersection + distance from previous stop + slope + distance from previous stop + (1 + item fed on + intersection + route's curvature + slope + distance from previous stop group ID ^b)
Ecological model 2	CP_{young leaves} ~ synchrony * tree's importance + intersection ^a + route's curvature ^a + slope ^a + distance from previous stop ^a + (1 + synchrony + tree's importance + intersection + route's curvature + slope + distance from previous stop + synchrony : tree's importance tree ID ^b)
Ecological model 3	CP_{fruits} ~ synchrony * tree's importance + intersection ^a + route's curvature ^a + slope ^a + distance from previous stop ^a + (1 + synchrony + tree's importance + intersection + route's curvature + slope + distance from previous stop + synchrony : tree's importance group ID ^b) + (1 + synchrony + tree's importance + intersection + route's curvature + slope + distance from previous stop + synchrony : tree's importance tree ID ^b)

The response variables of the models are presence/absence of change points (CPs) at and before locations where loud calling and feeding bouts took place (highlighted in bold).

^a Control predictors.

^b Random effect variables.

engage in loud calls. We included an interaction between overlap area and context because we predicted that howler monkeys would approach overlap areas in a goal-directed manner because they would anticipate the occurrence of intergroup encounters (see Table 1 for details in the structure of the models). Subsequently, we fitted three additional ecological models using presence/absence of CPs before and at feeding locations in which we included tree ID as a random effect variable. First, we tested whether the probability of approaching foraging trees in a goal-directed manner varied as a function of the item being eaten (i.e. mature leaves, young leaves, fruits) at the goal location (ecological model 1). Second, we tested whether the probability of approaching locations in a goal-directed manner to feed on young leaves changed as a function of the synchrony level of the tree species and the importance of that specific tree (ecological model 2). Third, we fitted a model with the same structure for fruit consumption (ecological model 3; Table 1).

For all social and ecological models, we included predictors to control for route network structure (i.e. proximity to route's intersections, route's curvature) and landscape structure (i.e. slope). For the social model, we also included a control predictor for internal motivation of the group to reach a goal (i.e. duration of the loud calling bout). For the ecological models, we controlled for the potential influence of sensory cues in the goal-directed behaviour of black howlers when approaching specific locations to feed (i.e. distance from starting location to CP).

We verified that the residuals of the models were normally and homogeneously distributed by visually inspecting qq-plots and plotting them against fitted values. We inspected the variance inflation factor of the models to rule out collinearity between variables using the function `vif` from the `car` package (all `vif` values in the models were below 1.3; Fox & Weisberg, 2011). Similarly, we assessed the stability of the GLMMs by comparing the estimates derived from a model based on all data with those obtained from models based on subsets that excluded levels of the random effects one at a time. No model assumptions were violated. In all cases, we compared the full model to a corresponding null model (with only random and control variables) using likelihood-ratio tests (anova function set to 'Chisq'). When an interaction term had no significant effect, we ran a reduced model including only the main effects. Finally, if the likelihood ratio test for full and null model comparison was significant, we inspected the significance of each predictor variable using likelihood ratio tests comparing full models with reduced models without that variable, using the `drop1` function (Barr et al., 2013).

RESULTS

We detected 318 CPs for the travel trajectories of five black howler monkey groups (mean \pm SD per group = 64.4 ± 22.5 CPs; Table 2, Fig. 1). The mean distance between CPs was 299.47 ± 165.54 m and that between CPs and the next stopping point was 80.46 ± 68.09 m. We recorded 454 loud calling bouts (mean \pm SD per group = 90.8 ± 26.9) indicating that black howler

monkeys engaged in a mean \pm SD = 1.5 ± 0.4 loud calling bouts per day during the study period. Of these bouts, 115 occurred during intergroup encounters and 328 were spontaneous or in response to neighbouring calls. Similarly, we recorded 1035 feeding bouts (mean \pm SD per group = 206.8 ± 39.1 ; Table 2) in 523 individual feeding trees of 38 species. Thus, black howler monkeys engaged in a mean \pm SD = 3.5 ± 0.6 feeding bouts per day.

A total of 133 trees were defined as important feeding trees (mean \pm SD per group = 26.6 ± 3.4 trees), in which 473 feeding bouts were recorded (mean \pm SD per group = 94.6 ± 16.4). Mean fruit tree synchrony \pm SD was estimated as 0.29 ± 0.18 and ranged between 0.05 (*Ficus insipida*) and 0.71 (*Spondias radlkoferii*). Similarly, mean young leaf synchrony \pm SD was estimated as 0.31 ± 0.26 and ranged between 0.03 (*Ficus pertusa*) and 0.80 (*Acacia glomerosa*). All *Ficus* spp. trees showed fruit (mean \pm SD = 0.14 ± 0.10) and young leaf (mean \pm SD = 0.10 ± 0.09) synchrony values below the average mean synchrony values. The mean \pm SD synchrony values were 0.18 ± 0.16 for important fruit trees and 0.35 ± 0.25 for unimportant fruit trees, while the mean synchrony values for young leaf trees were 0.16 ± 0.12 for important trees and 0.27 ± 0.17 for unimportant trees.

Influence of Social Events on Goal-directed Movements

The comparison between the full and null social models revealed that there were statistically significant differences in the probability of approaching in a goal-directed manner locations where loud calling bouts had taken place in the past (social model, likelihood ratio test: $\chi^2_5 = 14.12$, $P = 0.015$). We found that black howlers were more likely to approach a loud calling location in a goal-directed manner when intergroup encounters had taken place at that location (estimate \pm SE = 1.609 ± 0.574 ; confidence interval, $CI_{lower} = 0.484$; $CI_{upper} = 2.735$; $P = 0.005$; Fig. 2a) and with the accumulated number of times that they were observed loud calling at that specific location (estimate \pm SE = 0.433 ± 0.574 ; $CI_{lower} = 0.484$; $CI_{upper} = 2.735$; $P = 0.005$). We did not find a statistically significant influence of loud calling context or home range overlap area in the model (see Appendix Table A1).

Influence of Feeding Events on Goal-directed Movements

We found that food item type influenced the goal-directed behaviour of black howler monkeys towards feeding sites (ecological model 1, likelihood ratio test: $\chi^2_2 = 7.3$, $P = 0.026$). Black howler monkeys were more likely to approach a specific feeding site in a goal-directed manner to feed on fruits rather than on young leaves or mature leaves (Fig. 2b).

Neither the tree's phenological synchrony nor the feeding tree's importance influenced black howlers' goal-directed movements at feeding sites of young leaves (ecological model 2; Table 3). However, we found that goal-directed movement was influenced by both phenological synchrony and the feeding tree's importance at feeding sites of fruits (ecological model 3; Table 4). Black howlers

Table 2

Sample sizes of the detected number of change points (CPs) associated with feeding bouts ($CP_{ecological}$) and loud calling bouts (CP_{social}), and accumulated number of recorded feeding and loud calling bouts per study group

Group	No. of CPs	No. of feeding bouts	No. of loud calling bouts	$CP_{ecological}$		CP_{social}	
				At	Before	At	Before
Balam	70	161	83	8	14	6	3
Motiepa	60	233	56	15	15	3	5
Naha	100	252	79	13	30	3	9
Pakal	42	216	121	10	11	5	4
Unites	50	172	115	12	13	4	5

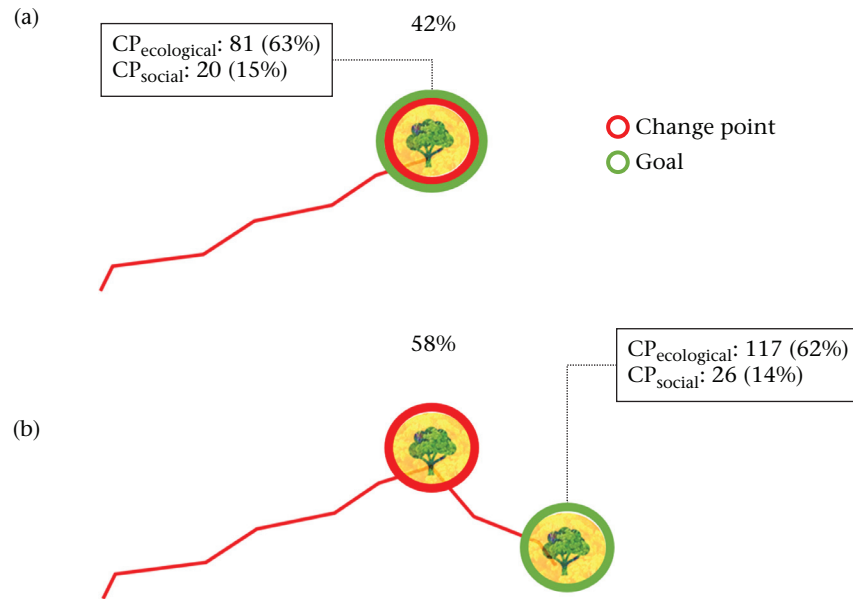


Figure 1. Significant directional changes (change points, CP) in the ranging patterns of black howlers that happened (a) at goal locations where feeding (CP_{ecological}) and loud calling (CP_{social}) bouts occurred and (b) while travelling before reaching a location where a feeding or loud calling bout occurred. The numbers observed and the percentage of the total number of CPs are shown.

were more likely to approach feeding trees in a goal-directed manner to feed on fruits when the trees were important but only when their phenology was synchronous (Table 4, Fig. 2c and d).

DISCUSSION

Our findings indicate that biologically meaningful events were associated with significant directional changes in black howlers at Palenque National Park. Specifically, we found that these changes were associated with social variables as well as ecological variables that were associated with temporal knowledge. After encountering neighbouring groups at specific locations, black howlers were more likely to return to these locations in a goal-directed manner to engage in loud calling bouts. This likelihood also increased with the number of times the focal group had engaged in loud calling bouts at that location before. Similarly, black howlers approached, in a goal-directed manner, feeding locations where fruits were present rather than young or mature leaves. Goal-directed behaviour towards fruiting trees was limited to important individual trees with phenological synchrony. Overall, our results are consistent with the hypothesis that previous experience of social and ecological events shaped black howlers' travelling trajectories reflecting potential incorporation of long-term memory in planning routes towards relevant locations.

To our knowledge, the ability to incorporate social information into route planning has not been reported before. By approaching locations where intergroup encounters had taken place in a goal-directed manner to engage in loud calls, black howlers appear to have knowledge of past social events and to integrate this information into their movement decisions. Since intergroup encounters in black howlers at Palenque National Park primarily happened at the borders of home ranges (Van Belle et al., 2013b, 2014), one could argue that an increase in turning directions at intergroup encounter locations might be a consequence of reaching the border of their home range instead of goal-directed behaviour (Nickaeen et al., 2017). However, the predictor variable overlap did not have a significant effect on the probability of goal-directed travel, making this alternative explanation highly unlikely. However, black

howlers probably remembered intergroup encounters that happened close to and further away from their home range's borders, which would be an adaptive behaviour against competitors. The outcome of intergroup encounters among conspecifics has been shown to determine prior access to valuable food sources (banded mongoose, *Mungos mungo*, Thompson, Marshall, Vitikainen, & Cant, 2017; spotted hyaenas, *Crocuta crocuta*, Boydston, Morelli, & Holekamp, 2001; bonobos, *Pan paniscus*, Lucchesi et al., 2020) but also to mates (humpback whales, *Megaptera novaeangliae*, Clapham, Mattila, & Vasquez, 1992; red deer, *Cervus elaphus*, Carranza, Alvarez, & Redondo, 1990). Anticipating the potential occurrence of encounters at specific locations has strong defensibility advantages in territorial animals, which might aid in minimizing the incursion of neighbouring groups (Christensen & Radford, 2018; Glowacki, Wilson, & Wrangham, 2017). Thus, memorizing strategic locations possibly contributes to the long-term stability of home ranges' demarcation as a cognitive adaptation of intergroup competition.

We found that black howlers typically approached locations where loud calls had taken place previously in a goal-directed manner. In fact, approximately 84.4% of all recorded loud calling bouts occurred at locations where at least one other loud calling bout had been recorded. Since animals typically recognize conspecifics through specific signals in their vocalizations (Yorzinski, 2017), it is possible that black howlers approached specific locations to purposefully advertise their position to neighbouring groups. In contrast to bats, which modify the frequency or duration of their calls to maximize the propagation of sound to inform conspecifics about their identity (Chaverri, Ancillotto, & Russo, 2018), black-and-gold howler monkeys, *Alouatta caraya*, did not adjust the duration, frequency or amplitude of their vocalizations across an open-to-close vegetation gradient (Holzmann & Areta, 2020). Thus, engaging in loud calling at locations that are recognizable by neighbouring groups might reinforce information regarding the identity of the group at a given location in time. Acoustic analyses are still needed to verify the reason underlying black howlers' tendency to approach specific sites in a goal-directed manner to engage in loud calls.

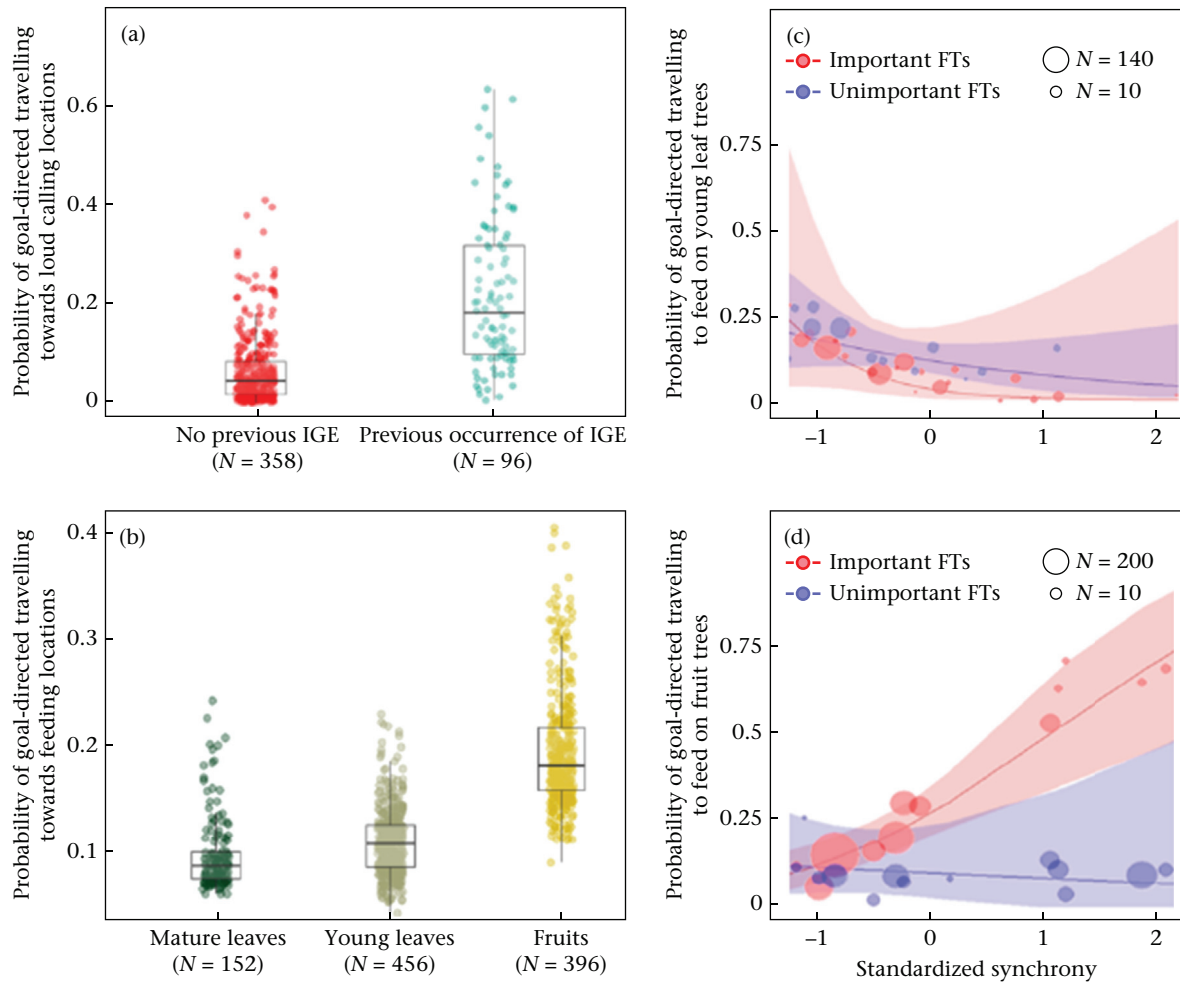


Figure 2. Probability of approaching feeding sites in a goal-directed manner as a function of: (a) the occurrence of previous intergroup encounters (IGE) at that location (i.e. each data point represents a loud calling bout); (b) the item eaten at that feeding site (i.e. each data point represents a feeding bout); (c) the importance of that feeding tree (FT) and phenological synchrony of young leaves of that tree species; (d) the importance of that feeding tree and phenological synchrony of fruits of that tree species. In (a) and (b) the box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are individual data points. In (c) and (d) lines represent the fitted model and circle size indicates the relative number of feeding bouts in the respective bin (i.e. sample size). The shaded area represents the 95% confidence interval.

Our findings on route planning involving ecological events extend the growing body of evidence reported for other animal taxa (Chiroptera, Harten, Katz, Goldshtein, Handel, & Yovel, 2020; Toledo et al., 2020; Corvidae, Raby, Alexis, Dickinson, & Clayton, 2007; Trochilinae, González-Gómez et al., 2011; Primates, Asensio et al., 2011; Joly & Zimmermann, 2011; Proboscidea, Polansky et al., 2015; English et al., 2014; Rodentia, Tolman, 1948; Epstein,

Patai, Julian, & Spiers, 2017). Black howlers approached feeding sites in a goal-directed manner more often when fruits were present rather than young or mature leaves. Owing to the ephemeral and energy-rich nature of fruits (Lambert & Rothman, 2015), anticipating ripening periods and planning routes accordingly is expected to be highly valuable for animals in rainforests (Janmaat

Table 3

Results of the ecological model testing whether black howler monkeys approached specific feeding sites in a goal-directed manner to feed on young leaves depending on the characteristics of the feeding tree (importance and level of synchrony)

Predictor variable	Estimate	SE	CI _{lower}	CI _{upper}	P
(Intercept)	-2.096	0.217	-2.522	-1.671	< 0.001
Synchrony	-0.330	0.202	-0.725	0.064	0.077
Importance of tree	-0.695	0.734	-2.133	0.743	0.223
Synchrony * Importance of tree	-0.649	0.697	-2.015	0.717	0.329
Intersection ^a	-0.029	0.365	-0.743	0.686	0.937
Slope ^a	-0.203	0.185	-0.565	0.159	0.245
Route's curvature ^a	-0.130	0.204	-0.529	0.269	0.557
Straight-line distance ^a	-0.087	0.163	-0.407	0.232	0.595

Ecological model 2, full versus null model comparison: likelihood ratio test: $\chi^2_3 = 5.03, P = 0.171$. CI: confidence interval.

^a Control predictors.

Table 4

Results of the ecological model testing whether black howler monkeys approached specific feeding sites in a goal-directed manner to feed on fruits depending on the characteristics of the feeding tree (importance and level of synchrony)

Predictor variable	Estimate	SE	CI _{lower}	CI _{upper}	P
(Intercept)	-1.851	0.356	-2.547	-1.153	< 0.001
Synchrony	0.212	0.221	-0.221	0.644	0.337
Importance of tree	0.869	0.374	0.136	1.602	0.020
Synchrony * Importance of tree	0.879	0.345	0.203	1.555	0.011
Intersection ^a	-0.174	0.299	-0.76	0.411	0.56
Slope ^a	0.238	0.175	-0.105	0.581	0.173
Route's curvature ^a	0.051	0.149	-0.242	0.344	0.734
Straight-line distance^a	0.343	0.166	0.017	0.668	0.039

Ecological model 3, full versus null model comparison: likelihood ratio test: $\chi^2_3 = 9.19, P = 0.027$. CI: confidence interval. Statistically significant results are shown in bold.

^a Control predictors.

et al., 2016; Milton, 1981). Howler monkeys, with a relatively small brain size in relation to body size (DeCasien, Williams, & Higham, 2017), appeared to have developed a cognitive strategy to cope with or simplify the spatiotemporal complexity of food resources (Hopkins, 2016). First, they seemed to minimize the number of spatial elements to include in the cognitive process, by remembering only a subset of important feeding trees. Second, by focusing on memorizing the phenological patterns of synchronous tree species across important individual trees, the cognitive process was simplified. While previous studies have highlighted independently the strategy of animals to memorize a specific subset of spatial locations (Ban, Boesch, & Janmaat, 2014; Ban et al., 2016; Delgado & Jacobs, 2017) and phenological patterns (Janmaat et al., 2012; Menzel, 1991), this is the first time both variables have been shown to influence route planning and active approach.

The importance of a limiting factor in the number of elements to be memorized in human and nonhuman animal species has already been highlighted in the literature (Tello-Ramos et al., 2019). For instance, humans are able to maintain friendship bonds with a maximum of 150 individuals (the so called 'Dunbar's number'; Dunbar, 2010) and to read urban transport maps with a maximum of 250 connections (Gallotti, Porter, & Barthelemy, 2016). Since animals inhabiting rainforests largely depend on keystone food resources to survive (Bleher, Potgieter, Potgieter, Johnson, & Böhning-Gaese, 2003; Peres, 2000; Terborgh, 1986), filtering environmental information to focus their cognitive effort on memorizing the location and phenological patterns of these valuable food resources would be highly advantageous. Therefore, animals are continuously acquiring information through interactions with the environment but are also actively selecting which locations are more beneficial to memorize. The overall number of spatial and temporal elements to be included in the cognitive process is likely to be dictated by the memory capacity of the species and the individual itself.

In addition to benefitting from fruit's high levels of easily digestible sugar, numerous animals also need the protein-rich content of young leaves to balance their diets (Raubenheimer, Simpson, & Mayntz, 2009). However, we found no evidence that black howlers either planned routes to feed on young leaves or selected a subset of trees with reduced spatiotemporal complexity to remember (as we found for fruits). Even though the CPT is a useful tool to detect goal-directed movement, the distribution of food resources can create a bias in the results (Byrne et al., 2009). The availability of leaves is often described as approximately one order of magnitude higher than that of fruits (Camaratta, Chaves, & Bicca-Marques, 2017; Janmaat et al., 2016). If trees used for foraging on leaves are more common in the environment than fruit-bearing trees, primates might be able to align resources and create a path between them that lacks a change point. Even though we did not find that travel bouts aimed to feed on young leaves were significantly shorter than those to feed on fruits (Appendix Fig. A2), black howlers could be travelling long distances to feed on young leaves in a straight manner simply because of the high availability of leaves in comparison to fruits. However, the synchronous production of young leaves during periods of maximum light radiation in tropical rainforests would be likely to contribute to reducing the uncertainty of finding young leaves in relation to fruits across the forest (Fagan et al., 2013; Lambert & Rothman, 2015; Riotte-Lambert & Matthiopoulos, 2020). Therefore, to ascertain lack of spatial memory associated with young leaf consumption, further research is needed to evaluate the influence of the distribution of food resources in the detection of goal-directed movement.

Conclusion

The ability to remember events at specific locations in highly heterogeneous landscapes such as rainforests can be a crucial determinant for animals to engage in efficient movement decisions. Black howlers at our field site appeared to direct their approach to locations where they had experienced meaningful social or ecological events to engage in loud calls or feed on fruit, respectively. The most parsimonious explanation of our findings is that black howlers, which have a relatively small brain, have developed a strategy to selectively store contextual information. We encourage future research to apply the present framework to other primate and nonprimate populations and to validate their findings by incorporating controls based on heuristic rules or spatially explicit random movement simulations (as in Teichroeb, 2015; Bracis & Mueller, 2017; Collet & Weimerskirch, 2020). Here, we ruled out alternative explanations in the interpretation of our results via observational control and a posteriori statistical modelling (Janmaat, 2019). The inclusion of a priori controls will provide the opportunity of explicitly testing specific cognitive hypotheses involved in the process of movement decision making and, therefore, provide additional support for our findings.

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References

- Adamescu, G. S., Plumptre, A. J., Abernethy, K. A., Polansky, L., Bush, E. R., Chapman, C. A., et al. (2018). Annual cycles are the most common reproductive strategy in African tropical tree communities. *Biotropica*, *50*(3), 418–430. <https://doi.org/10.1111/btp.12561>
- Asensio, N., Brockelman, W. Y., Malaivijitnond, S., & Reichard, U. H. (2011). Gibbon travel paths are goal oriented. *Animal Cognition*, *14*(3), 395–405. <https://doi.org/10.1007/s10071-010-0374-1>
- Ban, S. D., Boesch, C., & Janmaat, K. R. L. (2014). Tai chimpanzees anticipate revisiting high-valued fruit trees from further distances. *Animal Cognition*, *17*(6), 1353–1364. <https://doi.org/10.1007/s10071-014-0771-y>
- Ban, S. D., Boesch, C., N'Guessan, A., N'Goran, E. K., Tako, A., & Janmaat, K. R. L. (2016). Tai chimpanzees change their travel direction for rare feeding trees providing fatty fruits. *Animal Behaviour*, *118*, 135–147. <https://doi.org/10.1016/j.anbehav.2016.05.014>
- Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language*, *68*(3), 255–278. <https://doi.org/10.1016/j.jml.2012.11.001>
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Bebko, A. O. (2018). *Ecological and cognitive influences on Orangutan space use*. York University.
- Berdahl, A., Westley, P. A. H., & Quinn, T. P. (2017). Social interactions shape the timing of spawning migrations in an anadromous fish. *Animal Behaviour*, *126*, 221–229. <https://doi.org/10.1016/j.anbehav.2017.01.020>
- Berger-Tal, O., & Bar-David, S. (2015). Recursive movement patterns: Review and synthesis across species. *Ecosphere*, *6*(9), 149. <https://doi.org/10.1890/ES15-00106.1>

- Bjørnstad, O. N., Ims, R. A., & Lambin, X. (1999). Spatial population dynamics: Analyzing patterns and processes of population synchrony. *Trends in Ecology & Evolution*, 14(11), 427–432. [https://doi.org/10.1016/S0169-5347\(99\)01677-8](https://doi.org/10.1016/S0169-5347(99)01677-8)
- Bleher, B., Potgieter, C. J., Potgieter, C. J., Johnson, D. N., & Böhning-Gaese, K. (2003). The importance of figs for frugivores in a south African coastal forest. *Source: Journal of Tropical Ecology*, 19(4), 375–386. <https://doi.org/10.1017/S0266467403003420>
- Boydston, E. E., Morelli, T. L., & Holekamp, K. E. (2001). Sex differences in territorial behavior exhibited by the Spotted Hyena (*Hyaenidae, Crocuta crocuta*). *Ethology*, 107(5), 369–385. <https://doi.org/10.1046/j.1439-0310.2001.00672.x>
- Bracis, C., Bildstein, K. L., & Mueller, T. (2018). Revisitation analysis uncovers spatio-temporal patterns in animal movement data. *Ecography*, 41(11), 1801–1811. <https://doi.org/10.1111/ecog.03618>
- Bracis, C., & Mueller, T. (2017). Memory, not just perception, plays an important role in terrestrial mammalian migration. *Proceedings of the Royal Society B: Biological Sciences*, 284(1855), 20170449. <https://doi.org/10.1098/rspb.2017.0449>
- Burkart, J. M., Schubiger, M. N., & van Schaik, C. P. (2017). The evolution of general intelligence. *Behavioral and Brain Sciences*, 53(2), 90–93. <https://doi.org/10.1016/j.paidd.2011.05.015>
- Byrne, R. W., Noser, R., Bates, L. A., & Jupp, P. E. (2009). How did they get here from there? Detecting changes of direction in terrestrial ranging. *Animal Behaviour*, 77(3), 619–631. <https://doi.org/10.1016/j.anbehav.2008.11.014>
- Calenge, C. (2006). The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, 197, 516–519. <https://doi.org/10.1016/j.ecolmodel.2006.03.017>
- Camaratta, D., Chaves, Ó. M., & Bicca-Marques, J. C. (2017). Fruit availability drives the distribution of a folivorous-frugivorous primate within a large forest remnant. *American Journal of Primatology*, 79(3), Article e22626. <https://doi.org/10.1002/ajp.22626>
- Carranza, J., Alvarez, F., & Redondo, T. (1990). Territoriality as a mating strategy in red deer. *Animal Behaviour*, 40(1), 79–88. [https://doi.org/10.1016/S0003-3472\(05\)80667-0](https://doi.org/10.1016/S0003-3472(05)80667-0)
- Carroll, L. (1872). *Through the looking glass*. London, U.K.: Macmillan.
- Chaverri, G., Ancillotto, L., & Russo, D. (2018). Social communication in bats. *Bio-Logical Reviews*, 93(4), 1938–1954. <https://doi.org/10.1111/brv.12427>
- Christensen, C., & Radford, A. N. (2018). Dear enemies or nasty neighbors? Causes and consequences of variation in the responses of group-living species to territorial intrusions. *Behavioral Ecology*, 29(5), 1004–1013. <https://doi.org/10.1093/beheco/ary010>
- Clapham, P. J., Mattila, D. K., & Vasquez, O. (1992). Composition and dynamics of humpback whale competitive groups in the West Indies. *Behaviour*, 122(3–4), 182–194. Retrieved from https://brill.com/view/journals/beh/122/3-4/article-p182_3.xml
- Clayton, N. S., Bussey, T. J., & Dickinson, A. (2003). Can animals recall the past and plan for the future? *Nature Reviews Neuroscience*, 4(8), 685–691. <https://doi.org/10.1038/nrn1180>
- Clayton, N. S., & Dickinson, A. (1998). Episodic-like memory during cache recovery by scrub jays. *Nature*, 395(6699), 272–274. <https://doi.org/10.1038/26216>
- Collet, J., & Weimerskirch, H. (2020). Albatrosses can memorize locations of predictable fishing boats but favour natural foraging. *Proceedings of the Royal Society B: Biological Sciences*, 287, 20200958. <https://doi.org/10.1098/rspb.2020.0958>
- Crystal, J. D. (2016). Animal models of source memory. *Journal of the Experimental Analysis of Behaviour*, 105(1), 56–67. <https://doi.org/10.1002/jeab.173>
- da Cunha, R. G. T., de Oliveira, D. A. G., Holzmann, I., & Kitchen, D. M. (2015). Production of loud and quiet calls in howler monkeys. In M. M. Kowalewski, P. A. Garber, L. Cortes-Ortiz, B. Urbani, & D. Youlatos (Eds.), *Howler monkeys: behaviour, ecology and conservation* (pp. 337–368). New York, NY: Springer-Verlag. https://doi.org/10.1007/978-1-4939-1957-4_13
- Davies, N. B., & Houston, A. I. (1981). Owners and satellites: The economics of territory defence in the pied wagtail, *Motacilla alba*. *Journal of Animal Ecology*, 50, 157–180. Retrieved from https://www.jstor.org/stable/pdf/4038.pdf?casa_token=SvnYt8K-nEsAAAAA:Sy-wFfCd2oR2omPmj1jW6Cjrx0BNQbV92DXEIBqzm5Sg_rCYSrk8gmc1GNwMIPseju5bP_VuSbLL7M9im0qt_pi8V9MP-V90s2t_A135eAHB6A4-DOx
- DeCasien, A. R., Williams, S. A., & Higham, J. P. (2017). Primate brain size is predicted by diet but not sociality. *Nature Ecology and Evolution*, 1(5), 1–7. <https://doi.org/10.1038/s41559-017-0112>
- Delgado, M. M., & Jacobs, L. F. (2017). Caching for where and what: Evidence for a mnemonic strategy in a scatter-hoarder. *Royal Society Open Science*, 4(9), 170958. <https://doi.org/10.1098/rsos.170958>
- Di Fiore, A., & Suarez, S. A. (2007). Route-based travel and shared routes in sympatric spider and woolly monkeys: Cognitive and evolutionary implications. *Animal Cognition*, 10(3), 317–329. <https://doi.org/10.1007/s10071-006-0067-y>
- Díaz-Gallegos, J. R. (1996). *Estructura y composición florística del Parque Nacional zona arqueológica de Palenque, Chiapas, México* (Ph.D. thesis). Villahermosa, Tabasco, México: Universidad Juárez Autónoma de Tabasco.
- Dunbar, R. (2010). *How many friends does one person need?: Dunbar's number and other evolutionary quirks*. Cambridge, MA: Harvard University Press. Retrieved from https://books.google.de/books?hl=en&lr=&id=gQ_MFDC_F4kC&oi=fnd&pg=PP1&dq=info:ytYUGCRmTxxj:scholar.google.com&ots=4cmqy2mef&sig=A3nIT6eP8iWf9KcFzCMAkA-B&redir_esc=y#v=onepage&q&f=false
- English, M., Ancrenaz, M., Gillespie, G., Goossens, B., Nathan, S., & Linklater, W. (2014). Foraging site recursion by forest elephants *Elephas maximus borneensis*. *Current Zoology*, 60(4), 551–559. <https://doi.org/10.1093/CZOOLO/60.4.551>
- Epstein, R. A., Patai, E. Z., Julian, J. B., & Spiers, H. J. (2017). The cognitive map in humans: Spatial navigation and beyond. *Nature Neuroscience*, 20(11), 1504–1513. <https://doi.org/10.1038/nn.4656>
- Fagan, W. F., Lewis, M. A., Auger-Meth, M., Avgar, T., Benhamou, S., Breed, G., et al. (2013). Spatial memory and animal movement. *Ecology Letters*, 16, 1316–1329. <https://doi.org/10.1111/ele.12165>
- Fawcett, T. W., Marshall, & Higginson, J. A. R. (2015). The evolution of mechanisms underlying behaviour. *Current Zoology*, 61(2), 221–225. Retrieved from <http://eprints.whiterose.ac.uk/85510/>
- Feeney, M. C., Roberts, W. A., & Sherry, D. F. (2009). Memory for what, where, and when in the black-capped chickadee (*Poecile atricapillus*). *Animal Cognition*, 12(6), 767–777. <https://doi.org/10.1007/s10071-009-0236-x>
- Figuerola, F., & Sánchez-Cordero, V. (2008). Effectiveness of natural protected areas to prevent land use and land cover change in Mexico. *Biodiversity & Conservation*, 17(13), 3223–3240. <https://doi.org/10.1007/s10531-008-9423-3>
- Fox, J., & Weisberg, S. (2011). Multivariate linear models in R. In H. Salmon, O’Heffernan, M. K. DeRosa, & G. Dickens (Eds.), *An R companion to applied regression*. Thousand Oaks, CA: Sage. Retrieved from <http://staff.ustc.edu.cn/~zwp/teach/MVA/Appendix-Multivariate-Linear-Models.pdf>
- Gallotti, R., Porter, M. A., & Barthelemy, M. (2016). Lost in transportation: Information measures and cognitive limits in multilayer navigation. *Science Advances*, 2(2), Article e1500445. <https://doi.org/10.1126/sciadv.1500445>
- Gardner, R. J., & Moser, M.-B. (2017). Multiple mechanisms for memory replay? *Science*, 355(6321), 131–132. <https://doi.org/10.1126/science.aam5404>
- Glowacki, L., Wilson, M. L., & Wrangham, R. W. (2017). The evolutionary anthropology of war. *Journal of Economic Behavior & Organization*, 1–20. <https://doi.org/10.1016/j.jebo.2017.09.014>
- González-Gómez, P. L., Bozinovic, F., & Vásquez, R. A. (2011). Elements of episodic-like memory in free-living hummingbirds, energetic consequences. *Animal Behaviour*, 81(6), 1257–1262. <https://doi.org/10.1016/j.anbehav.2011.03.014>
- Grodzinski, U., & Clayton, N. S. (2010). Problems faced by food-caching corvids and the evolution of cognitive solutions. *Proceedings of the Royal Society B: Biological Sciences*, 365(1542), 977–987. <https://doi.org/10.1098/rstb.2009.0210>
- de Guinea, M., Estrada, A., Nekaris, K. A. L., & Van Belle, S. (2019). Arboreal route navigation in a neotropical mammal: Energetic implications associated with tree monitoring and landscape attributes. *Movement Ecology*, 7(1), 1–12. <https://doi.org/10.1186/s40462-019-0187-z>
- Harten, L., Katz, A., Goldshtein, A., Handel, M., & Yovel, Y. (2020). The ontogeny of a mammalian cognitive map in the real world. *Science*, 197(July), 194–197.
- Holzmann, I., & Areta, J. I. (2020). Reduced geographic variation in roars in different habitats rejects the acoustic adaptation hypothesis in the black-and-gold howler monkey (*Alouatta caraya*). *Ethology*, 126(1), 76–87. <https://doi.org/10.1111/eth.12962>
- Hopkins, M. E. (2016). Mantled howler monkey spatial foraging decisions reflect spatial and temporal knowledge of resource distributions. *Animal Cognition*, 19(2), 387–403. <https://doi.org/10.1007/s10071-015-0941-6>
- Janmaat, K. R. L. (2019). What animals do not do or fail to find: A novel observational approach for studying cognition in the wild. *Evolutionary Anthropology: Issues, News, and Reviews*, 28(6), 303–320. <https://doi.org/10.1002/evan.21794>
- Janmaat, K. R. L., Ban, S. D., & Boesch, C. (2013). Chimpanzees use long-term spatial memory to monitor large fruit trees and remember feeding experiences across seasons. *Animal Behaviour*, 86(6), 1183–1205. <https://doi.org/10.1016/j.anbehav.2013.09.021>
- Janmaat, K. R. L., Boesch, C., Byrne, R. W., Chapman, C. A., Goné Bi, Z. B., Head, J. S., et al. (2016). Spatio-temporal complexity of chimpanzee food: How cognitive adaptations can counteract the ephemeral nature of ripe fruit. *American Journal of Primatology*, 78(6), 626–645. <https://doi.org/10.1002/ajp.22527>
- Janmaat, K. R. L., Chapman, C. A., Meijer, R., & Zuberbühler, K. (2012). The use of fruiting synchrony by foraging mangabey monkeys: A ‘simple tool’ to find fruit. *Animal Cognition*, 15(1), 83–96. <https://doi.org/10.1007/s10071-011-0435-0>
- Janson, C. H. (2016). Capuchins, space, time and memory: An experimental test of what-where-when memory in wild monkeys. *Proceedings of the Royal Society B: Biological Sciences*, 283(1840), 20161432. <https://doi.org/10.1098/rspb.2016.1432>
- Janson, C. H. (2019). Foraging benefits of ecological cognition in fruit-eating primates: Results from field experiments and computer simulations. *Frontiers in Ecology and Evolution*, 7(125), 1–8. <https://doi.org/10.3389/fevo.2019.00125>
- Jelbert, S. A., Hurly, T. A., Marshall, R. E. S., & Healy, S. D. (2014). Wild, free-living hummingbirds can learn what happened, where and in which context. *Animal Behaviour*, 89, 185–189. <https://doi.org/10.1016/j.anbehav.2013.12.028>
- Joly, M., & Zimmermann, E. (2011). Do solitary foraging nocturnal mammals plan their routes? *Biology Letters*, 7(4), 638–640. <https://doi.org/10.1098/rsbl.2011.0258>
- Lambert, J. E., & Rothman, J. M. (2015). Fallback foods, optimal diets, and nutritional targets: Primate responses to varying food availability and quality. *Annual Review of Anthropology*, 44(1), 493–512. <https://doi.org/10.1146/annurev-anthro-102313-025928>
- Levey, D. J. (1988). Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. *Ecological Monographs*, 58(4), 251–269. <https://doi.org/10.2307/1942539>
- Lucchesi, S., Cheng, L., Janmaat, K. R. M., Mundry, R., Pisor, A., & Surbeck, M. (2020). Beyond the group: How food, mates, and group size influence intergroup encounters in wild bonobos. *Behavioral Ecology*, 31(2), 519–532. <https://doi.org/10.1093/beheco>

- Martin-Ordas, G., Haun, D. B. M., Colmenares, F., & Call, J. (2010). Keeping track of time: Evidence for episodic-like memory in great apes. *Animal Cognition*, 13(2), 331–340. <https://doi.org/10.1007/s10071-009-0282-4>
- Menzel, C. R. (1991). Cognitive aspects of foraging in Japanese monkeys. *Animal Behaviour*, 41(3), 397–402. [https://doi.org/10.1016/S0003-3472\(05\)80840-1](https://doi.org/10.1016/S0003-3472(05)80840-1)
- Milton, K. (1981). Distribution patterns of tropical plant foods as an evolutionary stimulus to primate mental development. *American Anthropologist*, 83, 534–548. Retrieved from <https://anthrosource.onlinelibrary.wiley.com/doi/pdf/10.1525/aa.1981.83.3.02a00020>.
- Morand-Ferron, J., Hermer, E., Jones, T. B., & Thompson, M. J. (2019, January 1). Environmental variability, the value of information, and learning in winter residents. *Animal Behaviour*, 147, 137–145. <https://doi.org/10.1016/j.anbehav.2018.09.008>
- Naguib, M., & Wiley, R. H. (2001). Estimating the distance to a source of sound: Mechanisms and adaptations for long-range communication. *Animal Behaviour*, 62(5), 825–837. <https://doi.org/10.1006/anbe.2001.1860>
- Naqshbandi, M., & Roberts, W. A. (2006). Anticipation of future events in squirrel monkeys (*Saimiri sciureus*) and rats (*Rattus norvegicus*): Tests of the Bischof-Kohler hypothesis. *Journal of Comparative Psychology*, 120(4), 345–357. <https://doi.org/10.1037/0735-7036.120.4.345>
- Nickaen, M., Novak, I. L., Pulford, S., Rumack, A., Brandon, J., Slepchenko, B. M., et al. (2017). A free-boundary model of a motile cell explains turning behavior. *PLoS Computational Biology*, 13(11), Article e1005862. <https://doi.org/10.1371/journal.pcbi.1005862>
- Noser, R., & Byrne, R. W. (2007). Mental maps in chacma baboons (*Papio ursinus*): Using inter-group encounters as a natural experiment. *Animal Cognition*, 10(3), 331–340. <https://doi.org/10.1007/s10071-006-0068-x>
- Noser, R., & Byrne, R. W. (2014). Change point analysis of travel routes reveals novel insights into foraging strategies and cognitive maps of wild baboons. *American Journal of Primatology*, 76(5), 399–409. <https://doi.org/10.1002/ajp.22181>
- Peres, C. A. (2000). Identifying keystone plant resources in tropical forests: The case of gums from Parkia pods. *Journal of Tropical Ecology*, 16(2), 287–317. <https://doi.org/10.1017/S0266467400001413>
- Plante, S., Colchero, F., & Calmé, S. (2014). Foraging strategy of a neotropical primate: How intrinsic and extrinsic factors influence destination and residence time. *Journal of Animal Ecology*, 83(1), 116–125. [https://doi.org/10.1111/1365-2656.12119@10.1111/\(ISSN\)1365-2656](https://doi.org/10.1111/1365-2656.12119@10.1111/(ISSN)1365-2656). MOVEMENTECOLOGY.
- Polansky, L., Kilian, W., & Wittemyer, G. (2015). Elucidating the significance of spatial memory on movement decisions by African savannah elephants using state–space models. *Proceedings of the Royal Society B: Biological Sciences*, 282(1805), 20143042. <https://doi.org/10.1098/rspb.2014.3042>
- Potts, J. R., Börger, L., Scantlebury, D. M., Bennett, N. C., Alagaili, A., & Wilson, R. P. (2018). Finding turning-points in ultra-high-resolution animal movement data. *Methods in Ecology and Evolution*, 9(10), 2091–2101. <https://doi.org/10.1111/2041-210X.13056>
- Presotto, A., Verderane, M. P., Biondi, L., Mendonça-Furtado, O., Spagnoletti, N., Madden, M., et al. (2018). Intersection as key locations for bearded capuchin monkeys (*Sapajus libidinosus*) traveling within a route network. *Animal Cognition*, 21(3), 393–405. <https://doi.org/10.1007/s10071-018-1176-0>
- R Core Team. (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. <http://www.r-project.org>.
- Raby, C. R., Alexis, D. M., Dickinson, A., & Clayton, N. S. (2007). Planning for the future by western scrub-jays. *Nature*, 445(7130), 919. <https://doi.org/10.1038/nature05575>
- Ramsier, M. A., Cunningham, A. J., Patiño, M. R., Glander, K. E., & Dominy, N. J. (2019). Audiograms of howling monkeys: Are extreme loud calls the result of runaway selection? *BioRxiv*, 539023. <https://doi.org/10.1101/539023>
- Rathcke, B., & Lacey, E. P. (1985). Phenological patterns of terrestrial plants. *Annual Reviews Ecological Systems*, 16, 179–214. <https://doi.org/10.1146/annurev.es.16.110185.001143>
- Raubenheimer, D., Simpson, S. J., & Mayntz, D. (2009). Nutrition, ecology and nutritional ecology: Towards an integrated framework. *Functional Ecology*, 23, 4–16. <https://doi.org/10.2307/40205497>
- Righini, N., Garber, P. A., & Rothman, J. M. (2017). The effects of plant nutritional chemistry on food selection of Mexican black howler monkeys (*Alouatta pigra*): The role of lipids. *American Journal of Primatology*, 79(4), 1–15. <https://doi.org/10.1002/ajp.22524>
- Riotte-Lambert, L., & Matthiopoulos, J. (2020). Environmental predictability as a cause and consequence of animal movement. *Trends in Ecology & Evolution*, 35(2), 163–174. <https://doi.org/10.1016/j.tree.2019.09.009>
- van Schaik, C. P., Terborgh, J. W., & Wright, S. J. (1993). The phenology of tropical forests: Adaptive significance and consequences for primary consumers. *Annual Review of Ecological Systems*, 24, 353–377. <https://doi.org/10.1146/annurev.es.24.110193.002033>
- Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, 1(2), 103–113. <https://doi.org/10.1111/j.2041-210x.2010.00012.x>
- Schielzeth, H., & Forstmeier, W. (2009). Conclusions beyond support: Overconfident estimates in mixed models. *Behavioral Ecology*, 20(2), 416–420. <https://doi.org/10.1093/beheco/arn145>
- Spiegel, O., & Crofoot, M. C. (2016). The feedback between where we go and what we know — information shapes movement, but movement also impacts information acquisition. *Current Opinion in Behavioral Sciences*, 12, 90–96. <https://doi.org/10.1016/j.cobeha.2016.09.009>
- Teichroeb, J. A. (2015). Vervet monkeys use paths consistent with context-specific spatial movement heuristics. *Ecology and Evolution*, 5(20), 4706–4716. <https://doi.org/10.1002/ece3.1755>
- Tello-Ramos, M. C., Branch, C. L., Kozlovsky, D. Y., Pitera, A. M., & Pravosudov, V. V. (2019). Spatial memory and cognitive flexibility trade-offs: To be or not to be flexible, that is the question. *Animal Behaviour*, 147, 129–136. <https://doi.org/10.1016/j.anbehav.2018.02.019>
- Templer, V. L., & Hampton, R. R. (2013). Episodic memory in nonhuman animals. *Current Biology*, 23(17), R801–R806. <https://doi.org/10.1016/j.cub.2013.07.016>
- Terborgh, J. (1986). Keystone plant resources in the tropical forest. In I. Soulé, & E. Michael (Eds.), *Conservation biology* (pp. 330–344). Sunderland, MA: Sinauer.
- Thompson, F. J., Marshall, H. H., Vitikainen, E. I. K., & Cant, M. A. (2017). Causes and consequences of intergroup conflict in cooperative banded mongooses. *Animal Behaviour*, 126, 31–40. <https://doi.org/10.1016/j.anbehav.2017.01.017>
- Toledo, S., Shohami, D., Schiffner, I., Lourie, E., Orchan, Y., Bartan, Y., et al. (2020). Cognitive map-based navigation in wild bats revealed by a new high-throughput wildlife tracking system. *Science*, 193(July), 188–193.
- Tolman, E. C. (1948). Cognitive maps in rats and men. *Psychological Review*, 55(4), 189–208.
- Torney, C. J., Lamont, M., Debell, L., Angohiatok, R. J., Leclerc, L.-M., & Berdahl, A. M. (2018). Inferring the rules of social interaction in migrating caribou. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373(1746), 20170385. <https://doi.org/10.1098/rstb.2017.0385>
- Van Belle, S., & Estrada, A. (2020). The influence of loud calls on intergroup spacing mechanism in black howler monkeys (*Alouatta pigra*). *International Journal of Primatology*, 41(2), 265–286.
- Van Belle, S., Estrada, A., & Garber, P. A. (2013a). Collective group movement and leadership in wild black howler monkeys (*Alouatta pigra*). *Behavioral Ecology and Sociobiology*, 67(1), 31–41. <https://doi.org/10.1007/s00265-012-1421-5>
- Van Belle, S., Estrada, A., & Garber, P. A. (2013b). Spatial and diurnal distribution of loud calling in black howlers (*Alouatta pigra*). *International Journal of Primatology*, 34(6), 1209–1224. <https://doi.org/10.1007/s10764-013-9734-4>
- Van Belle, S., Garber, P. A., Estrada, A., & Di Fiore, A. (2014). Social and genetic factors mediating male participation in collective group defence in black howler monkeys. *Animal Behaviour*, 98, 7–17. <https://doi.org/10.1016/j.anbehav.2014.09.023>
- Warren, W. H. (2019). Non-Euclidean navigation. *Journal of Experimental Biology*, 222, jeb187971. <https://doi.org/10.1242/jeb.187971>
- Yorzinski, J. L. (2017). The cognitive basis of individual recognition. *Current Opinion in Behavioral Sciences*, 16, 53–57. <https://doi.org/10.1016/j.cobeha.2017.03.009>

Appendix

Table A1

Results of the social GLMM testing whether black howler monkeys approached specific locations to engage in loud calling bouts in a goal-directed manner

Predictor variable	Estimate	SE	CI _{lower}	CI _{upper}	P
(Intercept)	-3.592	0.699	-4.963	-2.222	< 0.001
Context	-0.435	0.610	-1.631	0.760	0.475
Overlapping area	0.755	0.590	-0.401	1.910	0.201
No. of times loud calling occurred at that location before	0.433	0.230	-0.018	0.883	0.062
Occurrence of previous intergroup encounter	1.609	0.574	0.484	2.735	0.005
Context * Overlap area	0.116	1.144	-2.126	2.359	0.919
Duration of howling bout ^a	0.173	0.252	-0.320	0.666	0.491
Intersection ^a	-2.197	2.889	-7.860	3.466	0.447
Slope ^a	-0.136	0.279	-0.683	0.411	0.626
Route's curvature ^a	0.197	0.935	-1.635	2.029	0.833

CI: confidence interval.

^a Control predictors.

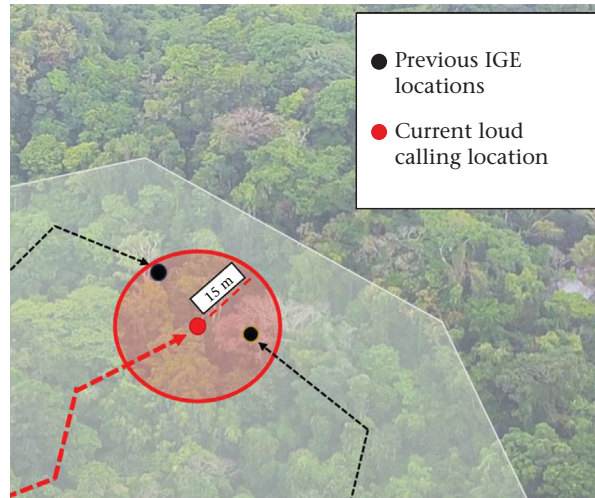


Figure A1. We determined that black howlers had experienced an intergroup encounter (IGE) at a given loud calling location if at least one intergroup encounter occurred within a 15 m radius from this loud calling location. The shaded area represents the home range of the observed group.

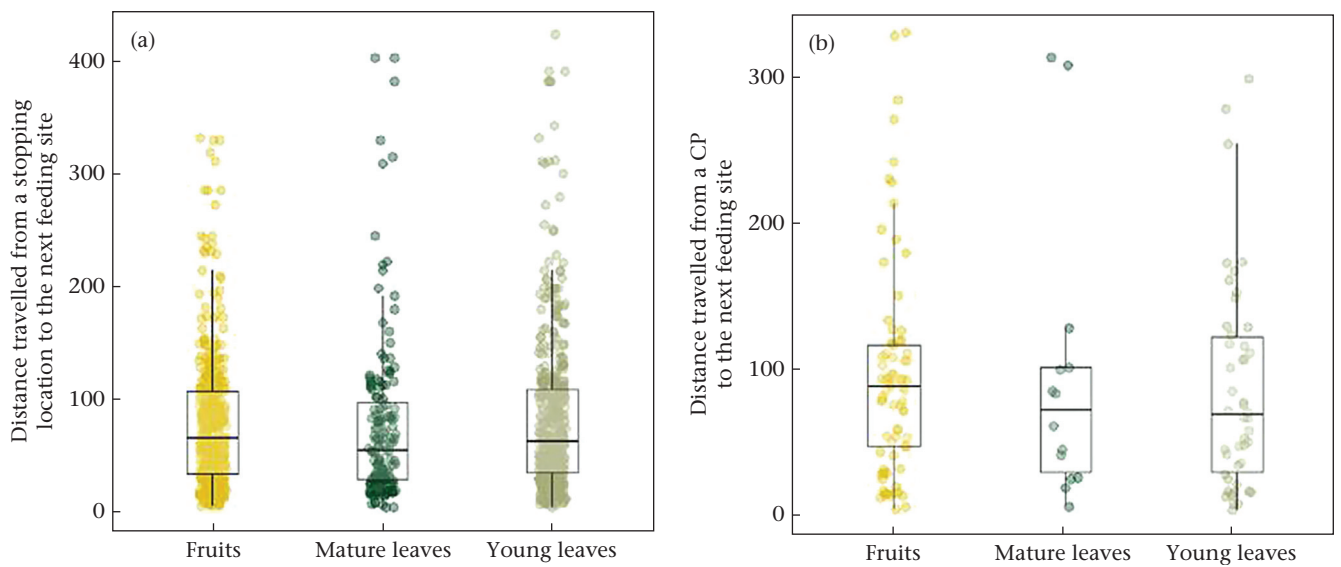


Figure A2. Distance travelled by black howlers to feed on fruits, mature leaves and young leaves (a) in the absence of directional changes and (b) after engaging in significant directional changes. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are individual data points. CP: change point.