Title: Change point analysis of travel routes reveals novel insights into foraging strategies and cognitive maps of wild baboons

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ABSTRACT

Efficient space use is a critical challenge for animals relying on stationary resources. It is often difficult with purely observational methods to gain unambiguous insight into any ability of primates to manage and process spatial information. Investigating the visible signs of the decision processes underlying space use often leaves open important issues. We applied the Change Point Test [Byrne et al. 2009], a statistical tool to objectively determine change points in animal travel paths, to investigate to what degree directional changes in our study group's *(Papio ursinus)* dry season ranging were associated with important resources and prominent landmarks. One third of directional changes were associated with fruit feeding, 1/3 with traveling, and 1/3 with dry matter feeding, travel feeding and with drinking. When directional changes were associated with traveling, the subsequent directional changes were likely to result in fruit feeding. Fruit feeding mostly occurred at the apex of the day journeys, while drinking, dry matter feeding and travel feeding often occurred along straight travel segments. The majority of directional changes did not occur in clusters at distinctive locations, but at distances of more than 120 m apart from each other, many of them along prominent landmarks. We conclude that the change points do not represent nodes or route bends of a network map. Rather, they represent 1) locations where the decision to turn back to their sleeping site was taken, and 2) locations next to important landmarks (changes of slope, car tracks) where slight adjustment of a movement direction was possible. We found no evidence for a Euclidean map and discuss our findings in the light of a network map representation of space.

Key words: spatial cognition, change point analysis, baboon travel routes, network map, large-scale space.

INTRODUCTION

Efficient space use is a critical challenge for animals relying on stationary resources. Finding patchily distributed fruit in large-scale space that cannot be perceived from the present location has been proposed as an evolutionary trigger for the brain enlargement and increased cognitive ability observed in primates and other animal taxa [Clutton-Brock and Harvey 1980; Milton 1981; 1988; 2000]. However, it is often difficult with purely observational methods to gain unambiguous empirical insight into any ability of primates to manage and process spatial information [but see Janson 1998; 2007; Noser and Byrne 2007b; Menzel 1999; Garber and Dolins 1996; Garber 2000, for experimental approaches). Investigating the visible signs of the decision processes underlying space use - a combination of travel journeys and resource use - often leaves open important issues: for example, we cannot know to what degree a visit to a resource place had been planned in advance [see Janson, this issue], and if so, where and when the decision was taken. Tantalizingly, the answers to these questions could potentially open up crucial insights into the mental processes involved in primate navigation.

In order to tackle these issues, we [Byrne et al 2009] have developed the Change Point Test (CPT), a statistical tool allowing researchers to apply objective criteria to interpret animal travel journeys. This test allows identification of the locations in space where, independently of the possible reasons, directional changes in travel paths occur. Once these 'change points' (CPs) are detected, biologically meaningful parameters associated with those locations can be investigated: for example, resource use, patterns of vocalizations, simultaneous movements of competitors, mates or predators, visibility of resources, topographical information, etc. If certain parameters systematically occur at CPs, we can conclude post hoc that they are likely to play an important role in the spatial decisions taken by the individuals or groups under investigation. Thus, the CPT opens up the possibility to study variation in spatial decision-making on the level of individuals, groups or species that live in a wide variety of habitats.

To date, two studies have used the CPT to investigate primate routes in combination with data on resource use at the locations where directional changes occurred. Joly and Zimmermann [2011] investigated the first CPs in mouse lemur *(Microcebus murinus)* travel paths ranging in a dry deciduous forest in NW Madagascar. They found that CPs were associated with important stationary food sources, such as gum or honeydew. Because these resources were situated more than 100 m away from the sleeping trees, and rejecting visual or olfactory cues as alternative explanations of directionality, the authors concluded that mouse lemurs routinely show intentional directional travel towards the first food source of a given foraging trip at the time when they leave their sleep tree. Asensio et al [2011] sampled 5 day travel routes of 11 gibbon groups *(Hylobates lar)* living in the wet, evergreen forest at Khao Yai National Park in Central Thailand. They found that the majority of CPs of all study groups was associated with preferred fruit tree species; few CPs were associated with feeding on other plant species or with group encounters, and few travel routes changed direction without any obvious behavioral changes. Distances between CPs ranged from 70 to 390m, and two subsequent CPs were often out of sight from each other. The authors concluded that gibbons travel in straight lines from one fruit tree to the next, and, since direct perception of the next food tree from a given tree was unlikely, that they use spatial memory to locate many trees.

Many baboons live in habitats where important resources are typically situated at large distances from each other, so that direct perception of the next resource at travel onset can be excluded a priori [eg. Sigg and Stolba 1981]. This was also the case in our study group, a small chacma baboon group living in a dry woodland savannah in Northern South Africa [Noser and Byrne 2007a]. Some of their most important resources (water holes, sleep site, fruit species available during the dry season) were extremely sparse. Since a random search strategy would not result in repeated visits to these locations, the observed spatial behavior could only be explained by the use of spatial memory for several resource locations [Noser and Byrne 2007a; 2010].

Our study group used a network map rather than a Euclidean map to find the 5 water holes in their home range [Noser and Byrne 2007b]. We drew this conclusion from their travel patterns in space after unexpected group encounters that often took place next to the water holes. After running away from the opponents, the baboons always waited for long time periods and then resumed their initial route rather than visiting the water hole directly from their new location. Thus, they seemed to be tied to a specific route that they were unable to abandon, rejecting the hypothesis that they encoded the distances and directions to the water holes by means of a Euclidean mental map. Rather, their behavior suggested that they represented information about how landmarks and potential goals were interconnected in space by means of a network map [sensu Byrne 2000; see also Poucet 1993, Garber 2000]. Converging evidence for the use of network maps in primates came also from other nonhuman primate species (Yellow baboons, [Altmann and Altmann 1970]; Orang Utans, [Mac Kinnon 1974]; Hamadryas baboons, [Sigg and Stolba 1981]; Howler and Spider monkeys, [Milton 1981], [Milton 2000]; Olive baboons, [Ransom 1981]; Tamarins, [Garber 1989], [Garber 2000]; Spider and Woolly monkeys, [Di Fiore and Suarez 2007]; Sifakas and Brown lemurs, [Erhardt and Overdorff 2008], whereas evidence for Euclidean maps remained limited (but see [Boesch and Boesch 1984], [Normand and Boesch 2009] for wild chimpanzees, and [Menzel et al. 2002], for a study with a captive bonobo).

Theoretically, network maps can be complex, containing a large number of routes to many goals, alternative routes to a single goal, and intersections of routes, where animals are likely to take spatial decisions. In practice, however, it is often difficult to decide what constitutes a "route". For example, Di Fiore and Suarez [2007] found that 95% of the locations recorded over several months of three Spider monkey *(Ateles belzebuth)* females living at Yasuni National Park in Ecuador fell within 50 m of a repeatedly traveled route. Thus, these spider monkeys traveled along relatively narrow repetitive routes. On the other extreme, Sigg and Stolba [1981] felt that a "buffer zone" of 500 m was appropriate to define a repeatedly traveled "street segment" in a

group of Hamadryas baboons living in the semi-desert of Erer-Gota, Ethiopia. To date it is unknown to what degree these differences in data analysis reflect differences in ecological parameters, navigational strategies and cognitive abilities.

We applied the CPT to investigate whether directional changes in our study group's dry season ranging were associated with important resources, to be comparable with the findings in gibbons [Asensio et al. 2011]. In particular, we investigated the degree to which fruit feeding was decisive for the observed travel patterns, that is, whether baboons, like gibbons, mainly travel from fruit tree to fruit tree. Second, we examined the nature of the baboon mental network maps more closely. Therefore, we investigated the locations where directional changes occurred in relation to each other, with the aim to identify their degree of clustering. By doing so we hoped to identify important network map "nodes", that is, locations where routes intersect and spatial decisions can be taken. Third, we examined CPs in relation to prominent landmarks in two topologically distinct areas: a hill where a large number of natural structures such as the slope, several valleys and views potentially guided movements, and a plain where (to us) vegetation was extremely uniform and only very few prominent landmarks were available. Assuming that these landmarks offer opportunities for reorientation for the baboons as well, we expected to find many directional changes next to them.

METHODS

We carried out fieldwork at Blouberg Nature Reserve (BNR; 22°58′S, 29°09′E) in the Limpopo Province, South Africa (see [Noser and Byrne 2007a] for details) between August 2000 and August 2002. The woodland savannah of BNR is naturally divided into two parts, mixed bushveld in the plain area ("the plain") and an arid mountain biome [Low and Rebelo 1996] on the foothills of Blouberg Mountain ("the hill"). The two areas were topologically distinct: on the hill a large number of natural structures such as the slope, several valleys and views potentially guided movement. In the plain orientation was difficult due to uniform vegetation and relatively low visibility (see below). However, changes in vegetation around the water holes, some car tracks and the distant hill offered opportunities for orientation.

At BNR, rainfall of 350 mm per year on average was confined to a single rainy season (October - April), while winter months were completely dry. In the plain, maximum distance from which a white, moving flag could be spotted at 1.5 m above ground was 104 m on average in peak dry season (July), while the highest branches of trees could be seen from a distance of 304 m maximally [Noser and Byrne 2007a for details). Visibility on the hill was highly variable and could not generally be determined. For example, some fig trees were visible from a distance of more than 1000m, whereas others could be seen only from a few meters distance (see [Noser and Byrne 2010] for details).

With approximately 25 members, the focal "Kloof group" was the smallest of at least 9 baboon groups living at BNR. In contrast to baboon groups observed elsewhere (eg. [Hamilton 1982]; [Kummer 1992]), this group used a single sleeping site throughout the study (24 months), situated in one of the very restricted cliffs at the foot of the hill. Also, a single male occupied the alpha position throughout the duration of this study. The group's home range was 13.5 km^2 in

size and contained five waterholes, including three natural pools carrying rainwater and two artificial dams that were fed by ground water.

For the present purpose, we used data collected during 370 h of observation on 35 days in the two dry seasons 2001 (May - Oct; 16 days of observation) and 2002 (May - August; 19 days). We met the Kloof group at their sleeping site at dawn, and followed them on foot to dusk. Every 5 min we took a GPS reading (Trimble Geoexplorer 3) of the individual at the rear of the group. At the same time, we scanned the behavior of all visible individuals (move, feed, stand, sit, lie, groom, drink). We estimated group spread ad libitum, when we were able to overlook a large part of the group. We determined 'potentially important' food sources *ad libitum*, when at least three animals fed from the same food source for a minimum of 3 min. Sometimes, this criterion was met in several nearby trees or bushes; we then viewed these locations as a single food resource, and took a single GPS reading in the center. For each food source, we determined which part was used (fruit, leaves, kernels, flowers, roots, etc). We collected samples of all food sources in the field and identified them in the lab.

In order to examine the extent to which natural and human-made landmarks affected spatial decisions, we mapped all roads of BNR by slowly driving along them and taking GPS readings at intervals of approximately 1 second. In addition we mapped the most prominent landmarks on the hill, three valleys, by walking along the line of the most prominent change of slope, and by taking GPS readings at intervals of 1 min approximately. We used a 1: 50'000 digital map of the area to plot contour lines.

GPS accuracy at the study site was around 16 m [Noser and Byrne 2007a for details). For this reason, we deleted the second of two subsequent GPS readings when they were less than 20 m apart. This was usually the case when slow "travel-feeding" occurred.

Before data analysis, we translated the individual behavior recorded at 5 min intervals (move, feed, stand, sit, lie, groom, drink) into "group behavior" by viewing the behavior of the majority of visible group members as characteristic for the group at the given location. Thereby, we collapsed the observed individual behavior into 5 categories: foraging, resting, moving, and drinking; travel-feeding was defined as occurring when all of the following criteria applied: 1) the majority of all visible group members foraged, 2) our criteria for an "important food source" did not apply (e.g. no synchronized feeding at the same food source was observed), 3) progression was so slow that two subsequent GPS readings were less than 20 m apart from each other. In contrast, when progression was faster, we defined the group as "moving", even when some individuals foraged. Furthermore, we subdivided foraging into two categories, fruit feeding (feeding on fruits and berries) and dry matter feeding (kernels, pods).

We applied the change-point test (CPT; [Byrne et al. 2009] to determine at which spatial locations baboon routes significantly changed direction, starting from the sleep site in the morning and ending at the sleep site in the afternoon. In brief, the CPT can be applied to a series of waypoints that represents an animal travel route (note that the CPT does not require waypoints to be equidistant). For any given waypoint of that route, the test compares whether a set of vectors before that point is collinear with a set of vectors after that point, whereby the lengths of the three resultant vectors R_q, R_k and R_{q+k} are used as indicators for collinearity (Figure 1, see [Byrne et al. 2009] for details). If R_q and R_k are collinear, then the test is re-applied at the next waypoint (note that the CPT works backwards in time). When R_q and R_k depart from collinearity at the preset level of significance, a change-point is identified.
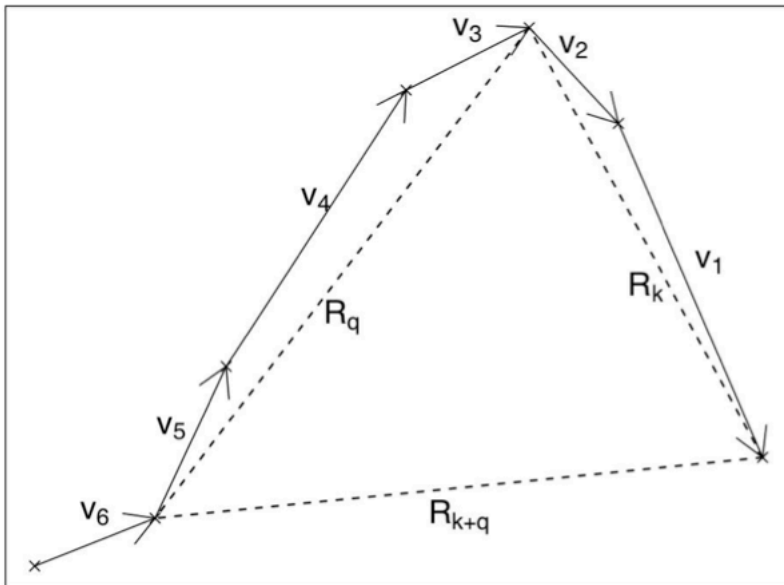
Figure 1

Figure 1
Basic idea of the change point test. An animal route is viewed as a series of vectors v_1, v_2, ..., v_n. The possibility of a change point between v_2 and v_3 is examined by comparing the distances $R_k + R_q$ with the length of the resultant R_{k+q} (figure originally published in [Byrne et al. 2009]).

Previous analysis [Byrne et al. 2009] had revealed that the CPT was most sensitive to directional changes in the Kloof group's dry season ranging when using q=6, and this was the criterion used here (that is, we considered six vectors describing travel *before* each potential change point to be compared with the vectors *after* each change point, see [Byrne et al. 2009] for details. Note that the value of q should be established anew for each data set). When a CP was detected, the CPT was re-run from this location. This procedure was repeated until all CPs of a given day were detected. In addition, we used an alpha level of $P < 0.01$.

We calculated day journey length by summing the distance between all subsequent GPS readings of a given day. We determined post hoc the behavior that the baboon group exhibited at each CP detected by the CPT. Since with q=6 the CPT had a tendency to sometimes "look around the corner" (that is, to identify as a CP the location next to the intuitive CP, see [Byrne et al. 2009], we also took into account the two GPS locations sampled before and after a CP for this analysis. As a control, we repeated this procedure with the same amount of Non-CPs along the same foraging routes; Non-CPs were random locations generated with R software (version 2.15.1).
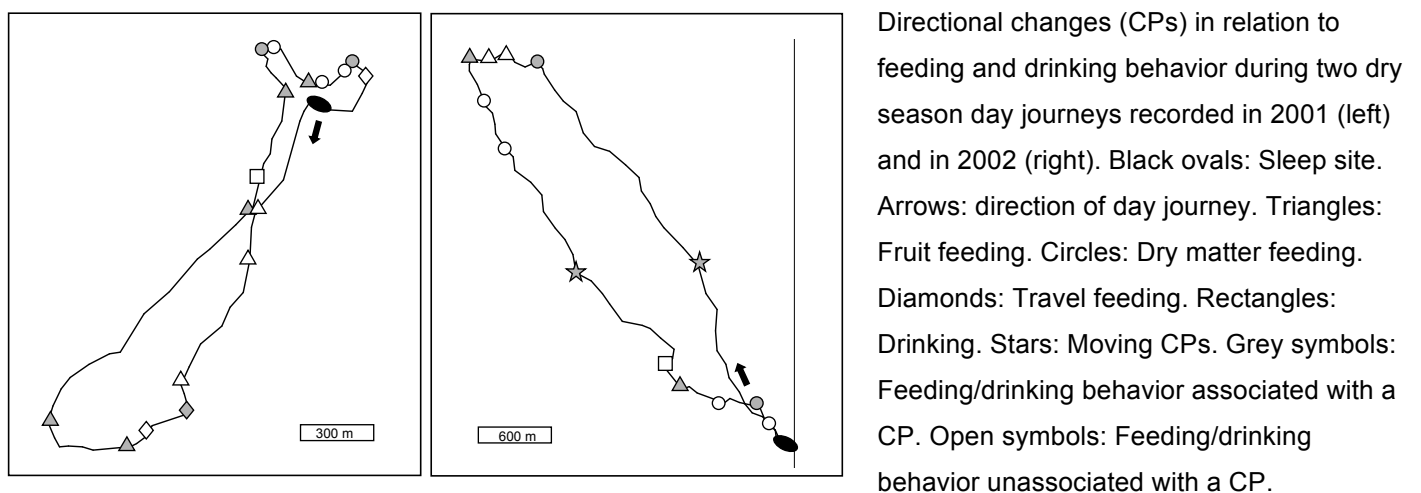
We investigated whether CPs occurred more often at some resource types than at others. We therefore counted how many times per day the study group visited a water hole, fruit or dry matter resources, and how many times they "travel fed". We then calculated the ratio of the number of resource types that were associated with a CP per day (water holes, fruit feeding, dry matter feeding, travel feeding) relative to the number of times these resource types were used. We named this the "CP ratio". For example, for fruit feeding, the CP ratio of a given day was the number of CPs associated with fruit feeding divided by the total number of GPS readings that were associated with fruit feeding that day. Since flower and leaf feeding did not occur every day, we discarded these two categories from the analysis. We interpreted a value close to 1 as an indication that the resource type preferentially elicited directional changes. For example, if travel feeding occurred at three locations on a given day, and we obtained a CP at all three locations, the CP ratio of that day would equal 1. In contrast, values close to 0 indicated that the number of CPs at a resource type was small relative to the number of locations where the focal group used this resource type. Thus, small CP ratios suggested that bee-line routes usually led beyond these resources, while high CP ratios suggested that directional changes often occurred next to them. We fitted a linear mixed-effect model with resource type (fruit feeding, dry matter feeding, travel feeding, drinking) as a fixed effect and day as a random effect [Pinheiro and Bates, 2000]. We used treatment contrasts to compare fruit feeding with the three other resource types.

In order to investigate to what degree CPs occurred in clusters, we calculated the distances between the CPs. We viewed two or more CPs as belonging to the same cluster when they were situated less than 120 m apart from each other. We based this criterion on our finding that the study group was seldom spread out over more than 100 m. Since GPS readings (accurate to 20 m) represented the location of the individual at the rear of the group, rather than the group's center, this definition gave us some confidence that we did not over- or underestimate the number of clusters.

This research adhered to the American Society Principles for the ethical treatment of primates, and permission to conduct this research was approved by our institutional animal care committee and the government of South Africa.

RESULTS

We detected a total of 222 CPs in the 35 day journeys of the Kloof group, that is, 6.34 ±1.98 CPs per day (mean ± SD). The 2001 dry season ranging gave a total of 112 CPs (7.0 ± 1.83 per day), with 69 CPs situated on the hill, and 43 next to the hill, in the plain. The 2002 dry season ranging data gave a total of 110 CPs (5.79 ± 1.99 per day), with only a single CP situated on the hill and 109 CPs situated in the plain. The difference reflects the overall home range use of the Kloof group: exclusively foraging on and next to the hill in 2001, but using this area only on the way to and from distant fruit feeding areas in the plain in 2002. For illustration, the locations of CPs and their relation to the resources used by the study group during two days are shown in Figure 2.

Figure 2

Directional changes (CPs) in relation to feeding and drinking behavior during two dry season day journeys recorded in 2001 (left) and in 2002 (right). Black ovals: Sleep site. Arrows: direction of day journey. Triangles: Fruit feeding. Circles: Dry matter feeding. Diamonds: Travel feeding. Rectangles: Drinking. Stars: Moving CPs. Grey symbols: Feeding/drinking behavior associated with a CP. Open symbols: Feeding/drinking behavior unassociated with a CP.

Day journey length was 6031 ± 2036 m in the dry season 2001, and 9557 ± 487 m in 2002. While the absolute number of CPs per day did not differ between the years, there were significantly more CPs per daily distance traveled in 2001 (1.18 ± 0.27 CPs per km traveled), compared to 2002 (0.60 ± 0.20 CPs; Figure 3). A random effects model, treating year effects as random variations around the population means [Pinheiro and Bates, 2000] gave an estimated mean intercept of 0.89, with an estimated between year SD of 0.4, while the within-year SD of 0.2 was considerably smaller.
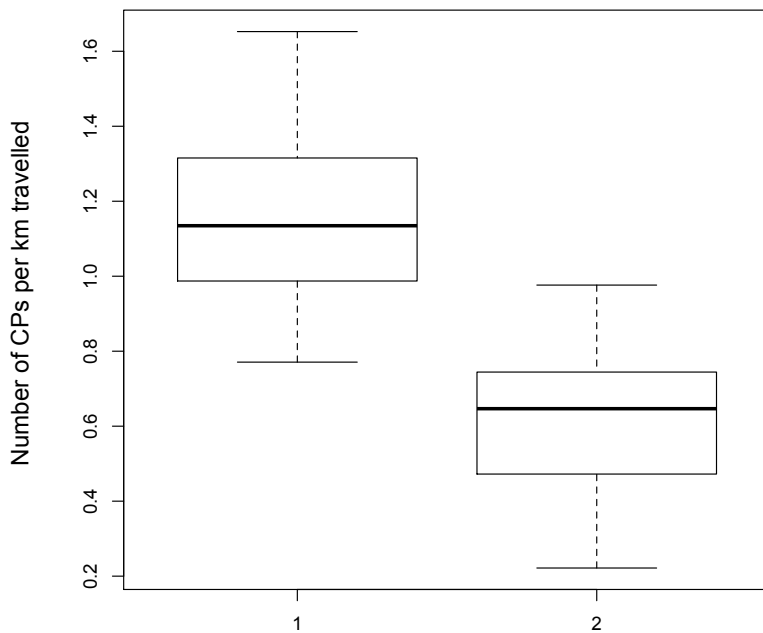
Figure 3
Number of change points per km travelled in 2001 (1) and 2002 (2). In 2001, the study group ranged on and next to the hill where a large number of landmarks such as the general slope, several valleys and views offered plenty of opportunities for orientation. In 2002, the baboons mainly used the plain where landmarks were rare: human observers could only use the shape of the hill at a distance and several car tracks for orientation.

Average distance between CPs (including distance from the sleeping site to the first CP of a given day) was 969 ± 852 m (mean ± SD; range 94 m to 3997 m). Note that, due to using q=6 in the CPT, any directional changes that may have occurred in the six first GPS readings of a given day could not be detected. This is critical when comparing the distance traveled to the first CP of a given day with the distance from which resources can be perceived. In order to account for this, we re-calculated the distances covered to the first CP of a given day by considering only the distance between the 6th GPS reading to the first CP of that day. This gave an average distance traveled between CPs of 922 ± 805 m (range 64 m to 3997 m), with an average of 632 ± 386 m for 2001, and of 1214 ± 993 for 2002. While visibility on the hill was highly variable and could not be generally determined [see methods; Noser and Byrne 2010], inter-CP-distances in the plain were far beyond the maximum distance (304 m) from which the highest branches of trees could be spotted. Thus, while at least some of two consecutive CPs were out of sight of each other in 2001, the vast majority of them were in 2002.

Investigating the behavior at the locations of directional changes revealed that approximately 1/3 (32.4 %) of the CPs were associated with fruit feeding. The corresponding fruiting trees or

bushes belonged to 16 different species, with 10 of them occurring on the hill and 6 on the plain of the baboon home range. An additional 1/3 of CPs were associated with other meaningful events such as feeding on dry matter (13.1%) and on flowers (3.2%), with travel feeding (12.2%), with drinking (8.6%), and with external disturbances (1.2%, a car driving by in 2 cases, repeated antelope alarm calling in a single case). The remaining 1/3 of the CPs were not associated with any behavior other than moving (29.3%); henceforth we refer to them as "moving CPs".

Investigating the behavior that was associated with the CPs following "moving CPs" (n=65, Table 1) we found that 43.1 % were associated with fruit feeding, and a total of 15.3 % were associated with feeding on other foods (dry matter, travel feeding, flowers), while 7.7% were associated with drinking. In 9.2% of the cases, "moving CPs" were followed by direct travel to the sleep site. In two additional cases (3.1%), the baboons were heading to the sleep site after a "moving CP", but they were disturbed by external factors. Notably, 21.5% of the CPs following a "moving CP" were again associated with moving. Examining the CPs following these "second order moving CPs" (N=14, Tab. 1), we found that they were associated with fruit feeding in 50% of the cases, with the sleep site in 21.4%, and with a water hole in 14.3 % of the cases. In one case, the CP was associated with an external disturbance (a car driving by), and in another case with travel feeding.

Fruit feeding occurred roughly twice as often at CPs, compared to Non-CPs (Table 1). Furthermore, when moving was associated with a CP, the subsequent CP was roughly three times as often associated with fruit feeding, compared to a Non-CP following a Non-CP that was associated with moving. Finally, when two subsequent CPs were associated with moving, the next CP was five times more likely to be associated with fruit feeding, compared to Non-CPs.

Table 1

Behavior at change points in baboon travel journeys.

Behaviour	A		B		C	
	Abs	%	Abs	%	Abs	%
Fruit feeding	72	**32.4**	28	**43.1**	7	**50**
	32	*14.4*	14	*15.9*	4	*11.1*
Moving	65	**29.3**	14	**21.5**	-	**-**
	88	*39.6*	36	*40.9*	11	*30.6*
Dry matter feeding	29	13.1	3	**4.6**	-	**-**
	30	*13.5*	10	*11.4*	6	*16.7*
Travel feeding	27	12.2	6	9.2	1	**7.1**
	38	*17.1*	14	*15.9*	8	*22.2*
Water hole	19	8.6	5	7.7	2	14.3
	21	*9.5*	5	*5.7*	1	*2.8*
Flower feeding	7	3.2	1	1.5	-	-
	9	*4.1*	1	*1.1*	2	*5.6*
Disturbed	4	1.2	2	3.1	1	7.1
	4	*1.8*	1	*1.1*	1	*2.8*
Sleep site	-	-	6	9.2	3	**21.4**
	-	-	7	*8.0*	3	*8.3*
Total	222	100	65	99.9	14	99.9
	222	*100*	88	*100*	36	*100*

Absolute number (Abs) and percentage (%) of A) all CPs (plain font style) and control locations (Non-CPs, italic), B) CPs preceded by a "moving CP" (plain font style), and Non-CPs preceded by a control location where moving occurred (italic), and C) CPs preceded by two "moving CPs" (plain) and Non-CPs preceded by two control locations where moving occurred (italic).

Table 1 further shows that when two subsequent "moving CPs" occurred, water holes and the sleep site were more often associated with the next CP, compared with Non-CPs. (Note that we did not formally test the sleep site with the CPT. However, it was obviously a crucial resource, given that the Kloof group returned to this site every night for two years). Although the Kloof group visited at least one of the water holes every day, there was no difference in the percentage of CPs and Non-CPs that were associated with drinking at water holes.

Figure 4 shows the overall mean CP ratio (horizontal line) relative to the mean CP ratio of the four categories of resource use (F = fruit feeding, H = drinking, D = dry matter feeding, S = travel feeding), relative to the days of observation (D1 - D35 = daily CP ratios), and relative to the two dry seasons (Y1, Y2 = yearly CP ratios). The CP ratio was largest for fruit feeding, and smallest for travel feeding, and suggests that both, "dry matter feeding" and "travel feeding" were more likely to occur in the course of straight travel, whereas "fruit feeding" and "drinking" were more likely to be associated with a CP. Also, Figure 4 shows that the variability between days was relatively large. Furthermore, the CP ratio was higher in 2001 than in 2002, suggesting that more CPs occurred at locations of feeding or drinking in 2001.
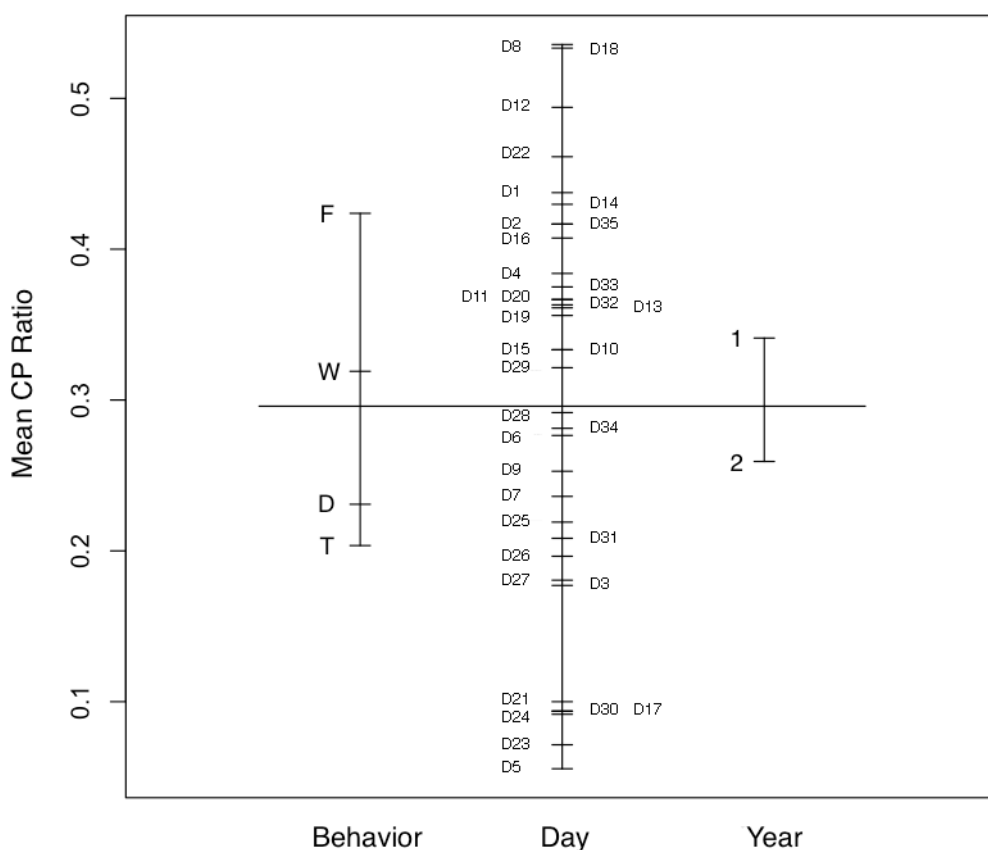

Figure 4
Overall mean CP ratio (horizontal line) relative to the mean CP ratio of four behavioral categories (F = fruit feeding, W = drinking, D = dry matter feeding, T = travel feeding), relative to the mean CP ratio of days of observation (D1 - D35 = daily CP ratios), and relative to the CP ratios of two years (1, 2). The differences between fruit feeding and dry matter feeding, and between fruit feeding and travel feeding were significant.

However, variability between years was relatively small relative to the variability between the categories of behaviors associated with CPs. The overall mixed-effects model was significant (n=134 observations, ANOVA, df=3, F=3.57, p=0.017), indicating that the variability between

usage of resource types was large. This was due to a significant difference between fruit feeding

and dry matter feeding (p = 0.0125) and between fruit feeding and travel feeding (p = 0.002),

whereas there was no difference between fruit feeding and drinking at water holes (p > 0.2).

Thus, travel routes of the Kloof group changed direction significantly more often after fruit feeding

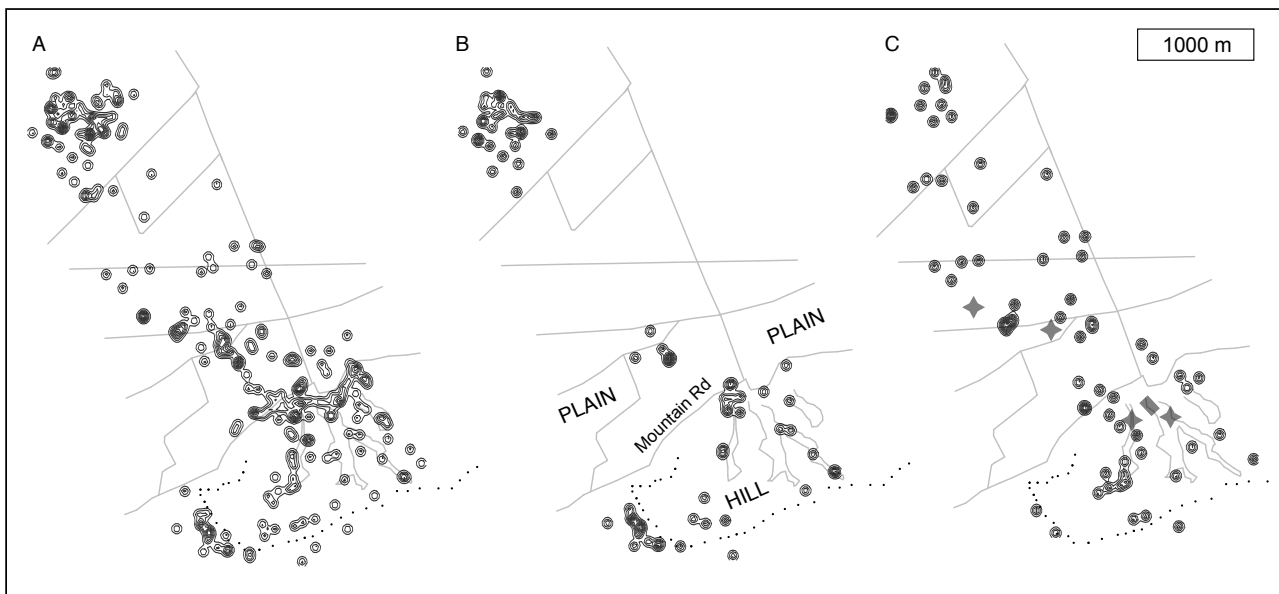compared to dry matter feeding, travel feeding and drinking.

Figure 5

Kernel density plots showing the spatial distribution of CPs in relation to landmarks in the plain (area N of
"Mountain Road") and on the hill (area S of "Mountain Road). Grey lines in the plain: car tracks. Grey lines on
the hill: valleys. Dotted line: 1080 m contour line, most prominent change of slope. (A) All CPs. A large number
of change points occurred along the car tracks in the plain, and along prominent slope differences (foot of the hill
running parallel to "Mountain Road", valleys). (B) CPs associated with fruit feeding. Fruit was relatively abundant
on the hill, but in the plain the baboons traveled long distances to reach a single, large fruit patch NW of the
sleep site, forming the apex of day journeys in 2002. (C) Moving CPs. In the plain, the majority of "moving CPs"
were associated with either the fruit patch NW of the sleep site, or with car tracks (the baboons did not usually

Figure 5 shows the locations of all CPs (A), of CPs that were associated with fruit feeding (B),

and of "moving CPs" (C) relative to the most prominent landmarks available to the study group:

car tracks in the plain and three valleys and the slope on the hill. (Note that the outermost CPs

approximately indicate the home range border).

CPs were not evenly distributed in this area. 127 CPs (57.2%) belonged to a cluster of at least two CPs, whereas 95 (42.8%) occurred singly, that is, with the next neighboring CP more than 120 m apart. 64 CPs belonged to a cluster of two, 34 to a cluster of three, 22 to a cluster of four, and 7 to a cluster of five CPs. However, Figure 5 also shows that many CPs did not occur in discrete clusters, but frequently occurred next to landmarks. Most prominently, a large number of CPs occurred at the foot of the hill, paralleling the "Mountain Road" to its South, or directly on the "Mountain Road" (Figure 5A). On the hill, almost all CPs were either situated in or next to one of the three valleys, or next to another very prominent change of slope, the dotted 1080 m contour line. Most obviously, the CPs associated with fruit feeding on the SW border of the home range were the turning points of most of day journeys recorded in 2001 (Figure 5B). In the plain, CPs were mainly clustered around one of the water holes, along the roads, and in a large patch on the N border of the home range where predominantly fruit feeding (and to a lesser degree also dry matter feeding and moving) occurred. These CPs illustrate the turning points of all day journeys recorded in 2002.

"Moving CPs" could potentially result from 1) external factors disrupting travel journey such as nearby baboon groups, or human activity, 2) re-orientation at the locations where important resources come into sight, 3) re-orientation based on landmarks that are out of sight of important resources, and 4) failure to find food at formerly productive resource places. We examined these possibilities, by first excluding external factors as a possible explanation. Therefore, we examined whether more CPs than Non-CPs were associated with the audible signs (wahoos, barks, screams) of neighboring baboon groups that foraged in the vicinity. We found that this was not the case: while a total of 58 CPs were associated with such vocalizations, 79 Non-CPs were. Vocalizations of neighboring groups were associated with roughly 1/4 of "moving CPs" (23.1%), but also of other CP classes; with 24.5% of CPs associated with fruit feeding, and with 27.6% of CPs associated with dry matter feeding. Thus, the presence of neighboring groups in the area

could be excluded as explaining "moving CPs". Human made disruptions of the study group's travel journey were not associated with "moving CPs", suggesting that external factors did not account for their occurrence. Also, we excluded reorientation when fruit trees came into sight as a possible explanation for the occurrence of "moving CPs": distance covered between a "moving CP" and the next CP associated with fruit feeding was 1348 ± 1126 m, ranging from 243 to 3978 m. When two "moving CPs" occurred consecutively, the distance between them was 1527 ± 605 m. And last, Figure 5C shows that only a few "moving CPs" occurred in areas where fruit feeding occurred. Rather, they were primarily situated in the areas connecting the sleep site area and the fruit feeding areas. This also excludes failure to find food at formerly productive resource sites as a possible explanation for the occurrence of "moving CPs". Rather, "moving CPs" indicate subtle directional changes along the directed movement from and to the two fruit feeding areas SW and N of the home range, and the sleep site area. In the plain, "moving CPs" often occurred next to roads. On the hill, "moving CPs" sometimes occurred next to the valleys, suggesting that the baboons used roads and valleys for subtle re-orientation along their directed travel from the sleep site to areas of high fruit density and back to their sleep site.

DISCUSSION

The Change Point Test [Byrne et al. 2009] is a useful tool to investigate the factors affecting the spatial decisions of animals. Variation of the relation between directional changes in travel routes and behavior of individuals, groups, populations or species at these locations can give important insight into foraging strategies and the underlying cognitive mechanisms. Our results allow the distribution of change points in the travel of baboons living in a dry woodland savannah to be compared with previously analyzed foraging journeys of gibbons living in a wet evergreen forest [Asensio et al. 2011]. Fruit feeding was very important for both species. In our baboons, fruit feeding accounted for roughly 1/3 of directional changes, and considerably more fruit feeding

occurred at change points compared to control locations along travel routes. Furthermore, directional changes occurred more often at locations of fruit feeding than at locations where other resources were used, suggesting that fruit played a crucial role in the spatial decisions taken by our study group. However, unlike the gibbon groups, our baboon group did not merely travel from one fruiting tree to the next. Fruiting trees determined day journey lengths: although comparatively scarce in the study group's range, fruiting trees constituted the turning points of day journeys, after which the baboons re-approached the sleep site. In between these extremes of day journeys, directional changes also occurred elsewhere: at water holes, at places where, on a behavioral level, dry matter feeding (kernels, pods) and slow travel feeding were observed. However, these resources only played a minor role in the spatial decisions of our study group: they occurred at change points and at control locations to the same extent. For kernels, pods, and probably also for most items ingested during travel feeding, this makes sense in the light of absolute abundance: in comparison to fruit and water, these resources occurred virtually everywhere in the Kloof group's home range so that no planning was required to reach them.

Water was an important, but scarce resource in the dry winters at the study site, and the baboons visited at least one of the four available water holes on a daily basis. Travel speed of the Kloof group was generally increased before reaching the water holes and route segments were particularly straight [Noser and Byrne 2007a], two features that researchers often associate with goal-directed travel and mental anticipation. Interestingly, the Kloof group did not systematically change travel direction shortly before or after drinking. Water holes were associated with directional changes to the same extent as with control locations along straight route segments. Thus, water holes were often situated on the straight route segments connecting two other resources. On a behavioral level, the baboons often drank "en passant", refraining from resting next to the water, especially when they were on their way to more distant fruiting trees in the mornings. Rather, they quickly descended the rocks (natural pools) or walls (artificial dams) to

the water one after the other, and the individuals in front of the group continued progression at high speed while group members at the rear still waited for their turn to drink. One possible, but not an exclusive explanation for this finding is that the baboons planned their routes *beyond* the water holes, and approached them with a more distant goal already in mind.

To our knowledge, a single study suggests that monkeys are capable of planning more than a single step ahead: captive vervet monkeys were tested with three grapes that were presented simultaneously, in a small arena that could be perceived at a glance. They did not travel first to the nearest grape, but collected the grapes in a sequence suggesting that they may have planned three steps ahead [Gallistel and Cramer 1996; Cramer and Gallistel 1997]. However, besides some methodological issues of the study (see [Janson, this issue]) this finding has never been replicated, and it is unclear how choices of simultaneously presented stimuli in small-scale space would translate into a natural foraging context. Empirical evidence coming from wild primates does not support the notion of a two-step planning mental capacity: gibbons mostly travel in straight lines between out-of-sight fruit trees, suggesting that they plan a single step ahead [Asensio et al. 2011]. Janson [1998] drew the same conclusion from the way a group of capuchin monkeys *(Sapajus nigritus,* formerly *Cebus apella nigritus)* traveled among several experimentally placed feeding platforms: the monkeys did not optimize the overall distance among platforms, but generally chose the nearest neighbor platforms even if they had previously experienced larger rewards at more distant ones. Thus, both empirical evidence from other primates as well as Ockham's razor applied to our data suggest that explanations other than a mental ability to plan two (or more) steps ahead should be considered (see also [Janson, this issue]).

Alternatively, baboons may sometimes travel in straight lines beyond water holes because they follow habitual routes that have been shaped in the course of a long time. Indeed, we found that

the Kloof group strictly followed a habitual route in a very specific condition [Noser and Byrne 2010]: during a comparatively short time period in summer, when they foraged for rare but highly preferred Mountain figs *(Ficus glumosa)* under pronounced time pressure due to intergroup competition. The corresponding travel routes, when superimposed on each other, were comparable to the narrow corridors that woolly monkeys and spider monkeys used daily when foraging in primary rain forest [Di Fiore and Suarez 2007].

However, during winter, when the present data set was collected, the Kloof group did not strictly use repetitive travel routes: a large number of directional changes occurred more than 120 m apart from the nearest neighbor, suggesting that many routes ran far from each other. Rather than occurring at specific locations, directional changes of travel routes were often associated with continuous prominent landmarks such as sudden changes in slope of the hill, and with car tracks occurring in the otherwise monotonous plain area of the home range. In addition, approximately 1/3 of the CPs did not correspond with any resources, but were simply associated with the study group "on the move". Sometimes, two subsequent directional changes of this type preceded a change point at a fruit tree. These "moving change points" were particularly often situated close to dominant landmarks (car tracks in the plain, along valleys and pronounced changes of slope on the hill).

How do these findings fit with our earlier work [Noser and Byrne 2007b] suggesting that the spatial representation underlying the observed foraging routes is a network map rather than a Euclidean or vector map? The behavioral manifestation of a simple form of a network map would be a network of travel routes, and as a result, clustering of change points, for example, at the nodes of the network, or at bends of certain repeatedly used routes. However, we found only a limited degree of clustering, suggesting that change points may not represent the nodes of a network map. In addition, many change points represented minor directional changes in the

course of highly directed travel, suggesting that at the corresponding locations the baboons slightly adjusted the movement direction they had already chosen rather than taking any novel decisions.

A possible explanation for these findings is that the baboons possess knowledge about an extremely complex network of routes, and our data set only captured a small part of it. However, a more parsimonious explanation is more likely: the network map of the Kloof group contained a few large, prominent landmarks, many of them out-of-sight of each other. When traveling between landmarks, the baboons either navigated by holding visual contact with a distant landmark (maybe a tall tree, or the overall shape of the hill when navigating towards the hill in the plain area), or held an approximate bearing, which they adjusted, if necessary, as soon as a the next landmark came into sight (for example a car track). This resulted in relatively broad corridors along which they travelled, and in relatively subtle directional changes when traveling in these corridors ("moving change points"). In addition, the baboons possessed finer-grained knowledge about the routes to a few discrete locations such as to a few water holes [Noser and Byrne 2007b] and to certain important trees (eg. Fig trees, *Ficus glumosa,* [Noser and Byrne 2010]*).* However, given that many food sources at Blouberg Nature Reserve were either more or less evenly distributed or else occurred in relatively large patches (eg the fruit trees used in winter 2002), the number of routes to discrete locations to remember in detail remained relatively small.

In contrast to Poucet [1993], who proposed that animals use a Euclidean (or vector) map when navigating in small-scale space and a network map when traveling in large-scale space, we found no evidence for a Euclidean map. Combining our earlier [Noser and Byrne 2007b, 2010] and the present findings, we conclude that baboons use a network map in both situations, for travel among prominent landmarks and large resource patches in large-scale space [this study] as well as for route-based travel to pinpoint relatively small resource locations ([Noser and Byrne

2007b]; [Noser and Byrne 2010]; see [Garber and Porter, this issue], for a similar conclusion for saddleback tamarins). This claim assumes that both travel along repetitive routes and travel along broad corridors is based on the same basic cognitive mechanism. For example, when traveling to a water hole over a large distance, the network map may become more detailed close to the water hole. As a result, when superimposing a large number of travel routes to that water hole, the physical width of the resulting route would narrow down in vicinity to the water hole. However, it is also possible that the varying travel patterns result from a hierarchy of navigational methods, a more general heuristic to get to an approximate resource area, and a local network map for pinpointing discrete, relatively small resources.

Sigg and Stolba [1981] found that, similar to our study group, a Hamadryas baboon group living in the Ethiopian semi-desert traveled along relatively broad corridors during a large part of their daily ranging, but used narrow, repetitive routes shortly before arriving at the water holes. Thus, this travel pattern applies to both a chacma baboon and a hamadryas baboon group living in a dry and a semi-arid habitat respectively, both covering large distances every day to find sufficient food and water. However, it contrasts with travel patterns found in spider monkeys, woolly monkeys [Di Fiore and Suarez 2007], and probably also in gibbons [Asensio et al. 2011] living in wet forest. Whether these differences correspond to the fundamental habitat differences of these primates, requiring differing navigational strategies, or whether they actually reflect variation of cognitive abilities remains to be clarified in the future. For example, a combination of the change point test [Byrne et al. 2009] with methods that asses area-restricted search [Knell and Codling 2012] may allow to control for ecological variation of habitats and for differences in foraging strategies and ultimately to shed more light on the question of interspecific variation in spatial cognition in wild primates.

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