Routes matter: the effect of seasonality on bamboo lemur navigational strategies

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Seasonal environments challenge animals, increasing the complexity of locating resources. Navigation may rely on ‘habitual routes’ or ‘Euclidean’ maps: following established routes or computing novel paths, respectively. Folivores are presumed to rely on evenly distributed resources and thus have a reduced reliance on navigation. We tested whether the navigation strategy of southern bamboo lemurs, *Hapalemur meridionalis*, a primarily folivorous strepsirrhine that periodically consumes fruit, varies across seasons. We recorded behaviour and location of three social groups during full-day, focal follows during January–December 2013. We analysed the macronutrient components of food items. Bamboo lemurs travelled through habitual routes during periods of food scarcity but relied on nodes (i.e. intersections where directional decisions are made) to navigate throughout the year. Likely, habitual route navigation promoted an energy-saving strategy during lean periods by easing lemur locomotion across the forest. In contrast, lemurs relied on Euclidean navigation during food abundant periods. The continuous use of nodes suggest that nodes may act as cognitive anchors to support efficient directional decisions across seasons. Linearity increased during periods of resource abundance when feeding on energy-rich items and during periods of scarcity to reach latrines. By travelling increasingly linearly towards energy-rich items, lemurs maximized energy intake during periods of food abundance. Overall, bamboo lemurs’ combination of both Euclidean and route-based navigational strategies demonstrates a cognitive adaptation for coping with seasonal resource variability in a way that challenges previous research postulating constrained spatial skills in folivorous strepsirrhines.

Keywords:

cognitive maps

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movement decision making

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Seasonal variation in resource availability plays an essential role in the strategy an animal uses to navigate; it influences both space use patterns within a territory (Ramos-Fernández et al., 2013; Spencer et al., 1990) and beyond their territory (Bracis & Mueller, 2017). As seasonal variation in food resources increases, animals need to recall more information to correctly anticipate where and when food will emerge (Fagan et al., 2013; Riotte-Lambert & Matthiopoulos, 2020) as well as balance their own energetic expenditure during navigation (Halsey, 2016; Nathan et al., 2008). In addition to monitoring variable food resources, animals need to constantly update and recall social information within their group, which may display its own seasonality (e.g. mating and breeding seasons; Prehn et al., 2019). Given the integral role of large-scale movement to access both ecological and social resources, animals have evolved behavioural and physiological adaptations to cope with the cognitive and energetic demands of navigating through seasonal habitats (Rosati, 2017; Sol, 2009).

To navigate their environment with ease, it is presumed that animals utilize a cognitive map: a mental representation of the landscape that informs travelling decisions among distant locations within the mapped area (Behrens et al., 2018; Tolman, 1948; but see Bennett, 1996). To date, two types of cognitive maps have been described (de Guinea et al., 2021b; Tujague & Janson, 2017). The first, a route-based cognitive map, structures home ranges as a complex network formed by a series of well-established routes interconnected by nodes, as has been recorded in Blattodea (Perna & Latty, 2014), Cetacea (Horton et al., 2017), Columbiformes (Freeman et al., 2011), Rodentia (McNaughton et al., 2006) and Primates (Trapanese et al., 2019). Nodes are locations where two or more habitual routes intersect, and additional information is perceived from the landscape to support efficient directional decisions (Presotto et al., 2018). The second is a Euclidean or coordinate-based map in which animals compute novel paths between known locations in the absence of habitual routes, e.g. as has been recorded in Chiroptera (Harten et al., 2020; Toledo et al., 2020), Primates (Normand & Boesch, 2009) and Proboscidea (Presotto et al., 2019).

Animals tend to deviate the trajectory of their travel bouts from a straight line when relying on route-based maps due to the shape of the habitual route (Porter & Garber, 2013), whereas a Euclidean map supports computing straight paths regardless of the origin and destination (Normand &

Boesch, 2009). Even though Euclidean maps support linear travel paths that minimize the time spent travelling by the animal, engaging in novel paths may increase the energetic costs of locomotion (Shepard et al., 2013). For instance, Wall et al. (2006) showed that even though African savannah elephants, *Loxodonta africana*, in northern Kenya would significantly shorten their paths by taking short cuts across a prominent hill, it would increase the cost of travelling by two orders of magnitude, which led them to travel around the hill instead. Similarly, chimpanzees, *Pan troglodytes*, inhabiting a mountainous terrain in Uganda travelled across routes that required the least energetic demands to reach their goal even though these were not necessarily the shortest options (Green et al., 2020). Since previous research highlighted chimpanzees' skills to travel using short cuts in Tai Forest (Normand & Boesch, 2009), it might be possible that computing short cuts may not always be the most optimal option to navigate (Green et al., 2020). By placing habitual routes across areas that minimize the cost of travelling (i.e. flat terrain, continuous substrate) and contributing to their clearance by continuously travelling through them (de Guinea et al., 2019; Halsey, 2016; Newmark & Rickart, 2012), animal route navigation can minimize the costs of travelling across complex landscapes such as forests.

An increasing number of species show ranging patterns associated with both route-based and Euclidean cognitive maps under varying conditions (Presotto et al., 2019; Presotto & Izar, 2010). For instance, the distribution and availability of food resources have been shown to influence animals' navigational strategy (Erhart & Overdorff, 2008; Morrison et al., 2021; Reese, 1989; Trapanese et al., 2019). Computing novel paths towards feeding sites becomes increasingly complex and more cognitively demanding in landscapes with a marked heterogeneous resource distribution than in landscapes with a homogeneous distribution of resources (Fagan et al., 2013; Morrison et al., 2021). For animals inhabiting seasonal habitats with complex and dynamic environments characterized by variable phenological resource patterns (Bollen & Donati, 2005; Janmaat et al., 2016), it may be advantageous to combine both cognitive map forms to navigate (Presotto & Izar, 2010). However, even during periods of food scarcity in which food resources are distributed patchily and ephemerally, animals may still compute novel, straight paths towards relevant locations related to social interactions or predator avoidance (de Guinea et al., 2021a; Isbell et al., 2018). While remembering the location of food resources may be more critical during food scarcity periods, the need to recall socially relevant locations remains constant throughout the year, e.g. sleeping sites, latrines (Fei et al., in press). The capacity to combine route-based maps and Euclidean maps to navigate across the same space in different temporal windows and to travel towards different types of goals remains unexplored in mammals.

Madagascar is a highly dynamic environment where forests have prolonged periods of fruit scarcity (Bollen & Donati, 2005; Dunham et al., 2018; Gould et al., 1999; Wright, 1999). Fruit trees not only show highly asynchronous intra-annual phenological patterns, i.e. irregular fruit production windows within a year, but also high supra-annual variability, i.e. fruit production might occur once every 2–3 years (Bollen & Donati, 2005; Ganzhorn et al., 1999). The combination of marked seasonal variation and unpredictable quantity and quality of food resources in Madagascar appears to have influenced the biological adaptations of lemurs (Dewar & Richard, 2007; Donati et al., 2017; Wright, 1999; but see Federman et al. 2017), a group of strepsirrhine primates that exhibit considerable variation in their social structure (van Schaik & Kappeler, 1996), feeding ecology (Eppley et al., 2020; Ganzhorn et al., 1999) and cognitive capacity (Fichtel et al., 2020). Such a variety of adaptations has been proposed as a response to the energetic constraints imposed during periods of food scarcity in order to efficiently cope with seasonal and unpredictable island environments, i.e. the energy frugality hypothesis (hereafter EFH; Wright, 1999). EFH states that most traits found in lemurs are either adaptations that allow for energy to be conserved or to maximize the use of scarce resources (Wright, 1999). Even though lemurs have shown different cognitive skills such as planning abilities towards food resources in the wild (e.g. grey mouse lemur, *Microcebus murinus*; Joly & Zimmermann, 2011, Lührs et al. 2009) or gaze following (e.g. ringtailed lemurs, *Lemur catta*; Sandel et al., 2011), the relationship between cognitive skills and the ecological characterization of the island has remained largely unstudied (but see Rosati, 2017).

The southern bamboo lemur, *Hapalemur meridionalis*, is a small-bodied, cathemeral (i.e. diel) primate (Eppley et al., 2015, 2017). They feed primarily on graminoid leaves throughout the year but increase the percentage of fruits in their diet from 23% during periods of food scarcity to

52% during periods of food abundance (Eppley, Donati et al., 2016; Eppley et al., 2011). Despite the presence of anatomical specializations for a folivorous diet (Campbell et al., 2004), fruits remain an important source of energy for bamboo lemurs, as shown in other mixed folivorous–frugivorous primates (Irwin et al., 2014; Masi et al., 2015). Within the littoral forest of southeastern Madagascar, a habitat characterized by sandy, nutrient-deficient soils (Bollen & Donati, 2005), lemurs experience elevated pressure to conserve energy during periods of food scarcity (Donati et al., 2011; Lahann & Dausmann, 2010).

Southern bamboo lemurs live in small female-dominant groups consisting of one or two breeding females and one breeding male with their offspring (Eppley et al., 2015). They are among the few known primates that use latrine sites as a multimodal means of intergroup communication within their home range (Eppley, Ganzhorn et al., 2016). Eppley, Ganzhorn et al. (2016) concluded that overmarking at latrine sites in the southern bamboo lemur may act as a form of mate guarding, and consistent with the EFH, latrines are a low-energy behavioural response that minimizes intergroup agonism. Further emphasising the importance of latrines, within this population they are often associated with stilt-rooted *Uapaca* spp., a preferred tree species that fruits multiple times a year (Eppley, Ganzhorn et al., 2016). Considering this bamboo lemur population lives in a bamboo-devoid habitat, their high degree of frugivory and latrine use provide a unique model to understand the link between dietary and social components (e.g. within- and between-group interactions) facilitating the movement ecology of a folivorous strepsirrhine.

Here, we examine the ability of bamboo lemurs to combine navigational strategies under varying food availability conditions (Appendix, Table A1). We predicted that, during periods of fruit scarcity, bamboo lemurs would increase their reliance on habitual routes and nodes to minimize energy expenditure and that travelling linearity would be low. On the other hand, during periods of fruit abundance, we predicted that bamboo lemurs would increase their travelling linearity by using Euclidean navigation to reach energy-rich food resources. Lastly, we predicted that bamboo lemurs would increase their linearity towards latrines during the period of resource scarcity despite travelling through habitual routes. By optimizing trajectories towards latrines, bamboo lemurs might benefit from advertising their presence in the area frequently and continuously during the mating season, thereby preventing neighbouring males from entering their territory.

<H1>METHODS

<H2>Data Collection

We collected data on southern bamboo lemurs in the Mandena Conservation Zone (24°57’S, 47°0’E; Fig. 1), a degraded and fragmented littoral habitat matrix in southeast Madagascar, approximately 10 km north of Fort-Dauphin (Eppley, Donati et al., 2015). This area consists of three different habitats, specifically: (1) littoral forest, i.e. wet coastal forest on a sandy substrate; (2) littoral swamp, i.e. seasonally inundated freshwater flood plain consisting of natural littoral forest swamp and mahampy (*Lepironia mucronata*) wetland; (3) freshwater *Melaleuca* swamp, i.e. a monodominant habitat of broad-leaved paperbark tree, *Melaleuca quinquenervia*, an invasive species native to Australasia (Eppley, Balestri et al., 2016; Eppley, Donati et al., 2015). Annual rainfall was asymmetrically distributed between a rainy season (November–April, hereafter ‘summer’; mean ± SE monthly rainfall: 311.66 ± 102.63 mm) and a drier season (May–October, hereafter ‘winter’; mean ± SE monthly rainfall: 156.29 ± 37.89 mm). The mean ± SE monthly temperature was 24.88 ± 0.42 ºC and 21.21 ± 0.61 ºC for summer and winter, respectively (Eppley, Donati et al., 2015).

To expedite the habituation process as well as ensure our ability to locate individuals quickly each morning, we captured and collared 10 adult *H. meridionalis* from four social groups between October and December 2012. As this was part of a larger behavioural ecology study, see Eppley et al. (2015) for specific details on the capture procedure.

We established phenological transects across littoral forest and swamp habitats to quantify variations in food availability. We selected the first five to six mature individual trees (i.e. with a diameter at breast height greater than 10 cm) of plant species (N=100) known to be consumed by bamboo lemurs encountered along these transects. We recorded presence/absence of fruits on phenology transect trees (*N*=517) twice per month, with food availability scored as the mean average of fruit present per month.

We conducted full-day focal follows (sunrise to sunset) from January through December 2013, on three habituated groups of bamboo lemurs (group size: Group 1 = 3–5 adults; Group 2 = 3–4 adults; Group 4 = 8–9 adults; (Eppley et al., 2015). Since we collected behavioural observations on 4–5 consecutive days per month in each of the study groups, we accumulated ca. 50 h of observations per month for each of the three focal groups.

We collected the geographical location of each focal individual at 15 min intervals using a GPS Garmin 62S. We estimated the error range of the GPS between 2 m and 3 m due to the degraded habitats of Mandena forest, taking ≤ 30 s to register an accurate waypoint. Since bamboo lemurs tend to travel in cohesive social units, we defined a travel bout as the spatial trajectory from the moment that at least two members of the group started travelling until they engaged in an activity other than travelling for at least 5 min.

We collected instantaneous behavioural focal samples at 5 min intervals (e.g. resting, feeding, moving, social), while also recording the habitat type (e.g. forest, *Melaleuca* swamp, swamp). We characterized habitats by sampling 25 × 100 m^2 botanical plots, 10 plots in littoral forest and littoral swamp and five plots in *Melaleuca* swamp. We recorded the scientific binomial name for all trees with a diameter at breast height ≥5 cm (Eppley et al., 2015). In addition, we collected continuous data on all feeding by the focal individual, specifying the plant species consumed, the specific food item(s) and the duration (to the second) of consumption. We defined a preferred feeding/resting tree as a tree in which the focal individual spent ≥ 15 min of continuous feeding or ≥ 15 min of inactivity, respectively. Similarly, we defined a preferred grazing site (i.e. graminoid) as a 10 m^2 terrestrial patch in which the focal individual spent ≥ 15 min of continuous feeding.

We collected samples for all food items consumed by the bamboo lemurs (i.e. grasses, piths, young leaves, mature leaves, stems, flowers/inflorescence, ripe fruits, unripe fruits, fungi and soil) directly from feeding trees and grazing sites. For details of the biochemical analysis of nutritional samples, see Eppley, Donati et al. (2016).

<H2>*Animal Welfare Note*

Research was conducted in accordance with the ASAB/ABS Guidelines for the use of animals in research. This study was carried out under the Accord de Collaboration among the University of Antananarivo and the Universität Hamburg. Research protocols were approved and permits authorized by Commission Tripartite of the Direction des Eaux et Forêts de Madagascar (Autorisation de recherche N 240/12/MEF/SG/DGF/DCB.SAP/SCB du 17/09/2012), adhering to the legal requirements of Madagascar.

<H2>*Data Analyses*

We loaded bamboo lemur ranging data into ArcGIS 10.2 using the Geospatial Modelling Environment spatial ecology interface. We used the R package 'adehabitatHR 0.4' (Calenge, 2015) to estimate the home range of the study groups as kernel density estimators (KDEs). For this, we settled on a threshold of 95% KDE isopleth for home ranges and 50% KDE isopleth for core areas (Calenge, 2015).

We generated the route network for each of the focal groups using Quantum Geographical Information System (QGIS) v.3.12.1. First, we overlaid all daily travel paths recorded during the same month per group and checked their concordance. Whenever a daily path fell within a 10 m buffer of another daily path of the same month for at least 20 m without deviating more than 45° from the other path, we considered it as the same travel segment (de Guinea et al., 2019; Porter, 2021). We constructed 'monthly paths', including only the unique daily paths of each sampled month to avoid a bias towards reused route segments due to short revisiting intervals. We overlaid each group's monthly paths and repeated the procedure to determine a suitable threshold for segment length (habitual route used in 2, 3, 4 and 5 months). To select a specific travel length threshold for our analyses, we generated route networks considering 20 m, 40 m, 60 m, 80 m and 100 m as minimum overlapping travelled length and produced an accumulation graph of the total distance travelled throughout the year for each group (Di Fiore & Suarez, 2007; Appendix, Fig. A1). Lastly, we calculated the proportion of daily distance travelled within a route network by dividing each daily path length by the distance travelled within a 10 m buffer of the route network (de Guinea et al., 2021b). We considered all travel paths that fell outside the route network described for each group as novel paths. To increase the power of our analyses, we only considered the habitual route segments that were used in ≥4 months as part of the route network (de Guinea et al., 2019; Presotto & Izar, 2010).

To detect the location of nodes, we first conducted the change point test (CPT) developed by Byrne et al. (2009). The CPT assesses the collinearity (i.e. alignment) between a predetermined number (q) of vectors before and after the location of each waypoint along a path (Noser & Byrne, 2014). If the sum of the length of the vectors is significantly longer than the length of the vector between the starting and ending locations, a significant change point (CP) is detected and the CPT starts again with the next waypoint (Byrne, 2009; Noser & Byrne, 2014). Since the CPT is sensitive to the selected number of vectors (q), we followed Byrne et al.'s (2009) indications 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). To account for any inaccuracies in GPS locations and any bias when creating the route networks, we determined, post hoc, whether CPs fell outside or within the intersection between at least two habitual route segments by generating a 20 m buffer around such intersections (de Guinea et al., 2019; Presotto et al., 2018). We considered all locations where CPs concurred with intersections as nodes (Presotto et al., 2018). Finally, we determined the characteristics of each area where CPs occurred: (1) we calculated the Euclidean distance between each CP and forest edge using the 'nearest neighbour analysis' function in QGIS; (2) we determined the number of fruit trees, graminoid sites (i.e. grazing areas), latrine sites and resting sites within a 20 m buffer from the centre of each CP (Appendix, Fig. A2).

We calculated the linearity of each travel bout by dividing the straight-line distance between the departure and arrival locations by the actual distance travelled, which was estimated as the sum of the distances between consecutive GPS points (Jang et al., 2019). We selected travel bouts with a straight-line distance larger than 40 m to minimize the potential influence of sensory cues in the travelling decisions of bamboo lemurs (Porter & Garber, 2013; Presotto et al., 2018; Presotto & Izar, 2010).

We estimated resource availability by calculating the monthly proportion of fruit available across the phenological transects. Similar to previous studies (Campera et al., 2014), Mandena resource abundance corresponded to October–March (i.e. approximately the austral summer), whereas resource scarcity corresponded to April–September (i.e. approximately the austral winter).

Finally, we estimated the dietary quality of each food item consumed by bamboo lemurs by weighting the daily proportional consumption of dry matter for each nutritional component, with the proportion of daily feeding records for each food item as the weighted coefficient following the equation in Kurland and Gaulin (1987). We calculated crude protein values following the Kjeldahl method (Ortmann et al., 2006). Lastly, we calculated metabolizable energy using standard conversion factors (6.25) for lipids, soluble protein, carbohydrates and the fraction of neutral detergent fibre digested by bamboo lemurs as assessed by Campbell et al. (2004) and Conklin-Brittain et al. (2006) and previously described by Eppley, Donati et al. (2016).

<H2>*Statistical Analyses*

To test our hypotheses, we designed four linear mixed models (Baayen et al., 2008) using R (v.4.0.1; R Core Team, 2020). First, we designed a linear mixed model with a Gaussian error structure and identity link function (McCullagh & Nelder, 1989) to test whether bamboo lemurs varied in their use of habitual routes across an annual cycle (‘route use model’). Our response variable was the proportional distance travelled within bamboo lemurs’ route network for each travel bout. As predictor variables, we included the estimated fruit availability and a seasonal term representing a single annual cycle using both sine and cosine of Julian date (divided by 365.25 and then multiplied by 2π) at which travel bouts were recorded (Stolwijk et al., 1999). By incorporating the sine and cosine predictor terms in the model, which represent a standardized circular oscillation of the response variable through time (Stolwijk et al., 1999), we tested whether the response variable showed significant peaks and valleys or followed a uniform distribution across the study period (i.e. a given response variable is expected to follow a single annual cycle with regular periodicity; see Wessling et al., 2018). As random effects, we included group identity (ID) and frequency of use of habitual route segments to avoid issues related with pseudoreplication. Second, we designed a generalized linear mixed model with a binomial error structure and a logit link function to test the probability of detecting a CP at nodes across an annual cycle ('nodes model'). We selected occurrence (yes/no) of CPs at nodes ($N_{CPs} = 286$) as a response variable. As predictor variables, we selected both sine and cosine of Julian date, fruit availability and proximity to fruit trees (i.e. number of fruit trees located within a 20 m buffer from each CP). Since we hypothesized that nodes could be used more often during periods of food scarcity but only if fruit trees were present, we included an interaction between sine and cosine of Julian date and number of fruit trees at CPs. In addition, we included habitat type and distance to forest edge as control predictors in the model. As random effects, we selected group ID and focal subject ID. We ran both models ('route-use model' and 'nodes model') using the package 'lme4' v.1.1-23 (Fox & Weisberg, 2011) and the functions 'lmer' and 'glmer', respectively. All predictors were included as random slopes in both models because all predictors varied among groups and subjects.

To examine the effect of different predictors in the linearity of bamboo lemurs' travel bouts, we fitted two generalized linear mixed models with a beta error structure and a logit link function (Bolker et al., 2009; Ferrari & Cribari-Neto, 2004) using the package 'glmmTMB' v.1.0.2.1 (Magnusson et al., 2020). In both models ('linearity model 1', $N = 1302$ travel bouts; and 'linearity model 2', $N = 259$ travel bouts), we selected as response variable the linearity of each recorded travel bout (see Data Analyses section). As predictor variables in linearity model 1, we selected seasonality (winter versus summer) and behaviour upon arrival (i.e. foraging on fruits, foraging on graminoids, resting and latrine). In addition, we included an interaction between seasonality and behaviour upon arrival. For linearity model 2, we selected as predictor variables seasonality (winter versus summer), metabolizable energy and crude protein content of the food item. We included two interactions: (1) seasonality and metabolized energy; (2) seasonality and crude protein content. For both models, we included habitat type (forest, *Melaleuca* swamp, swamp), proportion of travel within the route network, group size during travelling and straight-line distance as control variables. Similarly, for both models we selected group ID and month as random effects (Barr et al., 2013; Jang et al., 2019).

For all models, we compared the full model, which included all predictor variables, to the corresponding null model, which included only control predictors and random effects, using likelihood ratio tests ('anova' function set to 'Chisq'). If the comparison between full and null model was significant, we estimated the effect of each individual predictor variable and interaction by running the 'drop1' function in the full model. Subsequently, we ran the 'drop1' function in a reduced model with the same structure as the full model but excluding interactions (Barr et al., 2013). We facilitated model convergence and estimated comparability by *z* transforming all continuous variables with the exception of sine and cosine of Julian date. Similarly, all categorical variables were dummy coded to facilitate estimate comparability. We ensured that residuals were normally and homogeneously distributed by visually inspecting *q–q* plots and residuals fitted against fitted values for each model. We determined that all four models were sufficiently stable after excluding levels of the random effects one at a time and comparing the estimates derived from these data sets with those derived for the full data set. Finally, we calculated the variance inflation factors (VIF) using the package 'car' v.3.0-10 (Fox & Weisberg, 2011) for all models and concluded that there were no multicollinearity issues for any of the models because all VIF values were lower than three.

<H1>RESULTS

Over the study period, we collected a total of 1762 h of behavioural observations (mean ± SD = 58.3 ± 2.35 days per group) and 1355 travel bouts (mean 451.7 ± 46.48 travel bouts per group).

Bamboo lemurs travelled a median ± SD of 1.03 ± 0.4 km per day and an absolute distance of 57.25 km per group during the study period (quartiles: 53.84–57.71 km per group), of which a median of 39.93 km (quartiles: 32.48–41.15 km; median: 0.68%, quartiles: 0.60–0.71% of the total distance) were travelled within habitual route networks. Bamboo lemurs travelled a mean ± SD distance of 0.78 ± 0.32 km and 1.23 ± 0.76 km per day outside of their route network during periods of food scarcity and food abundance, respectively (mean ± SD proportion of travel outside habitual route networks: during food scarcity periods: 69.11 ± 16.36%; during food abundance periods: 76.17± 12.46%). We detected a total of 286 CPs, of which 119 concurred with intersections (i.e. nodes) and 167 fell along habitual routes or outside the route network (Fig. 2). We detected a total of 1373 goal sites comprising 561 feeding sites, 410 rest sites and 402 latrine sites.

Within habitual route networks, we found that the proportion of distance travelled by bamboo lemurs differed significantly between seasons (overlap model, likelihood ratio test: $\chi^2_3 = 9.229$, $P = 0.026$; Fig. 3). While both sine and cosine of Julian date were statistically significant (estimate ± SE: sine: -0.087 ± 0.033, $P = 0.023$; cosine: -0.162 ± 0.082, $P = 0.043$), fruit availability did not have a significant effect on the proportion of distance travelled within habitual route networks (estimate ± SE = 0.832 ± 0.849, $P = 0.980$). Conversely, we did not find a statistically significant effect in the use of nodes to navigate as a function of either the magnitude of seasonal variation, the number of fruit trees in their proximity or fruit availability in the study site (nodes model, likelihood ratio test: $\chi^2_6 = 6.022$, $P = 0.421$; Fig. 3).

The median length of a travel bout was 63.35 m (quartiles: 24.52–120.28 m) with a median straight-line distance of 46.36 m (quartiles: 19.74–81.26 m), which resulted in median linearity of 0.91 (quartiles: 0.68–1). The comparison between the full and null model examining differences in bamboo lemurs' travel bout linearity revealed clear differences (linearity model 1, likelihood ratio test: $\chi^2_9 = 10.009$, $P = 0.018$). We found that bamboo lemurs increased their travel linearity when approaching latrine sites but only during the resource scarce winter months (estimate ± SE = -0.042 ± 0.019, $P = 0.022$; Table 1, Fig. 4). Finally, we found statistically significant differences in the linearity of bouts aimed to reach feeding sites (linearity model 2, likelihood ratio test: $\chi^2_5 = 11.863$, P

= 0.037). While linearity increased when bamboo lemurs travelled to feed on more energetically valuable foods, the increment in linearity was higher when travelling to feed on relatively higher-quality food items during resource abundant summer months (Table 1, Fig. 5).

<H1>DISCUSSION

Our findings indicate that southern bamboo lemurs in Mandena combined navigational strategies within an annual cycle by relying primarily on habitual routes during periods of fruit scarcity and Euclidean navigation during periods of fruit abundance. As we predicted, bamboo lemurs' tendency to travel off-route during months of fruit abundance coincides with a tendency to travel more linearly towards energetically valuable food resources. During periods of fruit scarcity, on-route navigation increased, suggesting that the use of habitual routes may be a mechanism to facilitate foraging access at the expense of travelling linearity towards feeding sites. Although linearity may reduce the distance travelled compared to route navigation, the energetic cost of travelling across habitual routes that have already been cleared up by the frequent past travel of the group may decrease the cost of locomotion (Di Fiore & Suarez, 2007). However, bamboo lemurs were still able to increase the linearity of their travel bouts during periods of food scarcity to reach latrine sites. Lastly, we found that bamboo lemurs consistently relied on nodes throughout the study period, suggesting that nodes may be used as reference points in both navigation strategies.

The bamboo lemurs' tendency to overlap travelling paths onto habitual routes adds to an increasing body of literature highlighting that route networks are widespread across animal taxa (Trapanese et al., 2019; Wiener et al., 2011). Route navigation is commonly associated with constrained spatial skills (Garber, 2000; Poucet, 1993); however, we show that despite possessing Euclidean skills, bamboo lemurs chose to travel through habitual routes possibly to compensate for the seasonal decrease in energy-rich food resources. Therefore, bamboo lemurs likely increased their tendency to navigate through already cleared habitual routes during months of food scarcity driven by an energy-saving strategy in line with the expectations of the EFH (Wright, 1999). A similar pattern has been shown in black capuchin monkeys, *Sapajus nigritus*, inhabiting the Atlantic Forest, which increasingly travelled along habitual routes when they could not find high-quality food resources but used novel paths to reach fruit trees when they became available (Presotto & Izar, 2010). In addition, bamboo lemurs reduced their average ± SD travel bout length from 155.37 ± 112.62 m during months of food abundance to 91.81 ± 89.12 m during months of food scarcity. The clumped distribution of graminoids, which become the primary food item consumed by bamboo lemurs during food scarcity periods throughout the Mandena littoral habitats, likely supported this reduction in daily path length during months of food scarcity (Eppley, Balestri et al., 2016; Eppley, Donati et al., 2016).

While bamboo lemurs clearly rely on habitual routes to navigate during periods of food scarcity, the reduction of on-route navigation during periods of food abundance could potentially be explained by an increase in random movement. However, our data indicate that bamboo lemurs increased the linearity of their travelling trajectories when travelling off-route – during periods of food abundance – to feed on energetically valuable food sources, suggesting purposeful, rather than random, travelling behaviour. Such a pattern has only been shown before in chimpanzees and humans, which increase their travel linearly off-route to reach energetically valuable food resources when foraging across rainforests (Jang et al., 2019). Species that do not rely on routes to navigate have also shown the ability to travel in a relatively straight line between distant or out-of-sight food resources, balancing travel distance and prioritizing high-reward sites (e.g. buff-tailed bumblebees, *Bombus terrestris*: Lihoreau et al., 2011; Egyptian fruit bats, *Rousettus aegyptiacus*: Toledo et al., 2020; grey mouse lemur: Lührs et al., 2009). Similarly, bamboo lemurs did not appear limited to engage in random movement patterns or rely on habitual routes to navigate since they were able to compute novel, straight paths to approach high-quality food sources when needed. It has been argued that spatial memory is most advantageous in habitats featuring moderate levels of spatiotemporal complexity, in contrast to highly homogenous or highly heterogenous landscapes, which have either too few or too many conspicuous features, respectively, for efficient navigation (Fagan et al., 2013; Mann et al., 2014). Bracis et al. (2015) demonstrated that the incorporation of memory in simulated movement agents outperformed random walk agents only in landscapes with an intermediate distribution of food resources, while no differences were found in landscapes with a homogeneous distribution of resources. In Mandena, graminoids are clumped but also homogenously distributed in space and are continuously productive across annual cycles, suggesting that bamboo lemurs may be able to forage on them during fruit scarcity periods by relying on a less cognitively demanding navigational strategy such as route-based maps (see also Morrison et al., 2021). Conversely, during periods of fruit abundance, the distribution of food resources increases in complexity, favouring the use of Euclidean skills to forage and navigate. Thus, in addition to the energy-saving properties of habitual route navigation, bamboo lemurs likely benefit from reducing the cognitive load involved in movement decisions during periods of food scarcity by relying on habitual routes instead of Euclidean navigation.

Confirming our predictions, we found that bamboo lemurs increased their travelling linearity when approaching latrine sites during periods of food scarcity despite relying on habitual routes (mean ± SD number of latrine sites: food abundant season: 98.67 ± 35.12 per group; food scarcity season: 169.63 ± 9.24 per group). Even though habitual routes have been argued to condition the linearity of the travel paths performed by the user (Jang et al., 2019), bamboo lemurs were still able to optimize their trajectories to reach latrine sites. Although a previous analysis of the function of latrines does not appear to be related to sexual advertisement or territoriality in bamboo lemurs, latrine use supports the EFH (Eppley, Ganzhorn et al., 2016). More specifically, this latrine behaviour plays a functional communication role aimed at minimizing the energetic costs associated with intergroup agonistic interactions, a strategy suggested to be in response to the relatively low productivity and quality of forest resources in Madagascar (Donati et al., 2017; Wright, 1999). By approaching latrine sites in a highly linear manner, bamboo lemurs show the skills to remember not only the location of high-quality food resources (latrine sites were disproportionately located at *Uapaca* spp. trees, which produce a preferred fruit), but also locations involved in intergroup scent-marking and social interactions as observed in black howler monkeys, *Alouatta pigra* (de Guinea et al., 2021a), common marmosets, *Callithrix jacchus* (Abreu et al., 2021) and North American river otters, *Lutra canadensis* (Karnes & Tumlison, 1984).

Despite our findings supporting the use of differing navigational strategies across seasons, bamboo lemurs consistently revisited nodes throughout the entire annual cycle. The use of nodes as cognitive anchors to ease the process of directional decision making is traditionally associated with route-based cognitive maps (de Raad & Hill, 2019; Garber, 2000). However, our results indicate that bamboo lemurs benefit from using nodes during Euclidean navigation as well, which may be extended to other species (Porter et al., 2021; Presotto et al., 2019). Previous research has highlighted that nodes are frequently located at emergent trees and mountain ridges where animals enhance their visibility over the landscape (Pereira, 2008; Presotto et al., 2018). While Mandena is characterized by a flat terrain where visibility is relatively constant across the forest, nodes were frequently associated with fruit trees and latrines, suggesting that additional information might have been perceived primarily via olfactory rather than visual cues (Cunningham et al., 2021). Lemurs can track odour plumes associated with fruits in forests up to an estimated distance of 17 m (Cunningham et al., 2021), which suggests that a potential bias in our linearity results due to olfaction is seemingly unlikely because we selected travel bouts longer than 40 m. However, olfactory cues may have contributed to lemur navigational flexibility by mapping odorants across the landscape, which may be continuously updated by revisiting nodes where social (e.g. location of intraspecific groups; Eppley, Ganzhorn et al., 2016; Jordan et al., 2007) and ecological (e.g. fruit availability; Ban et al., 2014; de Guinea et al., 2021a) information is obtained (Jacobs, 2012). It is possible that such an ability to process fine-scale olfactory information runs in parallel to an internal cognitive map to support flexible navigation patterns and optimal movement decisions in bamboo lemurs (Jacobs, 2012; Wu et al., 2020).

Overall, our results suggest a trade-off between adaptations to conserve energy and the necessity to maximize the intake of nutrients and metabolizable energy during windows of food abundance. In fact, lemurs can maximize the possibility for their offspring to survive by improving food intake during the period of food abundance, prior to the upcoming lean season, when they need to conserve energy (Donati et al., 2011; Ganzhorn, 2002; Irwin et al., 2014; Simmen & Rasamimanana, 2018). The wet season in Madagascar matches with the key times of lactation and weaning for most lemur species, which tend to be highly synchronized with their reproductive phases (Wright, 1999). In line with this, it has been shown that survival of offspring depends on body conditions of females prior to the upcoming lean season (e.g. ringtailed lemur: Gould et al., 1999; red-tailed sportive lemur, *Lepilemur ruficaudatus*: Ganzhorn, 2002; *Eulemur* sp.: Ganzhorn, 2002; Simmen et al., 2010). Therefore, bamboo lemurs' combination of both Euclidean and route-based navigational strategies demonstrates a cognitive adaptation for coping with marked seasonal resource variability in a way that challenges previous research postulating constrained spatial skills in folivorous strepsirrhines.

Data Accessibility

All data and code supporting this article are available on Dryad: https://datadryad.org/stash/share/V90A50mvoxiHP6SaZ3ETSOdNu0ntzP3InznZZX8nk9Q

Author Contributions

T.M.E. designed the data collection protocols and collected all behavioural ecology data and nutritional samples. Data analysis was performed by B.W., M.d.G. and S.P. The manuscript was written by B.W. and M.d.G. and revised by T.M.E., S.P., J.U.G. and G.D.

Declaration of Interest

None.

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Appendix

Table A1

Summary of the predictions exploring the combination of navigation strategies in bamboo lemurs in response to changes in resource availability

Resource availability	Reliance on routes to navigate	Reliance on nodes to navigate	Increase linearity to approach food resources	Overall navigation strategy
High	–	–	+	Flexible, Euclidean navigation
Low	+	+	-	Route navigation

Table 1

Results of the linear-mixed models testing for differences in linearity among southern bamboo lemur travel bouts

Effect	Estimate	SE	$\mathrm{CI}_{\mathrm{lower}}$	$\mathrm{CI}_{\mathrm{upper}}$	χ^2	*df*	*P*
Linearity model 1							
(Intercept)	1.274	0.176	0.955	1.595			*
Seasonality (winter vs summer)[1]	0.071	0.073	-0.075	0.218	0.895	1	0.344
Behaviour upon arrival (latrine)	**0.175**	**0.091**	**-0.005**	**0.351**	**8.116**	**3**	**0.044**
Behaviour upon arrival (rest)	0.249	0.091	-0.068	0.415			*
Behaviour upon arrival (ripe fruit)	0.243	0.114	-0.021	0.444			*
Habitat type (*Melaleuca* swamp)	0.133	0.096	-0.067	0.320	4.189	2	0.123
Habitat type (swamp)	-0.113	0.107	-0.348	0.097			*
Straight line[2]	-0.301	0.088	-0.423	-0.119	5.049	1	0.025
Group size	-0.048	0.017	-0.082	-0.011	5.146	1	0.023
Proportion of travel within network[3]	0.017	0.032	-0.061	0.077	0.310	1	0.578
Seasonality: Behaviour upon arrival (latrine)	**-0.044**	**0.190**	**-0.814**	**-0.072**	**9.562**	**3**	**0.023**
Seasonality: Behaviour upon arrival (rest)	-0.015	0.185	-0.041	0.318			*
Seasonality: Behaviour upon arrival (ripe fruit)	0.027	0.227	-0.440	0.450			*
Linearity model 2							
(Intercept)	1.455	0.257	0.889	1.859			*
Seasonality (winter vs summer)[1]	0.241	0.138	-0.031	0.517	2.666	1	0.102
Metabolized energy (kcal/g)[4]	**0.178**	**0.074**	**0.036**	**0.325**	**4.892**	**1**	**0.027**
Crude protein [5]	-0.096	0.135	-0.352	0.147	0.467	1	0.494
Straight line [2]	-0.143	0.131	-0.442	0.109	1.008	1	0.311
Proportion of travel within network[3]	0.193	0.076	0.037	0.353	3.844	1	0.049
Seasonality: Metabolized energy (kcal/g)	**0.257**	**0.138**	**-0.016**	**0.538**	**3.425**	**1**	**0.064**
Seasonality: Crude protein	0.119	0.136	-0.135	0.385	0.747	1	0.387

Statistically significant predictor variable results appear in bold. CI: confidence interval.

*Not shown due to having a limited interpretation.

[1] Seasonality divides annual cycles into a winter period (food scarcity) and a summer period (food abundance).

[2, 3, 4] *Z*-transformed; mean ± SD of the original values: [2]81.26 ± 69.01, [3]0.63 ± 0.53, [4]185.84 ± 17.57.

[5] Log- and then *z*-transformed; mean ± SD of log-transformed value: 8.05 ± 3.86.

[6, 7] Behaviour upon arrival and habitat type were dummy coded with the reference category: [6]Graminoids, [7]Forest.

Figure 1. Location of our study site (Mandena) in Madagascar and home ranges (95% kernel density estimators (KDEs)) of the study groups.

Figure 2. Habitual route networks of the three study groups together with change points and nodes. Daily travel paths for summer (red) and winter months (blue) are shown to right of each group's route network.

Figure 3. Proportion of daily path length travelled within habitual route networks (left) and probability of using nodes to redirect travel patterns during navigation across an annual cycle (right). Variability in fruit abundance is shown as a colour gradient for each recorded daily path (left) and each significant directional change (right).

Figure 4. Differences in the linearity of trajectories (log-transformed) as function of the behaviour in which bamboo lemurs engaged upon arrival (i.e. foraging on graminoids, visiting latrines, resting and foraging on fruits) separated between austral summer (blue; resource abundance season between October and March) and austral winter (red; resource scarcity season between April and September).

Figure 5. Differences in the linearity of trajectories as subject to the nutritional value of the feeding site where bamboo lemurs fed upon arrival: (a) feeding site metabolized energy; (b) feeding site crude protein content. The dashed lines represent the fitted model (with all other predictors being centred), dots represent the averaged linearity, and their area corresponds to the number of travel bouts in the respective bin ($N = 1–25$ per bin). Shaded areas represent 95% confidence intervals of the fitted model.

Figure A1. Comparison of interpath overlap within groups of bamboo lemurs across the year. Comparing segments that overlap in (a) at least 2 months, (b) at least 3 months, (c) at least 4 months and (d) at least 5 months for an accumulative distance that occurred within the route network for 20 m (red), 40 m (orange), 60 m (green), 80 m (blue) and 100 m (black).

Figure A2. Location of goals for each group with route network and tracking data: location of latrine and rest sites (top); location of fruit and graminoid sites (bottom).