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Gibbon travel paths are goal oriented

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Abstract Remembering locations of food resources is critical for animal survival. Gibbons are territorial primates which regularly travel through small and stable home ranges in search of preferred, limited and patchily distributed resources (primarily ripe fruit). They are predicted to profit from an ability to memorize the spatial characteristics of their home range and may increase their foraging efficiency by using a 'cognitive map' either with Euclidean or with topological properties. We collected ranging and feeding data from 11 gibbon groups (*Hylobates lar*) to test their navigation skills and to better understand gibbons' 'spatial intelligence'. We calculated the locations at which significant travel direction changes occurred using the change-point direction test and found that these locations primarily coincided with preferred fruit sources. Within the limits of biologically realistic visibility distances observed, gibbon travel paths were more efficient in detecting known preferred food sources than a heuristic travel model based on straight travel paths in random directions. Because consecutive travel change-points were far from the gibbons' sight, planned movement between preferred food sources was the most parsimonious explanation for the observed travel patterns. Gibbon travel appears to connect preferred food sources as expected under the assumption of a good mental representation of the most relevant sources in a large-scale space.

Keywords Travel change-point · Cognitive map · Spatial memory · Gibbons · *Hylobates lar*

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Introduction

Animals can solve the critical task of navigating and efficiently locating food resources in space using various mechanisms (e.g. Bingman and Jones 1994; Etienne et al. 1998; Held et al. 2005; Menzel et al. 2000; Ponticorvo and Miglino 2010; Shettleworth 1998; Wallraff 2001). In particular, the ability to locate an ephemeral and patchily distributed resource such as ripe fruit in tropical forests (van Schaik et al. 1993) is a serious challenge for frugivorous animals (Hemingway and Bynum 2005; Olupot et al. 1997). For instance, the need for finding fruit in large areas may have been a trigger for the evolution of the relatively large brains and intelligence of simian primates (Clutton-Brock and Harvey 1980; Milton 2000; Potts 2004). An effective mechanism to manage the discovery and memory of the locations of ephemeral resources in large-scale space (i.e., the area that cannot be seen entirely from a single vantage point, *sensu* Byrne 2000) is to monitor food plants' reproductive cycles and to build an internal, spatial representation of the physical environment or 'cognitive map', which connects locations of important resources with each other and with other structural elements of a home range (Tolman 1948).

There is continued debate over the use of two broad categories of cognitive maps: geometrical and topological (Garber 2000). A geometrical map, also known as Euclidean map or metric map, is viewed as a quantitative representation of the environment (Gallistel and Cramer 1996). Euclidean navigation ideally preserves the metric angles and distances between locations and thus provides accurate representation of all geometric relations between all points of the environment. It allows directly assessing distance and direction to a potential destination from virtually any point of the home range. A cognitively simpler alternative to the Euclidean map, a topological map, also called network map or route-based map, allows an animal to use information about the ways in which landmarks and destinations are qualitatively connected in space (Byrne 2000). Topological maps represent the connectivity of the environment in a graph-structured network where vertices (also called nodes or junctions) represent well-deÞned locations such as food trees in the environment (Schkolkopf and Mallot 1995). Each node is connected to others by links in the form of segments that represent the edges or corridors (e.g. arboreal pathways) for traveling between locations. Di Fiore and Suarez (2007) suggested that nodes in a topological map may be points at which animals make decisions about where to travel next. Although there is some evidence to support the possession of a Euclidean map in some species (e.g. Gould 1986; Normand and Boesch 2009), the existence of such mental map has been seriously challenged (Benhamou 1996; Bennett 1996; Byrne 1979, 1982; Poucet 1993; Sturz et al. 2006), and most studies rather support the use of a less demanding topological representation of the environment (e.g. Byrne 2000; Di Fiore and Suarez 2007; Dyer 1991; Erhart and Overdorff 2008; Foo et al. 2005; Gillner and Mallot 1997; MacKinnon 1974; Milton 2000; Noser and Byrne 2007; Wehner 1981).

Linear travel paths to out-of-sight food resources have traditionally been used as evidence that animals had a travel goal in mind at the beginning of a bout of travel and therefore knew where they were heading (Benhamou 2004; Cunningham and Janson 2007; Garber 1989; Janmaat et al. 2006; Janson and Di Bitetti 1997; Normand and Boesch 2009; Noser and Byrne 2007; Valero and Byrne 2007). However, animals may deviate from ideal straight-line routes because of constraints of the landscape, to reduce predation pressure or to exploit a small resource becoming visible and accessible along the way. Furthermore, linear paths to out-of-sight resources would not necessarily imply a travel goal in mind, unless the animals are seen to by-pass detectable, but inferior resources in the route. However, animals might still have a general notion of the productivity of speciÞc resources in their home range and by-pass small relatively unproductive resources until they encounter desirable resources without the use of spatial memory. Under these circumstances, it is difÞcult to objectively identify the travel goal for an animal or a group on a path as well as the points at which they supposedly decided to move to a goal. A possible alternative to the use of travel linearity between food sources as a window into cognitive mechanisms underlying travel paths is a mathematical test that integrates and compares consecutive travel locations (the change-point test [CPT]) as proposed by Byrne et al. (2009). The test calculates retrospectively at which point of a given travel route a signiÞcant change in travel direction occurred. Thus, the CPT method allows assessing (independently of the possible reasons of the change) points at which animals or groups of animals travelled in a new direction (e.g. to a food tree) based on the statistical characteristics of the route they already passed. Byrne et alÕs (2009) method suggests that systematically identifying travel direction points via the CPT method is a Þrst step to understanding how animals navigate their environment, and ultimately, how they represent and store spatial information of their home range in the brain.

White-handed gibbons (*Hylobates lar*) provide excellent models to study mechanisms of primate travel and its underlying cognitive basis, because they are highly specialized on ripe fruit (Elder 2009; Gittins and Raemaekers 1980; Leighton 1987; McConkey 2009; Savini et al. 2008), and their brains reßect their hominoid ancestry in both gross anatomy and volumetric proportions (MacLeod et al. 2003). Thus, they can be expected to having evolved efÞcient spatial skills to economically use their environment. Although the speciÞc cognitive skills of gibbons are largely unknown, it is noteworthy that they are, like all apes, more encephalised than expected from their small body size (Rilling and Insel 1998). In particular, the lateral cerebellum is larger in gibbons than in monkeys (MacLeod et al. 2003), which, among other functions, is activated during planning of movement and in visuo-spatial problem solving (Kim et al. 1994). Moreover, gibbons share with the larger hominoids a clear separation between the superior and inferior parietal lobules and a distinction between the supermarginal and angular gyri (MacLeod 2004). In humans, these neocortex areas are primarily auditory and visuo-spatial association centers (MacLeod 2004), which suggests that the gibbonsÕ spatial skills are more similar to those of great apes than those of monkeys. Gibbon communities are also well known for their mosaic organization of closely interlocking, relatively small territories (Bartlett 2009; Brockelman et al. 1998; Reichard 2003; Savini et al. 2008), which increases their potential to effectively organize travel routes across their entire home range on a daily basis compared to primates whose daily travel can only cover a small fraction of a large home range (e.g. *Ateles* spp., Di Fiore and Campbell 2007). In addition, because gibbons live in small groups compared to most other primate species, decision making is simpler because it is shared between fewer individuals. Therefore, by having small groups gibbons can theoretically change travel directions more quickly without compromising the individual preferences of many group members. As a consequence, gibbons are expected to have evolved efficient strategies for exploiting dispersed food resources. If this assumption is true, gibbons can be expected to forage by traveling directly to food sources that are out of view. In support of such scenario, Brockelman (2009) has argued that visibility in the forest canopy of gibbons' natural environments is too short to allow a gibbon group to find preferred food trees efficiently enough through random search.

We aimed to use the CPT to detect locations at which white-handed gibbon groups at Khao Yai National Park (Thailand) change the direction of travel and to examine whether these points are related to biologically relevant activities (e.g. feeding, duets). Specifically, we tested whether preferred food resources encountered with neighboring groups and the loud duets predictably influenced the gibbons' movements by comparing change-point locations with locations of these important activities for gibbons. Instead of using linearity between biologically relevant locations to arbitrarily decide the start and end of a potential planned trajectory from a hypothetical decision point to its corresponding goal, we used consecutive change-points to objectively identify from which locations gibbons started a path segment and in which location they ended. This portion between two consecutive change-points of a daily travel trajectory was analyzed to test the potential for planned movement in gibbons. If trajectories are planned, change-points should occur significantly more frequently at biologically important locations than at unimportant locations, whereas during random search, change-points would be found aimlessly across the home range and daily path. Janson (1998), however, developed a heuristic travel model that generates straight pathways with random directional changes at high quality resources just based on visual search cues, which does not require planned travel or spatial knowledge. To evaluate the extent to which our results support planned travel rather than a "mindless" travel trajectory of a heuristic model, we tested the observed efficiency of gibbon movement at finding important food sources against travel predicted by a heuristic model based on straight pathways in randomly selected directions from food locations. We assume that gibbons used spatial knowledge to reach a goal they had in mind at the preceding change-point if the following two conditions are met: (1) consecutive change-points were out of sight of each other and significantly corresponded to events that were biologically meaningful for gibbons (e.g. feeding trees) and (2) observed gibbon travel trajectories are more efficient at detecting important resources than the heuristic random travel model predicts. Finally, we aimed to evaluate the extent to which our results support planned travel to points out of view and cognitive mapping in light of the characteristics of Euclidean and topological navigation.

Methodology

Study sites and animals

The study was carried out at Khao Yai National Park (2,169 km^2), situated in central Thailand (101°22′E, 14°26′N), in a seasonally wet, evergreen forest with few, small patches of old secondary growth at an elevations of 730–870 m a.s.l. We followed 11 habituated gibbon groups that are part of a long-term investigation of gibbon socioecology at the Central Mo Singto study site (Barelli et al. 2007; Barelli et al. 2008; Brockelman et al. 1998; Brockelman 2009; Reichard 2009; Reichard and Sommer 1997). Group composition varied from 3 to 6 individuals during the study (Table 1). Figure 1 shows the locations of the 11 study groups' home ranges. The canopy at the study site has an average height of 20 m (range 14–34 m, Brockelman 1998). Brockelman (2009) estimated the visibility at the field site using four tree platforms placed at various heights in the main canopy. With an optical rangefinder, he measured the distance to the farthest branch on which a gibbon might be able to detect fruit through the foliage in eight compass directions. The estimated visibility at the forest main canopy where gibbons usually travel was estimated to average 21 m. We took a conservative approach to reduce data bias due to a possible underestimation of visibility and assumed that under average conditions the gibbons could not identify food sources beyond double the estimated visibility in the forest, or 42 m, from their immediate location.

Data collection

Data were collected from July 2009 to February 2010 when the 11 study groups were followed for a total of 55 days; each group was followed for five consecutive days with an average of 6.5 h per day. The location of the focal group was continuously recorded at 1-min intervals using the track point setting on a hand held global positioning unit (GPS Garmin Etrex Vista HCX) from roughly the center of the group. To estimate the relative precision of the GPS at the study site, we collected location data 180 times on the

Table 1 Age-sex composition of study groups in Khao Yai National Park (July 2009 to February 2010)

Group	Number of individuals	Composition
A	4	3AM, 1AF
B	3	1AH, 1AF, 1I
C	4	1AM, 1AF, 1JM, 1I
H	5	2AM, 1AF, 2JF
M	3	1M, 1AF, 1JM
N	6	3AM, 1AF, 1JF, 1I
NOS	6	3AM, 1AF, 1SAM, 1I
R	4	1AF, 3AM
S	5	2AM, 1AF, 1SAF, 1I
T	6	2AM, 1AF, 1SAF, 1JM, 1I
W	5	2AM, 1AF, 1JM, 1I

M male, *F* female, *SA* subadult, *J* Juvenile, *I* infant

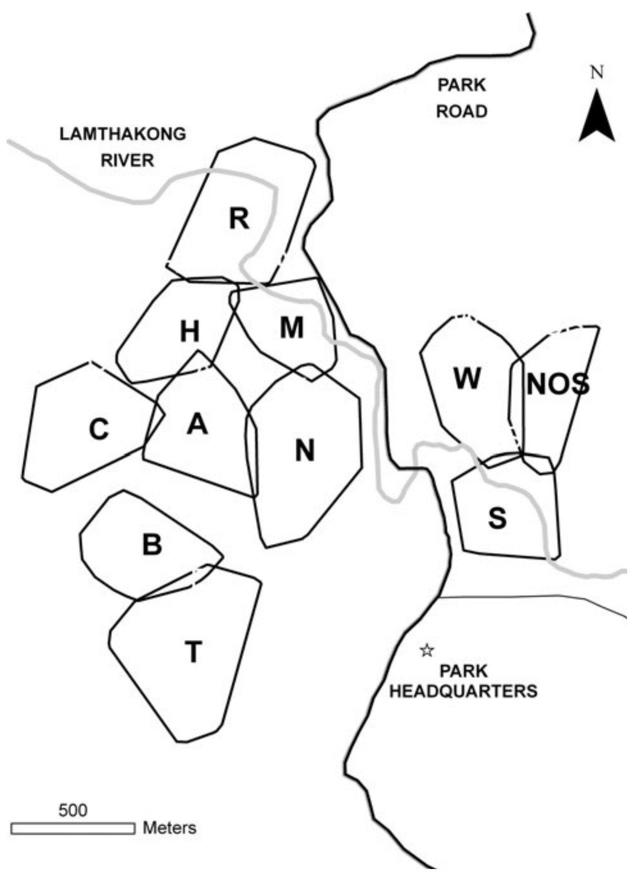

Fig. 1 Location and home range of the 11 study groups at Khao Yai National Park (Thailand). *Created with ArcGIS 9.2*

exact same spot and calculated the average distance based on a distance matrix with all locations ($x = 13.1$ m; SD $\pm$ 7 m; $n =$ 16,111). We collected feeding data on all food plants (trees and woody climbers) and used plant parts (fruit, flower or leaves) in which at least one adult fed for C5 min during a single visit. These sources were then identified at least to the genus level and their position in the home range was georeferenced with a GPS unit. The height of the tree or liana was measured with a laser range finder. We chose a 5-min cut-off period to broadly separate less important from more important food sources in accord with previous research on this population (Bartlett 1999; for *Ateles geoffroyi* see Link and Di Fiore 2006). Although a 5-min period to define "important" seems arbitrary, it was an appropriate compromise in our study between identifying and locating many sources meaningful to the gibbons and not producing an unmanageably large sample of potential travel destinations. Additionally, we classified preferred food sources for each group separately as the individual food plants belonging to species that made up at least 10% of the total feeding time of each gibbon group during the five consecutive day follows. We also georeferenced points of intergroup encounters with neighboring gibbon groups and locations of duets (distinct vocal calls made simultaneously by the male and female in a group) because we expected that such behaviors potentially affected movement decisions.

Once a group's 5-day follow was completed, we calculated the group's 5-day home range outline using the minimum convex polygon (MCP: i.e. the delineation of the area by drawing the lines that connect the outermost points, Fig. 1) to locate all individual trees of preferred food species within this area. We walked the 5-day home range and mapped all individual trees and woody climbers belonging to the preferred food species by using 50-m-wide transects until the entire home range was covered. Mapping all available sources of preferred species was necessary to understand the choices the gibbons had made during the previous 5-day data collection period compared to all individual trees of the preferred sources that had potentially been available to gibbons. This setup allowed us to directly compare realized travel between preferred trees and woody climbers compared to the overall spatial distribution of the preferred species. We also mapped individual sources of preferred species even if they did not bear food if their diameter at breast height (DBH) equaled or was greater than that of preferred species containing food in which the gibbons had been seen feeding, because we assumed that non-food bearing trees of preferred species would represent potential goal targets of high interest to the gibbons to monitor their fruiting status. Similarly, we also mapped all large fig trees (C60 cm DBH) in the 5-day home range with or without fruit, as *Ficus* spp. are known to be key foods of many frugivores (Shanahan et al. 2001) and are also important for Khao Yai gibbons (Savini et al. 2008). Thus, *Ficus* trees were likewise assumed to represent potentially important target locations for feeding or status monitoring of individual trees. Botanical transects for each 5-day home range of a single group were completed in less than four consecutive days directly following our behavioral data collection to ensure that plant monitoring (i.e. phenology of plant species) and behavioral observations were as closely synchronized as possible.

Data management

In order to draw realistic pathways of movements of gibbons, we used consecutive locations separated by a minimum of 20 m. A minimum distance of 20 m was selected for two reasons: (1) to reduce the errors in the representation of gibbon movement caused by the observer movements under the gibbons' locations while recording other behavioral data and (2) to obtain a minimum range distance, because we were interested in gibbons' long-range movements (i.e. movements between trees). Geographical coordinates were collected using the projected coordinate system datum WGS84 and recorded in Universal Transverse Mercator (UTM, Zone 47N) units. To obtain an estimate of route overlap for the 5-day follow of a group, we first considered that travel segments overlapped if they were within B20 m of each other for a distance of C40 m. An index of route overlap was then calculated by dividing the total distance of overlapping trajectories of a gibbon group by the total distance travelled during the 5-day follow period. For instance, if all 5 hypothetical travel routes made by a gibbon group overlapped in a 100-m segment and the total distance travelled during 5 days was 2,000 m, the index of overlap was calculated as 500/2,000, or 0.25 (25% of route overlap).

Travel change-point detection

We applied the change-point test (CPT) created by Byrne et al. (2009) to reliably determine at which points the gibbons significantly changed their travel direction. The CPT examines routes composed of short linear segments (vectors) to detect points at which the direction of these vectors changes significantly, that is, 'change-points' in otherwise more uniform or undirected travel. Accordingly, we applied the CPT to a daily travel path by calculating travel segments starting from the gibbons' last potential goal location of a given day (i.e. a food source, duet site, sleeping tree or intergroup encounter site) until a change-point was discovered. This location then became the starting point for applying the CPT until the previous change-point was found and so on, until no further change-points were detected for a daily path. We initially ran eight variants of the test (q = 1–8) on the 55 gibbon daily pathways (5 routes per group) to detect the most appropriate level of analysis, which meant the point at which the test was most sensitive to detecting change-points with an alpha level of $P < 0.01$. We ran the test 1,450 times and found that the CPT was most sensitive at $q = 6$. Thus, we restricted further analysis to change-points detected in gibbon routes at variant level $q = 6$ (for further details of level detection and detailed description of the CPT see Byrne et al. 2009).

In short, we obtained and analyzed daily "snapshots" of gibbon movement in which we plotted and integrated all visited important resources, potential important resources, intergroup encounter locations, duet locations, and the locations at which travel directions changed significantly (Fig. 2).

Data analysis

We tested if change-points obtained using the CPT were spatially independent events that occurred at locations

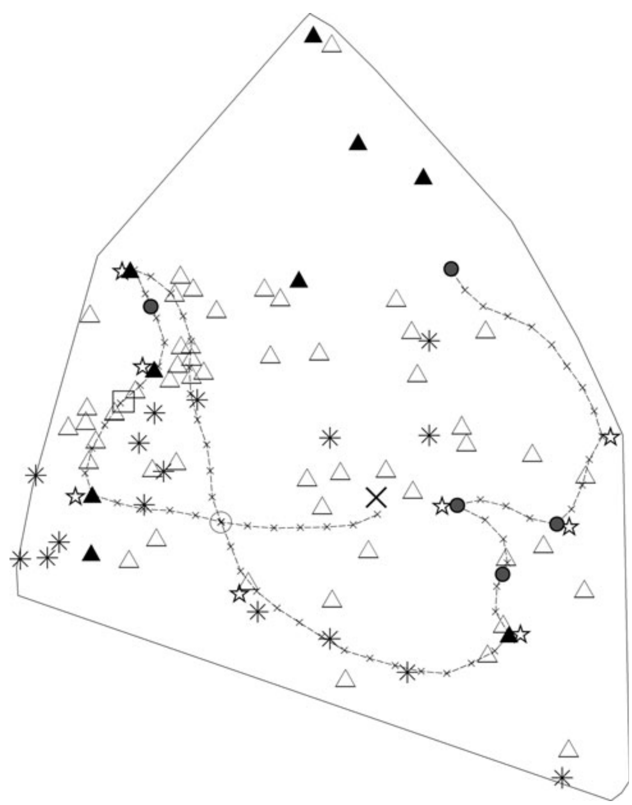

Fig. 2 Home range of *group A* (*outer line*) in which a daily travel path and all available preferred food sources are shown. The "*X*" represents the start of the movement following the *dotted line* and consecutive waypoints (*small "x"*) separated by 20 m. *Solid triangles* indicate food sources belonging to a preferred plant species (10% of the total feeding time) and *empty triangles* individuals of preferred species with no food available within home range. *Solid points* indicate food sources from other eaten species. The *squares* are locations in which an encounter occurred and *circles* represent locations where duets occurred. *Asterisks* indicate the location of fig trees (*Ficus* spp.). *Stars* represent the places in which the travel direction significantly changed according to CPT. *Created with ArcGIS 9.2*

where biologically meaningful activities were observed (i.e. change-points that represented visits to feeding sources, an intergroup encounter with another group, or a location of a duet). For that purpose, we used a Wilcoxon paired test comparing the total number of food trees that were found in the 5-day pathways per group with randomized points along such pathways. This is to say that we tested how likely it would be to find a change-point at a biologically meaningful location compared to finding a change-point along the daily travel path by chance. We used the same statistical test to determine if preferred food sources were more significantly related to change-points than non-preferred food sources by comparing the proportion of preferred food sources that were change-points with the proportion of non-preferred food sources that were at change-points. To examine if the height of trees may affect the occurrence of change-points, because tall trees could be used as vantage points to locate distant resources, we compared the average height of trees and lianas at change-points to the height of those used by gibbons at other locations using a Mann–Whitney *U*-test.

Finally, we developed a heuristic travel model to determine the relative efficiency of finding preferred food sources using a random search method. In this model, a route began from the starting point of a gibbon daily route, from where it continued in a straight line in a random direction using a given detection radius of visibility until it encountered a preferred food source or hit the border of the MCP home range (Fig. 3). A new vector was then calculated in a 360° random direction from the previous location until it again detected a new target. This operation was repeated until the total distance covered in the model exactly equaled the observed gibbon groups' travel distance for that day. For the heuristic travel calculations, we used a conservative approach of six distinct detection radii of visibility range to simulate the entire possible gibbon detection distances: the 21 m (average visibility range estimated by Brockelman 2009), 30 m range, 42 m range (double of the theoretical visibility range for gibbons at the study site), 63 m range, 84 m range, and 105 m range. We calculated an index of search efficiency for each daily route of gibbon groups by subtracting the number of preferred tree or woody plant individuals detected by the heuristic model to the ones detected by gibbons and divided by the total of preferred individuals in that home range. The model efficiency values would range from - 1 to ? 1 with negative efficiency values implying that the random search model is performing better than gibbons at detecting preferred foods, whereas positive values imply that the gibbons are more efficient. A two-way ANOVA was designed to compare the effects of the search model (6 levels of detection radii) and groups on the search efficiency values. The error term was derived from the 5 days (replicates) for each group. Variance homogeneity was examined plotting the error variance against the mean for the group-visibility radii treatments ($n = 66$), because this relationship was not significant (Pearson's $r = 0.0016$; $P = 0.75$), and no statistical transformation was applied to the data.

Results

During the 5-day observation periods, the gibbons based their diet on a wide array of trees and woody plant species, but only two to four species comprised preferred species (C10% of feeding time) for each group (ESM 1). For all 11 gibbon groups, most feeding time (90.5%) was dedicated to fruits, whereas other items such as leaves and flowers were consumed in small proportions. We detected a total of 195 change-points for the travel trajectories of the 11 gibbon groups (Table 2). Most travel change-points (93.8%) were associated with biologically meaningful parameters for gibbons (e.g. feeding), and only for 12 travel change-points (6.2%), we did not detect a biologically meaningful reason why a change in travel direction had occurred. In most cases (153 out of 195 change-points, 78.4%), change-points coincided with food sources of which 126 were preferred food sources and only 27 were 'other' sources. In 26 cases (13.3%), the gibbons changed their travel direction at preferred sources that did not have food (including 4 times at fig trees), but otherwise change-points occurred at

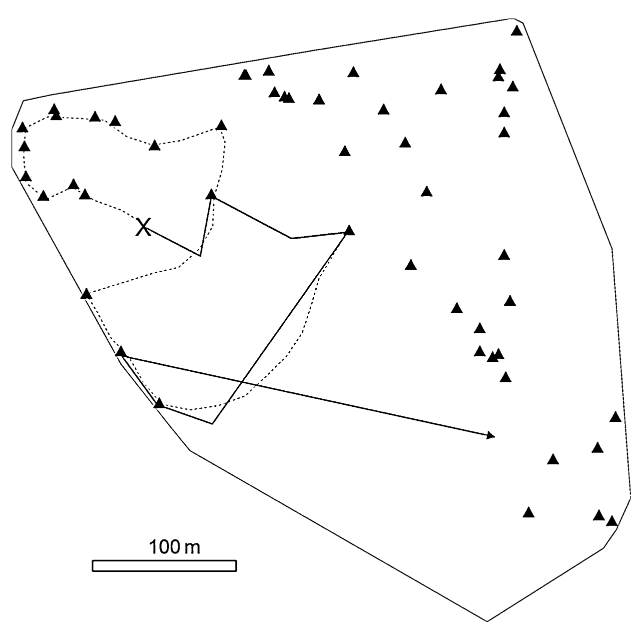

Fig. 3 Example of a heuristic search with a detection radius of 42 m to detect preferred food sources (*solid triangles*) in group M home range. The "*X*" represents the start of the movement of the heuristic search and the *dashed line* the actual path made by gibbons. *Created with ArcGIS 9.2*

Table 2 Change point distribution in study groups

Group	Home range (ha)	Mean distance (m) between consecutive CP (range)	Total distance length (m)	Total observation time (h)	Route overlap (%)	Feeding time				Change-point locations						
						Fruits (%)	Leaves (%)	Flowers (%)	Others (%)	Preferred species	Other plant species	Preferred species with no food	Ficus with no fruit	Encounters	Others	Total
A	17.4	142.8 (75–272)	5,860	36.5	36.7	100.0	0	0	0	13	4	6	0	2	3	28
B	16.1	187.3 (87–336)	4,240	30	36.6	94.7	5.3	0	0	15	3	2	0	0	1	21
C	18.9	146.1 (73–262)	4,520	29	35.1	78.7	21.3	0	0	14	2	1	0	1	1	19
H	14.1	171.7 (86–231)	3,900	32	27.5	87.5	7.8	4.7	0	13	1	0	0	0	0	14
M	12.1	200.3 (120–286)	2,840	31	28.1	94.0	0.8	5.3	0	10	2	0	0	0	0	12
N	25.3	157 (87–277)	4,120	32	17.3	94.5	1.0	2.3	2.3	7	3	2	2	0	2	16
NOS	15.5	163.2 (92–271)	4,040	33	38.0	98.9	1.1	0	0	14	1	2	0	1	2	20
R	23.6	126.2 (82–215)	3,260	32	25.7	88.0	9.0	0	3.0	4	2	1	3	0	0	10
S	13.7	172 (87–314)	3,240	32.5	8.0	95.6	4.4	0	0	9	0	3	0	0	1	13
T	27.8	218.1 (120–386)	5,960	31.5	41.2	72.7	23.4	3.9	0	13	3	4	2	0	2	24
W	18.3	132.2 (78–202)	4,060	32.5	49.3	92.7	7.3	0	0	14	1	1	2	0	0	18

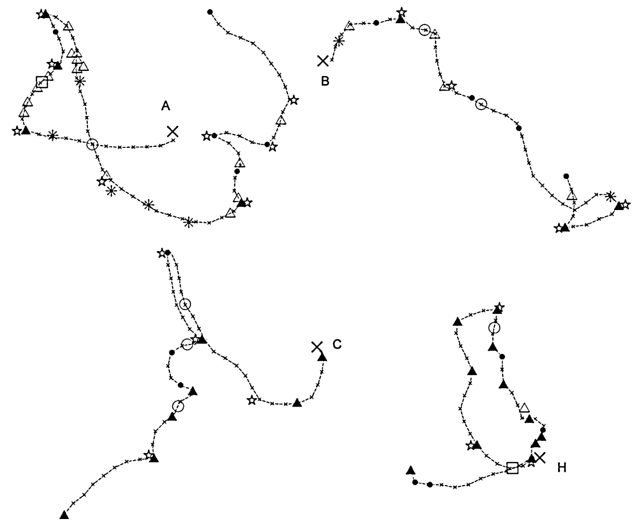

Fig. 4 Examples of daily travel path made by *group A*, *group B*, *group C*, and *group H*. The "*X*" represents the start of the movement following the *dotted line* and consecutive waypoints (*small "x"*) separated by 20 m. *Solid triangles* indicate food sources belonging to a preferred plant species (10% of the total feeding time) and *empty triangles* individuals of preferred species with no food available within home range. *Black points* indicate food sources from other eaten species. *The squares* are locations in which an encounter occurred and *circles* represent locations where duets occurred. *Asterisks* indicate the location of fig trees (*Ficus* spp.). *Stars* represent the places in which the travel direction significantly changed according to CPT. *Created with ArcGIS 9.2 and Adobe Photoshop*

preferred species in fruit. In four occasions, (2.1%) travel direction changes coincided with intergroup encounters, but change-points were never associated with locations of duets. Figure 4 shows four examples of daily routes made by groups A, B, C and H, respectively.

The straight-line distance between consecutive change-points ranged from 73 to 386 m with a mean of 165.2 m (Table 2). The average height of trees and lianas at change-point locations was 20.2 m, which closely mirrored the average canopy height of 20 m previously estimated by Brockelman (1998) in the study site. The average height at change-points was not significantly higher than the average height of 19.9 m of trees and lianas used otherwise, which were not associated with change-point locations (Mann–Whitney $U_{11} = 59$, $P = 0.95$). Given that distance range between consecutive change-points (73–386) was more than double the assumed normal visibility within the canopy and that change-point locations were not above the average canopy range, we conclude that all consecutive travel change-points were generally associated with food sources out of sight from each other. Route overlap averaged 31.2% per gibbon group and ranged from 8% in group S to 41.2% in group T (Table 2).

We found that the gibbons' travel direction change-points were significantly more associated with feeding sites, encounter sites, or potential feeding locations (those with no food but of considerable size) than would be expected if change-points were randomly selected locations along the gibbons' daily path (z_{11} = 2.93; $P < 0.001$), for example, where gibbons were more likely traveling (88.2% of the random cases). In other words, if travel change-points were distributed randomly, they should have occurred primarily while the gibbons were traveling. As most food resources at change-points belonged to preferred food species (126 out of 153 change-points), we asked if such food sources were significantly more often the travel change locations of gibbon pathways and found indeed that the proportion of preferred food sources occurred more at change-point locations (median = 47.2%) than did other food resources (11.3%) visited by gibbons (z_{11} = 2.85; P = 0.004). Finally, we compared the travel efficiency of the heuristic model at detecting preferred food sources in the relation to the observed movement made by gibbon groups (Fig. 5). An ANOVA test revealed that the efficiency values varied with detection radius were significant according to the 6 levels of detection radii (F = 124, df = 5, $P < 0.001$). This conclusion is very robust because our design included variability between groups. Gibbon travel was more efficient than the model for the 21, 30, 42 and 63 m test detection radii. Only at long distances exceeding four times the estimated visibility distance (84 and 105 m) did the heuristic model perform better than the actual movements in detecting preferred food sources. We also detected highly significant differences between groups (F = 7.64, df = 10, $P < 0.001$), but because we confounded groups with months, it is not clear whether this effect was due to differences between groups, months, distances or home-range sizes, and future research is needed to clarify this aspect.

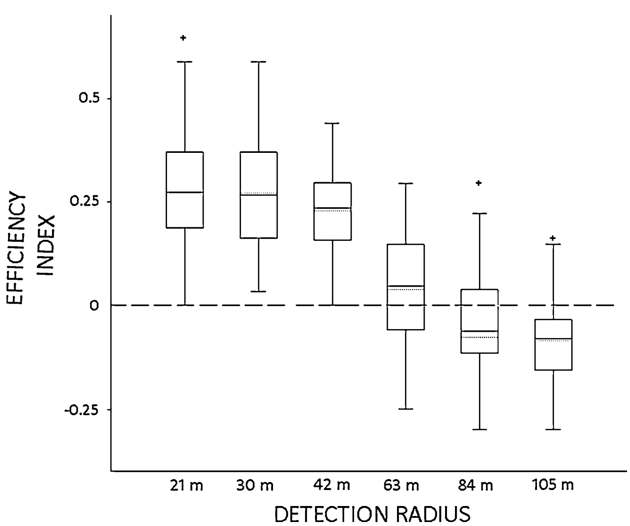

Fig. 5 Index of search efficiency for each detection radius. Each *box* encompasses the 25th thorough 75th percentile, and the *horizontal lines* mark the median, minimum and maximum values. *Dotted lines* represent the average values. Outliers are shown as *dots* outside the *boxes*. *Created with Office 2007 and Photoshop*

Discussion

In the Khao Yai study area, gibbon travel change-points were significantly associated with biologically meaningful activities such as feeding on preferred food sources or encounters with other gibbon groups, but they were not associated with duets. In particular, individual trees or woody climbers of preferred food resources were the primary cause underlying the gibbons' daily travel, because these predominantly coincided with change-points. We conclude that foraging behavior dominates the pattern of daily travel decisions, whereas social stimuli, i.e. intergroup encounters, are less frequently the gibbons' travel goals based on observed changes in travel direction. This result is not unexpected because deviation from foraging pathways is expected to occur opportunistically and on short notice when a neighboring group is spotted or heard nearby. This movement pattern also suggests that Khao Yai white-handed gibbons do not regularly patrol the boundaries of their home ranges and hence save time and energy required for maintaining their territories (e.g. Schoener 1983) by integrating territorial defense into foraging movements.

Overall, we interpret our results to indicate that the spatio-temporal distribution of preferred food trees structures gibbons' daily travel. Similarly, travel routes of sakis appear to be determined by a few selected feeding sites, and other feeding sites are visited along the way (Cunningham and Janson 2007). Preferred individual food trees serve a dual function, because they are travel goals at the end of feeding bouts and also the places from where new travel directions and routes toward the next preferred food source are taken. Accordingly, Valero and Byrne (2007) found that spider monkeys do not generally continue in the same direction after exploiting a resource; they change their direction to reach with high linearity another resource that is out of sight. An alternative explanation that would exclude spatial memory under these circumstances is that animals could follow a straight path until an important resource is detected and then randomly choose a new direction (Janson 1998). However, our data show that a model of travel in randomly selected directions would result in fewer encounters with preferred food sources than in actually observed paths of the same length. The random model was tested with a variety of detection radii and only at long distances (four times further the estimated visibility) was the random travel model superior to the gibbons' observed movement. Our findings strongly suggest that new travel goals are already set at the time of leaving a current food source, judging from the long distances between consecutive change-points far out of sight for the gibbons, and the travel efficiency of gibbon movements. Our study design did not allow us to control for situations in which other foragers' activities (e.g. feeding birds) or olfactory cues could have aided the gibbons' perception to find preferred foods. However, the long distances between consecutive change-point locations make these possibilities an unlikely explanation in most observed cases. Our results rather indicate that gibbons must have an excellent spatial representation of food locations in their mind and that they build a spatial cognitive map of their home range that allows them a sense of direction to reach out of sight preferred food species in an efficient manner. They may even include spatial knowledge of less important resources, as change-points occurred sometimes at non-preferred food locations. The efficiency of travel between preferred food trees suggests that the gibbons plan their daily travel routes based on the knowledge they have of the availability of resources in a large-scale space; however, our current analyses only allow us to suggest that gibbons may plan a travel one step at a time, i.e. from one travel change-point to the next one, and further analyses must address if gibbons can plan several steps ahead. In contrast to navigating toward distantly spaced, out-of sight preferred food sources, the remaining minor resources are probably found visually along the way between preferred resources.

Gibbons could use a topological map in which preferred plant species are key nodes of a network of arboreal pathways (Milton 2000). The relatively high route overlap in periods of 5 days, and the association of preferred foods with change-point locations also supports the possibility of the topological representation of space in gibbons. In some instances, travel change-points were preferred food resources containing no fruit for gibbons, or fig trees (*Ficus* spp.) without figs, which can reasonably also be considered keystone nodes in a topological map given their high fruit production and asynchronous phenological cycles (Shanahan et al. 2001). In addition, travel to non-fruiting trees of preferred species and visits to *Ficus* trees without figs may be a strategy to incorporate in daily travel paths the monitoring of important resources, which would likewise be consistent with topological navigation. Di Fiore and Suarez (2007) suggested that nodes in a topological map could be locations where gibbons make decisions about where to travel, which is in accordance with the main assumption of associating change-points with travel decision points (Byrne et al. 2009). These pathways appear to connect areas that have high densities of preferred food sources, which supports that available preferred food species might dictate regular travel routes (Cant et al. 2001; Noser and Byrne 2010). Similarly, Garber (2000) found that tamarins used turning areas to reorient travel toward productive feeding sites. However, even if preferred trees are intersecting nodes of a route network, preferred food sources were related to a relatively short period of time (5 days), and the state of gibbon fruiting trees at the site changes quickly from month to month (Savini et al. 2008). Therefore, individual trees providing fruit at a certain point in time are unlikely to be useful as permanent nodes on a topological map. If the travel targets and nodes change over time as important plant species alternate in providing food for gibbons, this rather suggests a continuous modification of travel paths. Still, the possession of a highly complex topological map with numerous nodes and pathways would guarantee an efficient travel to cope with the continuous modification of the available preferred resources for gibbons. It is also likely, however, that cognitive abilities beyond the demands of maintaining a static topological map are necessary to continuously integrate the changing phenological status of a large number of preferred individual food trees of a home range over annual or perhaps super-annual time intervals. Unfortunately, our 5-day observation window was too short to address long-term aspects of gibbon travel, and further tests using longer-term observations are clearly necessary to better understand the level at which gibbon cognition is compatible with more advanced sets of cognitive spatio-temporal navigation skills.

Our observations support the idea that gibbons can store locations of preferred food sources and perhaps other non-preferred sources in their memory, and that they can move efficiently over long distances to reach them. Given that gibbons have relatively small home ranges and an ability to quickly range over them (Bartlett 2009; Savini et al. 2008), they may have evolved or retained some of the metric characteristics of Euclidean navigation recently also found in another ape (Normand and Boesch 2009). Poucet (1993) suggested a model of spatial cognition in which landmarks are encoded as Euclidean representation in small-scale ranges and as topological representation in a large-scale range. Normand and Boesch (2009) expected more Euclidean navigation when chimpanzees where traveling in core areas rather than in peripheral areas of their home range. Because they did not find differences in how chimpanzees move through either core areas or the rest of their home range, they favored the possibility of Euclidean over topological navigation for chimpanzees ranging both in small and large areas. It may be argued that the daily use of the same small territory provides gibbons with numerous opportunities to encounter and view key food sources and other landmarks, which would benefit the creation of a Euclidean representation in a primate species that may have a ''spatial intelligence'' more similar to great apes than to monkeys (MacLeod 2004).

Our findings do not entirely support the view that gibbons solely use a set of route networks to navigate, nor allow us to abandon or confirm the use of Euclidean traveling. Probably both mental representations of space are likely present in gibbons and are used in complementary ways, depending on circumstances. In any case, observed gibbon travel patterns appear to connect preferred food sources as expected under the assumption of a functional cognitive representation of the most relevant sources in a large-scale space.

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   [✓] Research results

[✓] Conclusions and recommendations

[✓] References

[ ] Appendices (if necessary)

I do hereby certify that all of the above given checks are true.

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EXECUTIVE SUMMARY

How precisely animals navigate is still poorly understood and thus more contrasting information is needed for most species. Core areas are small regions of intense use within the home-range of animals. Despite these core areas are theoretically the most significant regions (e.g. refuges, food availability) of the home-range, little comparative work has been made demonstrating this implicit idea. Remembering locations of food resources is critical for animal survival and therefore affects movement decisions and core areas ¶ J H R J U D S K L F D O F K R L F H Gibbons are territorial primates which regularly travel through small and stable home ranges in search of preferred, limited and patchily distributed resources. This project investigated 1) spatial memory and cognitive mapping abilities of white-handed gibbon groups and 2) the quality of core areas at Khao Yai National Park by using a Geographical Position System (GPS) unit and Geographical Information Systems (GIS) software (ArcGIS 9.2). Gibbons were predicted 1) to profit from an ability to memorize the spatial characteristics of their home range; and 2) to use core areas of high food quality. We collected ranging and feeding data from 11 gibbon groups (*Hylobates lar*) to test their navigation skills and the use of core areas. We calculated the locations at which significant travel direction changes occurred using the CPT (change-point direction test). Travel direction locations primarily coincided with preferred fruit sources. Within the limits of biologically realistic visibility distances observed, gibbon travel paths were more efficient in detecting known preferred food sources than a heuristic travel model based on straight travel paths in random directions. Because consecutive travel change-points were far from th H J L E E R Q V ¶ sight, planned movement between preferred food sources was the most parsimonious explanation for the observed travel patterns. Gibbon core areas had consistently higher densities of preferred food species than the rest of their corresponding home-ranges, containing an average of the 31.8% of their total basal area. Therefore, gibbon ranging appears to connect preferred food sources as expected under the assumption of a good mental representation of the most relevant sources in a large-scale space.

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BACKGROUND AND RATIONALE

The nutritional characteristics of the landscape play a determinant role in animal movement ecology and the evolution of spatial cognition. Particularly, preferred food resources, i.e. those that are eaten more often than would be predicted based on their availability, affect animal ranges by shifting their movement patterns to take advantage of the spatial distribution of such key foods (Milton, 2000). It is hypothesized that the evolution of large brains and advanced thinking of primates are related to meeting the challenges of finding food within a large-scale environment (Potts, 2004). Forested habitats, where primates evolved, are characterized by complex spatial and temporal patterns of fruit production that require primates to solve the problem of efficiently visiting highly dispersed fruit trees (Milton, 2000). Particularly, deciding where and when to look for fruit and which routes to travel economically to reach fruiting trees would have been advantageous for primates that relied on fruit. And indeed, primate brain sizes seem closely linked to diet, with leaf-eaters (folivore primates) having smaller brains than fruit eating primates (Milton, 2000).

Core areas are defined as small regions of intense use within the home-ranges (the area where animals restrict their normal activities during a set period of time) of solitary or group-living animals (Leuthold 1977). The delineation of animal core areas provides vital information for understanding movement ecology as they are thought to represent the minimum area that an individual or a group needs to survive (Powell 2000). Because core areas constitute regions in which most activities are concentrated, such regions must contain key resources such as refuges, key food locations or patches of high forest quality. However, there is still little quantitative data comparing core area quality versus the rest of the home-range.

How animals remember travel paths and fruit locations is still not fully understood. One approach to fill this research gap is to study how animals memorize and strategically find food. 6SHFLILFDOO\ KRZ VSDWLDO LQIRUPDWLRQ ie: a mental LV UHSUHVH representation of environmental information, Tolman, 1948). Two debating types of cognitive maps are usually distinguished: 1) A geometrical cognitive map, is a projective mental image of the environment in the sense of a metric cartographic map with coordinates in which environmental landmarks (unique objects at fixed locations) are represented. Theoretically, this type of mental map allows for determining angles of interconnecting landmarks and thereby predicts the most efficient movement from one point to another. 2) In contrast, route-based navigation uses information on how landmarks and destinations are connected spatially by a system of pathways (e.g. Di Fiore and Suarez, 2007).

White handed gibbons (*Hylobates lar*) live in small family groups, usually containing one breeding pair, and one or two offspring individuals (Fuentes 2000). Gibbons are ripe fruit specialists with an extensive diet based on numerous plant species, however just a few preferred ones constitute the core of their main diet (McConkey 2009). Indeed, Savini et al (2008) reported that an average of just 4 food species made the 80% of the monthly feeding time for 5 groups of gibbons in Khao Yai (Thailand). Gibbons have small (ca 25 ha) and stable home-ranges throughout years, which they can quickly crossover in a single day (Bartlett 2009), while other primates of similar size and nutritional needs have much larger home-ranges and use different portions of their range seasonally (e.g. *Ateles* spp, Di Fiore and Campbell 2007). Due to the relatively small size of their home-range, gibbons may need to maximize their foraging efficiency by continuously discovering and remembering food resource locations (Brockelman 2009). Brockelman (2009) suggests that by having small mobile groups, gibbons are expected to be able to exploit their knowledge of a small size forest to the maximum in order to locate their food resources.

In addition, the presence to numerous habituated gibbon groups at Khao Yai (Reichard 2009) offers an excellent opportunity to investigate this relation across several gibbon groups. In this study we collected systematic data on 11 gibbon groups at Khao Yai study the cognitive spatial abilities and the use of core areas.

RESEARCH OBJECTIVES

This project investigated the spatial memory and cognitive mapping abilities of white-handed gibbon groups and the quality of core areas at Khao Yai National Park by using a GPS unit and GIS software (ArcGIS 9.2). Specific objectives were:

1. 7R GHWHUPLQH JLEERQV¶ SUHIHUUHG IRRG VRXUFH and their geographical location.

2. To plot all daily movements of gibbons and determine at which location there was a significant chance in travel direction.

3. To identify core areas and study whether they had high quality in comparison to the rest of the home-range.

Study site and animals

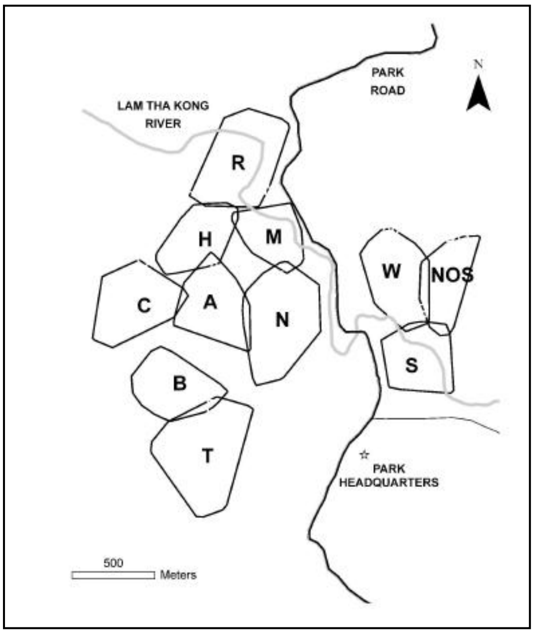
Khao Yai National Park, situated in central Thailand (2169 km^2 ƒ •(ƒ •1 F R Q V L of a seasonally wet, evergreen forest interdispersed with few, small patches of secondary growth at an elevations of 730 ±870 m. We studied 11 habituated gibbon groups at the Central Mo Singto study site from July 2009 to July 2010. Group composition varied from 3 to 6 L Q G L Y L G X D O V G X U L Q J W K H V W X G \ 7 D E O H) L J V K R Z V home-ranges during the study time.

TABLE 1. STUDY GROUPS AND COMPOSITION

Group	Number of Individuals	Composition
A	4	3AM, 1AF
B	3	1AH, 1AF, 1I
C	4	1AM, 1AF, 1JM, 1I
H	5	2AM, 1AF, 2JF
M	3	1M, 1AF, 1JM
N	6	3AM, 1AF, 1JF, 1I
NOS	6	3AM, 1AF, 1SAM, 1I
R	4	1AF, 3AM
S	5	2AM, 1AF, 1SAF, 1I
T	6	2AM, 1AF, 1SAF 1JM,
W	5	2AM, 1AF, 1JM, 1I

M= male, F = female, SA =subadult, J=Juvenile, I= infant

FIGURE 1. LOCALIZATION OF STUDY GROUPS



Data collection

Each group was followed for 5 consecutive days with an average of 6.5 hr per day. A GPS was used to record the location of groups at 1-min intervals. Each point was assumed to represent the approximate central location of the group. Geographical coordinates were collected using the coordinate system WGS84 and projected into Universal Transverse Mercator (UTM, Zone 47N) units. We collected feeding data of all food plants (trees and woody climbers) and used part (fruit, flower or leaves) in which at least one DGXOW IHG IRU • PLQXWHV GXULQ the plant DBH (diameter at breast height) was recorded.

2QFH D JURXS¶V IROORZ ZDV FRPSOHWHG ZH FDOFXODW -day home range outline using the minimum convex polygon (MCP: i.e. the delineation of the area by drawing the lines that connect the outermost points) to locate all individual trees of preferred food species within this area. We walked the 5-day home range and mapped all individual trees and woody climbers belonging to the preferred food species by using 50 m wide transects until the entire home range was covered. These botanical transects for each 5-day home range of a single group were completed in less than 4 consecutive days directly following our behavioral data collection to ensure that plant monitoring and behavioral observations were as closely synchronized as possible.

Core Areas

Core areas were calculated following Harris et al (1990), by calculating the exact percentage that corresponds to the inflection point in the utilization distribution. The inflection point was therefore calculated by plotting the area contour values at 5% increments from 5% to 95%

contours against the percentage of area enclosed. Contour area values were calculated with the least squares cross-validation. Then, we fitted an exponential regression function (y = e^{bx}) forced WKURXJK WKH RULJLQ :H XVHG WKH UHVLGXDOV UHJUHVV where the slope of the exponential regression curve was 1 by solving x = [ln (1/b)] / b for each group locations. To calculate kernel core areas we only used the geographical coordinates of the focal group separated by 15 minutes intervals to minimize non-independence among observations.

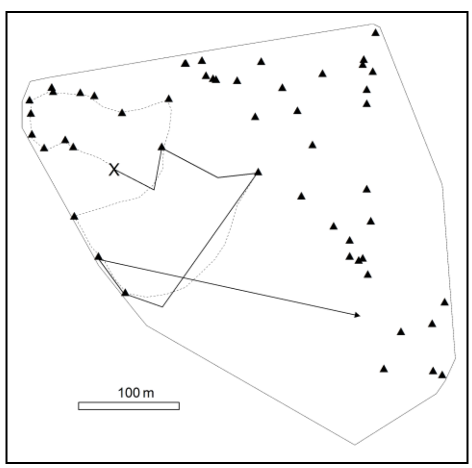
Data management

In order to draw realistic pathways of movements of gibbons we used consecutive locations separated by a minimum of 20 meters. To obtain an estimate of route overlap for the 5-day follow of a group we first considered that travel segments overlapped if the \ ZHUH ZLWKLQ ” PHWHUV RI HDFK RWKHU IRU D GLVWDQFH RI • PHWHUV S by dividing the total distance of overlapping trajectories of a gibbon group by the total distance traveled during the 5-day follow period.

We tested if change-points obtained using the CPT were spatially independent events that occurred at locations where biologically meaningful activities (e.g. visit to food sources) were observed. To that purpose we used a Wilcoxon paired test comparing the total number of food trees that were found in the 5 day pathways per group with randomized points along such pathways. We used the same statistical test to determine if preferred food sources were more significantly related to change-points than non-preferred food sources by comparing the proportion of preferred food sources that were change-points with the proportion of non-preferred food sources that were at change-points. To examine if the height of trees may affect the occurrence of change-points, because tall trees could be used as vantage points to locate distant resources, we compared the average height of trees and lianas at change-points to the height of those used by gibbons at other locations using a Mann Whitney U-test.

Finally, we developed a heuristic travel model to determine the relative efficiency of finding preferred food sources using a random search method. In this model, a route began from the starting point of a gibbon daily route, from where it continued in a straight line in a random direction using a given detection radius of visibility (see below) until it encountered a preferred food source or hit the border of the MCP home range (Fig. 2).

FIGURE 2. EXAMPLE OF A HEURISTIC SEARCH WITH A DETECTION RADIUS OF 42 METERS TO DETECT PREFERRED FOOD SOURCES (SOLID TRIANGLES) IN GROUP M HOME RANGE. THE ³ ; ´ REPRESENTS THE START OF THE MOVEMENT OF THE HEURISTIC SEARCH AND THE DASHED LINE THE ACTUAL PATH MADE BY GIBBONS.



A new vector was then calculated in a 360º random direction from the previous location until it again detected a new target. This operation was repeated until the total distance covered in the

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travel calculations we used a conservative approach of six distinct detection radii of visibility range to simulate the entire possible gibbon detection distances: the 21 m (average visibility range estimated by Brockelman 2009), 30 m range, 42 m range (double of the theoretical visibility range for gibbons at the study site), 63 m range, 84 m range and 105 m range. We calculated an index of search efficiency for each daily route of gibbon groups by subtracting the number of preferred tree or woody plant individuals detected by the heuristic model to the ones detected by gibbons and divided by the total of preferred individuals in that home range. The model efficiency values would range from -1 to +1 with negative efficiency values implying that the random search model is performing better than gibbons at detecting preferred foods; whereas positive values imply that the gibbons are more efficient. A Two-Way ANOVA was designed to compare the effects of the search model (6 levels of detection radii) and groups on the search efficiency values.

Travel change-point detection

We applied the change-point test (CPT) created by Byrne et al. (2009) to determine at which points the gibbons significantly changed their travel direction. Accordingly, we applied the CPT to a daily travel path by calculati Q J W U D Y H O V H J P H Q W V V W D U W L Q J I U R P W location of a given day (i.e. a food source, duet site, sleeping tree or intergroup encounter site) until a change-point was discovered. This location then became the starting point for applying the CPT until the previous change-point was found and so on, until no further change-points were detected for a daily path.

As an estimate of area productivity in preferred food species we used the basal area of preferred food species, i.e. the cumulative DBH of the preferred food species per hectare. We calculated the basal area of preferred species within core areas and rest of the home-ranges (non core area). The basal area between core area and non core area for the 11 groups was compared using a Wilcoxon paired test.

RESEARCH RESULTS

During the 5-day-period of time were gibbon groups were observed, they covered an average home-range of 18.4 ha (range 12.1 - 25.8 ha), and core areas of 3.6 ha (range 1.1 ±4.7 ha), which made an average of the 20.1% of the home-ranges. Gibbons based their diet on a wide array of trees and woody plant species from which they generally obtained ripe fruit (90.5% of their total feeding time), but only an average of 3 species comprised preferred species (range 2-5 species, table 2). Solely preferred food species made an average of 79% of the total feeding time per group and constituted mostly sources of ripe fruit from tree species.

TABLE 2. PERCENTAGE OF TOTAL FEEDING TIME USED IN EATING PREFERRED RESOURCES OF STUDY GROUPS

Family	**Species**	**Growth form**	**Part eaten**	**A**	**B**	**C**	**H**	**M**	**N**	**R**	**S**	**NOS**	**T**	**W**
Fabaceae	*Acacia pennata*	C	YL	-	-	-	-	-	-	-	-	-	21%	-
Cannabaceae	*Aphananthe cuspidata*	T	FR	-	39%	-	-	-	-	-	-	-	-	-
Euphorbiaceae	*Balakata baccata*	T	FR	16%	-	-	-	-	-	-	-	-	-	-
Elaeocarpaceae	*Elaeocarpus robustus*	T	FR	-	-	-	-	27%	10%	-	-	-	-	12%
Elaegnaceae	*Elaegnus conferta*	C	FR	-	-	-	-	-	-	46%	-	-	-	-
Myrtaceae	*Eugenia cerasoides*	T	FR	40%	-	-	-	-	-	-	-	-	-	-
Moraceae	*Ficus* spp.	T	FR	-	-	21%	27%	16%	38%	-	-	23%	-	-
Clusiaceae	*Garcinia benthamii*	T	FR	-	10%	-	-	-	10%	-	-	-	29%	-
Cannabaceae	*Gironniera nervosa*	T	FR,YL,ML	-	-	-	10%	16%	-	25%	57%	18%	-	18%
Annonaceae	*Miliusa lineata*	T	FR	22%	-	-	-	-	-	-	-	-	-	-
Escalloniaceae	*Polyosma elongata*	T	FR	-	-	-	-	-	-	-	12%	-	-	-
Anacardiaceae	*Choerospondis axilaris*	T	FR	-	28%	-	13%	-	27%	-	24%	41%	15%	52%
Meliaceae	*Sandoricum koetjape*	T	FR	-	-	64%	-	-	-	-	-	-	-	-
Vitaceae	*Tetrastigma laotican*	C	FR	-	-	-	-	21%	-	-	-	-	-	-
Rutaceae	*Toddalia asiatica*	C	FR	-	-	-	19%	-	-	-	-	-	-	-
	% TOTAL FEEDING TIME			78%	77%	86%	69%	79%	84%	71%	94%	83%	65%	82%

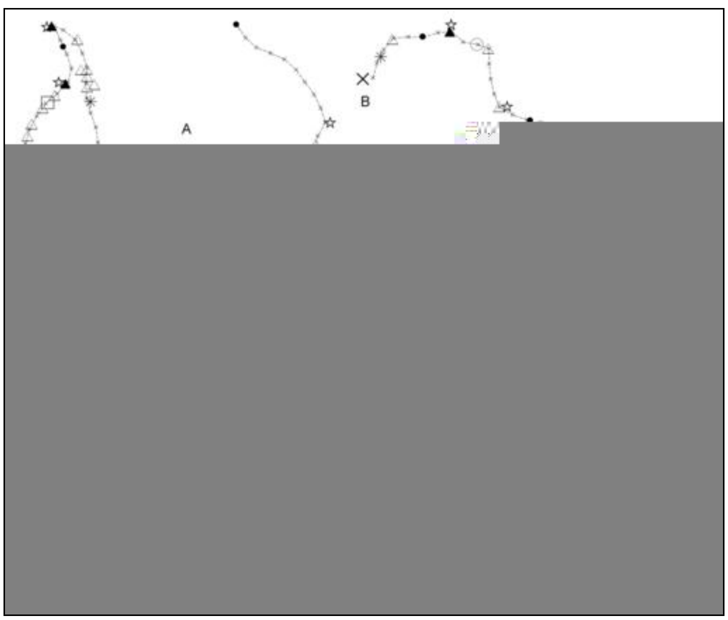
We detected a total of 195 change-points for the travel trajectories of the 11 gibbon groups (Table 3). Most travel change-points (93.8%) were associated with biologically meaningful parameters for gibbons (e.g. feeding), and only for 12 travel change-points (6.2%) we did not detect a biologically meaningful reason why a change in travel direction had occurred. In most cases (153 out of 195 change-points, 78.4%), change-points coincided with food sources of ZKLFK ZHUH SUHIHUUHG IRRG VRXUFHV DQG RQO\ ZHU gibbons changed their travel direction at preferred sources that did not have food (including 4 times at fig trees), but otherwise change-points occurred at preferred species in fruit. In 4 occasions (2.1%) travel direction changes coincided with intergroup encounters, but change-points were never associated with locations of duets.

TABLE 3. CHANGE POINT DISTRIBUTION IN STUDY GROUPS.

				CHANGE-POINT LOCATIONS						
Group	**Mean distance (m) between consecutive CP (range)**	**Total distance length (m)**	**% Route overlap**	**Preferred species**	**Other plant species**	**Preferred species with no food**	**Ficus with no fruit**	**Encounters**	**Others**	**Total**
A	142.8 (75-272)	5860	36.7%	13	4	6	0	2	3	28
B	187.3 (87-336)	4240	36.6%	15	3	2	0	0	1	21
C	146.1 (73-262)	4520	35.1%	14	2	1	0	1	1	19
H	171.7 (86-231)	3900	27.5%	13	1	0	0	0	0	14
M	200.3 (120-286	2840	28.1%	10	2	0	0	0	0	12
N	157 (87-277)	4120	17.3%	7	3	2	2	0	2	16
NOS	163.2 (92-271)	4040	38.0%	14	1	2	0	1	2	20
R	126.2 (82-215)	3260	25.7%	4	2	1	3	0	0	10
S	172 (87-314)	3240	8.0%	9	0	3	0	0	1	13
T	218.1 (120-386	5960	41.2%	13	3	4	2	0	2	24
W	132.2 (78-202)	4060	49.3%	14	1	1	2	0	0	18

The straight-line distance between consecutive change-points ranged from 73 to 386 m with a mean of 165.2 m (table 3). The average height of trees and lianas at change-point locations was 20.2 m, which closely mirrored the average canopy height of 20 m previously estimated by Brockelman (1998) in the study site. The average height at change-points was not significantly higher than the average height of 19.9 m of trees and lianas used otherwise, that were not associated with change-point locations (Mann Whitney $U_{11}=59$, $p=0.95$). Figure 3 shows four examples of daily routes made by groups A, B, C and H, respectively.

Figure 3. Figure 4. Examples of daily travel path made by group A, group B, group C, and group H. The ³ ; ´represents the start of the movement following the dotted line and consecutive waypoints (small ³x ´ separated by 20 meters. Solid triangles indicate food sources belonging to a preferred plant species (10% of the total feeding time) and empty triangles individuals of preferred species with no food available within home range. Black points indicate food sources from other eaten species. The squares are locations in which an encounter occurred and circles represent locations where duets occurred. Asterisks indicate the location of fig trees (*Ficus* spp). Stars represent the places in which the travel direction significantly changed according to CPT.



Given that distance range between consecutive change-points (73-386) was more than double the assumed normal visibility within the canopy and that change-point locations were not above the average canopy range, we conclude that all consecutive travel change-points were generally associated with food sources out of sight from each other. Route overlap averaged 31.2% per gibbon group, and ranged from 8% in group S to 41.2% in group T (table 3).