Travel Routes and Spatial Abilities in Wild Chacma Baboons (Papio ursinus)

ANNE LOUISE DE-RAAD

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TRAVEL ROUTES AND SPATIAL ABILITIES IN WILD CHACMA BABOONS (*PAPIO URSINUS*)

Dissertation submitted to Durham University
for the Degree of Doctor of Philosophy

Anne Louise de Raad

Department of Anthropology
Dawson Building, Durham
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ABSTRACT

The primary objective of this research was to give insight into the spatial cognitive abilities of chacma baboons (*Papio ursinus*) and to address the question whether chacma baboons internally represent spatial information of large-scale space in the form of a so-called topological map or a Euclidean map. Navigating the environment using a topological map envisions that animals acquire, remember and integrate a set of interconnected pathways or route segments that are linked by frequently used landmarks or nodes, at which animals make travel decisions. When animals navigate using a Euclidean map, animals encode information in the form of true angles and distances in order to compute novel routes or shortcuts to reach out of view goals. Although findings of repeatedly used travel routes are generally considered evidence that animals possess topological-based spatial awareness, it is not necessarily evidence that they navigate (solely) using a topological map or lack complete Euclidean spatial representation. Therefore, three predictions from the hypothesised use of a topological map and Euclidean map were tested to distinguish between them. It was investigated whether there was a difference in travel linearity between the core area and the periphery of the home range, whether travel goals were approached from all directions or from one (or a few) distinct directions using the same approach routes and lastly, whether there was a difference between the initial leaving direction from a travel goal and the general direction towards the next goal. Data were collected during a 19-month period (04/2007-11/2008) at Lajuma research centre in the Soutpansberg (Limpopo Province, South Africa). A group of baboons were followed from their morning sleeping site to their evening sleeping site for 234 days, during which location records, behavioural data and important resource data were recorded. A statistical procedure termed the change-point test (CPT) was employed to identify locations at which baboons started orienting towards a goal and baboons showed goal-directed travel towards identified travel goals. Subsequently, hotspot analysis was employed to delineate clusters of such change-points, termed ‘decision hotspots’. Decision hotspots coincided with highly valuable resources, towards which baboons showed significantly faster travel. It thus seemed that they ‘knew’ when they were nearing their goals and adapted their speed accordingly. Decision hotspots were also located at navigational landmarks that delineated a network of repeatedly used travel routes characteristic of a topological map. Therewith, this method reveals an important utility to the study of decision-making by allowing a range of sites to be selected for detailed observations, which were previously limited to sleeping sites or ‘stop’ sites, which would be impossible if the decision hotspots had not been previously identified. Furthermore, baboons travelled as efficiently in the periphery as in the core area of their home range, which was suggested to be more consistent with Euclidean spatial awareness. However, comparatively low travel linearity throughout the home range revealed it is more likely that the baboons accumulated a similar knowledge of the periphery as of the core area, which allowed them to navigate with a similar efficiently through both areas. The mountainous terrain at the study site provided ample prominent landmarks to aid the baboons in navigation and allowed baboons to initiate navigation to a travel goal with the same direction as when they reached that goal. Baboons did not approach travel goals from all directions, but instead they approached their goals from the same direction(s). In conclusion, the findings of this research are more consistent with the use of a topological spatial representation of large scale space, where landmarks aid baboons to navigate efficiently through large scale space. A review of the literature shows that until date, evidence for the existence of Euclidean spatial representation in both animals and humans is extremely limited and often unconvincing. It is likely that a high level of experimental control is necessary to unambiguously demonstrate the existence of Euclidean spatial awareness in the future.

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PREFACE

The material herein has not been submitted for a degree, diploma or other qualification to this or any other university. This dissertation is the result of my own work and includes nothing which is the outcome of the work done in collaboration. All photographs included were taken by the author during the course of this work. The copyright of this thesis rests with the author. No quotation from it should be published without the prior written consent and information derived from it should be acknowledged.

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TRAVEL ROUTES AND SPATIAL ABILITIES IN WILD CHACMA BABOONS

CHAPTER 1

NAVIGATING THE LITERATURE

In this chapter literature regarding spatial mapping and navigation is reviewed and definitions of the types of internal spatial representations animals may possess are presented in Section 1.1. The objective of this thesis is discussed in Section 1.2 and finally an overview of the thesis is presented in Section 1.3. Table 1.1 provides a set of definitions of key concepts utilised in this thesis.

Table 1.1 Key concepts in this thesis (adapted from Urbani 2009)

Concept	Definition
Cognition	Animals' internal mechanism of information processing. Integration of previous learned information and/or newly discovered information for understanding the relationship of elements in the individual's environments (Tomasello & Call 1997; Shettleworth 1998; Sternberg 1999; Reznikova 2007)
Spatial representation	Animal's ability to internally represent, encode and integrate the relative or specific locations of points in the environment, and use information of spatial relationships to reach goals (Gallistel 1990; Wehner & Wehner 1990; Poucet 1993; Benhamou 1996; Cheng & Spetch 1998; Etienne *et al.* 1998; Dyer 1998, 2000; Menzel *et al.* 2006)
Landmarks	Fixed points in the environment used during navigation in order to reach a goal. Landmarks can be used solely or as an array. A landmark array is defined as configurations of beacons that function as associative cues for navigation (Cheng 1986; Braithwaite 1998; Save *et al.* 1998; Sherry 1998; Kamil & Cheng 2001).

1.1 Introduction

In the wild, animals face the challenge of navigating through the environment to find the most productive resources in the most effective way. The domain of spatial orientation has been extensively discussed in the animal navigation literature and one of the key questions is *how* animals find their way around and how they 'know' where to go?

Three different mechanisms of spatial memory and their underlying spatial representations have been proposed. The initial concept of the *cognitive map* was introduced by Tolman in 1948 and corresponds to the idea that animals possess highly detailed information about the spatial relationships among relevant features of the environment. This mechanism, also referred to as the *vector map* (Byrne 2000), *mental map* (Boesch & Boesch 2000), *geometrical map* (Asensio *et al.* 2011) or *Euclidean map* (Normand & Boesch 2009), allows animals to compute distance and direction from any one place to any other known place, based on a Euclidian representation of space. True angles and distances between landmarks are represented within some kind of coordinate system, which allow an animal to compute routes between points that are out of view and, thus, to bridge informational gaps.

This mechanism allows animals to assess distance and direction to a potential destination from virtually any point of the home range and to travel in straight-lines and to make novel short-cuts between points. In this thesis the term Euclidean map (Normand & Boesch 2009) will be used to characterize this mechanism.

The first alternative mechanism was initially called *dead reckoning*, but is now more often referred to as *path integration*. This type of orientation mechanism allows animals to locate an object in relation to an egocentric (also called auto-centered, self-centered, self-referenced or viewer-referenced) reference system (or frame) (Klatzky 1998; Poti *et al*. 2005; Presotto & Izar 2010). Exceptions notwithstanding, there is general understanding that in an egocentric reference frame, locations and orientation are represented with respect to the organism itself, that is in body-centered coordinates (Klatzky 1998; Poti *et al*. 2005). Path integration does not require a Euclidean map (in the sense of memory) of locations in large-scale space, but allows for computation of current position with reference to a point of departure – without the help of landmark information (Etienne *et al*. 1996). Path integration is therefore of special importance for central place foragers or species living in open habitat where visual landmarks are scarce (Lührs *et al*. 2009). For instance, Saharan ants (*Cataglyphis bicolour*) forage in a flat open landscape generally lacking landmark information. These ants track their own movements from the nest by memorizing the corresponding distances and angles, and compute a direct homing route to their nest from any position in space (Wehner & Srinivasan 1981; Collet & Collet 2000). Examples of path integration also include studies on humans. For example, Polynesian sailors use path integration to navigate long distances in open sea during the day, rather than travelling at night while relying on spatial cues from known stellar configurations (Oatley 1974). The sailors maintained a detailed record of distances in relation to travel time between islands and additionally made corrections of the speed and bearing of the boats during navigation relative to wind and wave directions and strength (Oatley 1974). To rely solely on path integration for navigation, often results in navigational errors that become amplified the further along the path the animal travels (Wehner 1992; Bennet 1996; Collet & Zeil 1998). So while most animals use path integration in their movements (Etienne *et al.* 1998), they may also possess additional spatial cognitive abilities.

Path integration is often supplemented by route-based navigation that uses the topological relation between objects (Collet & Zeil 1998). This second alternative mechanism is referred to variously as a *route-based, network* or *topological map*. In contrast to path integration, this type of orientation mechanism allows animals to locate an object in relation to an allocentric (also referred to as environmental, external, exocentric or geocentric) reference system (or frame) (Klatzky 1998; Poti *et al*. 2005; Presotto & Izar 2010). In an allocentric reference system locations are represented within a framework external to the holder of the representation and independent of his or her position (Klatzky 1998). Spatial relations are thus defined with respect to elements of the environment, especially reference objects or landmarks (*i.e.*, perceptible elements are used as cues to the position of other objects) (Poti *et al*. 2005). A topological map mechanism requires associative memory and allows animals to navigate following network of commonly re-used routes and landmarks. Animals store information about the way in which landmarks and targets are connected to one another in space (only topological relationships between objects and paths are preserved). Based on the topological relation between objects, this mechanism implies a representation of space in which the animal is not able to compute distances, direction or short cuts to a known location, but uses a travel route based on landmarks as a succession of instructions containing approximate local information about direction and distance (Byrne 2000; Garber 2000). Animals using a route-based representation are expected to re-use the same set of travel paths to reach travel goals that are located in the same part of their home range (Suárez 2003).

Animals that possess Euclidian map-like spatial awareness and topological map-like spatial awareness rely on fixed features of the environment to orient in space and landmarks function as points of information. However, the degree and manner in which landmarks are used in these two different types of spatial representation are different. Using a topological map an animal needs to encode a set of landmarks that are used as prominent beacons (*e.g.*, nodes or topographic features such as mountain ridges) and that are located along habitual used travel routes (Byrne 2000; Garber 2000; Di Fiore & Suarez 2007; Presotto & Izar 2010). The same landmark may be encoded as different views and possibly different points (Urbani 2009). In contrast, animals using a Euclidean spatial representation encode different views of the same landmark as a single point or reference to compute a novel route (Urbani 2009). In conclusion, animals using a Euclidean spatial representation will travel by computing a relatively straight or direct route to reach travel goals and have the ability to take novel routes and short cuts, whereas animals using a topological spatial representation, will travel along habitually used travel routes and re-orient travel at frequently used nodes. Table 1.2 provides a brief description and summarises synonyms of the different types of spatial representations discussed above as found in the literature.

The topological map has been suggested to be an efficient system for storing environmental spatial information (Poucet 1993; Di Fiore & Suarez 2007) and is considered less cognitively demanding than a Euclidean map, because instead of remembering where resources are, animals have only to associate the resources along familiar routes and memorise this association between landmarks and the nearby food source (Garber 2000; Poti *et al.* 2005; Presotto & Izar 2010).

Table 1.2 Types of mental maps, their synonyms and a brief description.

Spatial representation	Synonyms	Description
Euclidean map	Cognitive map Coordinate(-based) map Vector map Metric map Geometric map	Spatial representation in which an animal encodes information in the form of true angles and distances in order to compute novel routes or shortcuts to reach out of view goals (Byrne 2000; Garber 2000).
Topological map	Route-based map Topological mental map Topology-based mental map Network map	A spatial representation, in which an animal acquires, remembers and integrates a set of interconnected pathways or route segment that are linked by a set of landmarks or nodes (Byrne 1982; Bennet 1996).
Path integration	Dead-reckoning	Spatial representation in which an animal tracks changes in the position of its body relative to the environment and uses this information to return to a target or goal (Benhamou *et al.* 1990).

1.2 Thesis aim

A central issue in biological anthropology involves the understanding of primate cognition and how prosimians, monkeys, apes, and humans store, encode, represent and integrate spatial and ecological information (*e.g.*, Janson 1998; Milton 1988, 2000; Boinski & Garber 2000; Bicca-Marques & Garber 2004, 2005; Janson & Byrne 2007). Living primates navigate through home ranges that vary in size from 0.1 ha in red fronted lemurs (*Eulemur fulvus rufus*) to several hundreds of hectares in gorillas (*Gorilla gorilla gorilla*) (Milton & May 1976) and therefore individual species face different challenges associated with resource exploitation (Tomasello & Call 1997; Boinski & Garber 2000; Byrne & Janson 2007). Several studies of range use and foraging behaviour have demonstrated that primates have the ability to relocate widely distributed food patches (Janson 1998, 2007; Garber 1989), to travel in relatively straight-line paths to widely distributed, out-of-sight resources, to weigh the relative values of particular food items, and to maintain detailed spatial representation of the distribution of these resources in their home range (*e.g.*, New World primates: *Alouatta palliata*: Milton 1980; Garber & Jelinek 2005; Hopkins 2011; *Ateles geoffroyi*: Milton 1981; Chapman *et al*. 1989; Valero & Byrne 2004, 2007; *Ateles belzebuth*: Di Fiore & Suarez 2004, 2007; *Cebus apella*: Janson 1990a, 1990b, 1996, 1998; Janson & Di Bitetti 1997; *Lagothrix lagotricha*: Di Fiore & Suarez 2004, 2007; *Pithecia pithecia*: Cunningham 2003; *Saguinus fuscicollis*: Garber 1989, 2000; Garber & Hannon 1993, Bicca-Marques & Garber 2003; *Saguinus iperator*: Bicca-Marques & Garber 2003, 2005, *Saguinus mystax*: Garber 1989, 2000; Garber & Hannon 1993, Old World primates: *Papio ursinus*: Noser 2004; Pochron 2001, 2005; Noser & Byrne 2007a, 2007b; Byrne 2000; Apes: *Pan troglodytes*: Boesch & Boesch 1984, Bates & Byrne 2004, Normand & Boesch 2009 and Prosimians: *Eulemur fulvus rufus* and *Prophithecus edwardsi*: Erhart & Overdorff 1999, 2008; Overdorff & Erhart 2001). These abilities themselves, however, do not offer insight into the underlying spatial representation used for navigation. In this thesis, spatial mapping and decision-making in wild chacma baboons (*Papio ursinus*) are examined with the aim to give insight to their spatial cognitive abilities. The primary objective of this research is to address the question whether chacma baboons ranging and travel patterns are consistent with a route-based or a Euclidean-based spatial representation.

1.3 Thesis overview

Following this introduction, the study site and basic information on the biology, behaviour and ecology of baboons (*Papio* spp.) are presented in Chapter 2. Chapter 2 also provides a description of the baboon troop studied and describes general methods of data collection. In Chapter 3, the concept of home range is discussed and the baboon's ranging is examined and compared to existing home range data of other baboon populations. Two home range estimators are discussed in more detail and methodological issues related to these estimators are considered. In Chapter 4 a recently introduced statistical test used to identify locations at which animals start orienting towards a goal (Byrne *et al*. 2009), is presented. This so-called change-point test is explained in detail and an elaborate sensitivity test is conducted to investigate potential effects of sampling protocol and to establish the optimal change-point test parameter values to analyse baboon travel routes. In Chapter 5, the change-point test is applied to baboon travel routes and results are compared to an alternative method to identify locations where animals significantly change travel direction, termed the turn angle method. The utility of the two methods to identify locations at which animals start orienting towards a goal and to identify locations where travel decisions are being made is examined. In Chapter 6, the utility of the change-point test is extended with a hotspot analysis to provide the first quantitative analysis of the spatial distribution of locations where animals repeatedly change direction on multiple travel days. These so-called "decision hotspots" are classified according to their association with resources and topological features. In Chapter 7, the concept of goal-directed travel is discussed and it is investigated to what extent baboon travel routes are goal-directed. Finally, Chapter 8 aims to determine whether movements of chacma baboons are more consistent with topological spatial awareness or Euclidean spatial awareness. First, it is investigated whether baboons use a network of routes to navigate through the landscape and several methods to delineate such a network are discussed. Then a series of hypotheses are tested, concerning the degree to which chacma baboons rely on a route-based spatial representation or a Euclidean-based spatial representation to integrate ecological information. Chapter 9 summarises and discusses the major findings of this thesis.

CHAPTER 2

GENERAL METHODOLOGY

2.1 Baboons

Data were collected on chacma baboons (*Papio ursinus*) (Kerr 1792). Two subspecies have been recognised with *Papio ursinus griseipes* (Pocock 1911) occurring in south-west Zambia, Botswana (Okavango Delta), Zimbabwe, and Mozambique (south of the Zambezi) and *Papio ursinus ursinus* (Kerr 1792) occurring in the remainder of the range, in all provinces in South Africa and throughout Namibia (Figure 2.1). Groves (2005) listed *Papio ursinus ruacana* (Shortridge 1942) from northern Namibia and Angola as a valid subspecies, although this had been questioned by Grubb *et al*. (2003). In this thesis the study animals are referred to as chacma baboons or simply baboons.

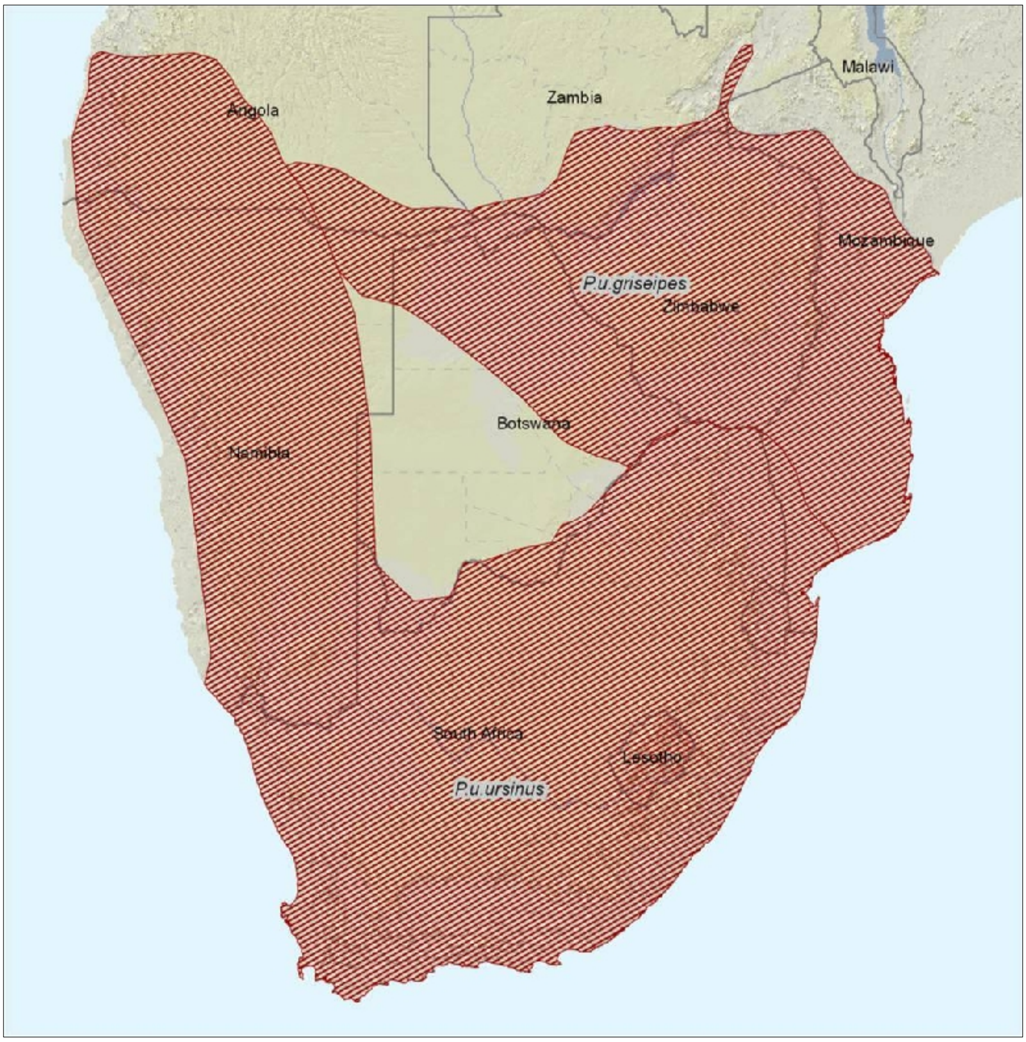

Figure 2.1 Range of chacma baboons (*Papio ursinus*) (*red shaded area*) throughout Southern Africa (IUCN [International Union for Conservation of Nature] October 2009).

Chacma baboons live in permanent groups, of anywhere from 4 up to about 200 individuals that contain several males and multiple females with their offspring (Hamilton *et al.* 1976; Hill & Lee 1998). For male baboons, the transition to sub-adult from the juvenile stage is marked by rapid testes enlargement and the development of a large dog-like muzzle and enormous canine teeth (Alberts & Altmann 1995) and as a result there is pronounced sexual dimorphism in adult baboons. After about 2–3 years spent as sub-adults, males achieve a size and competitive ability that enables them to defeat some adult males in fights, thereby accomplishing the transition to adulthood and gaining potential access to fertile females (Alberts & Altmann 1995; Alberts *et al.* 2006). When males become fully adult, at around nine years of age, they disperse from their natal troop (Cheney & Seyfarth 2007). The number of adult males in a baboon group at any given time ranges widely, from as few as 1 to as many as 12 (Cheney & Seyfarth 2007; Hoffman & Taylor 2008). As in most Old Word monkeys, female baboons stay throughout their lives in their natal groups. The social organization of baboon groups is therefore based around females and closely related females tend to associate with one another, forming kin-based subgroups (*i.e.*, matrilines) within the larger troop (Smuts 1995; Silk *et al.* 2006).

Chacma baboons are promiscuous and both males and females tend to mate with several different members of the opposite sex. Females usually have their first estrous cycles, which last for about 28 days (Cheney & Seyfarth 2007), when they are 4–6 years old, although they do not conceive until 1 or 2 years later (Altmann *et al*. 1977; Smuts 1995). When their perineum begins to swell during their estrous cycles, adolescent and adult females will solicit copulations from males of all ages, although only juveniles and adolescents usually show much interest (Cheney & Seyfarth 2007; Smuts 1995). As ovulation approaches and a female's perineum reaches maximum size, females often form a sexual consortship with an adult male, in which the male closely follows the female and they groom and mate at high rates (Cheney & Seyfarth 2007). Apart from the short-term relationships in sexual context between males and females, they may form long-term bonds which have been described as "special relationships" (Strum 1975), "friendships" (Smuts 1995) and "intense long-term pair bonds" (Ransom & Rowell 1972). Females may thus form short-term bonds with males and strong long-term bonds with males and with other females, but adult male baboons rarely associate with members of their own sex (Smuts 1995).

Chacma baboons are found in a range of habitats from the wet, cold Drakensberg Mountains in South Africa (Barton *et al.* 1996; Byrne *et al.* 1990, 1993; Whiten *et al.* 1987) to the dry, hot Namib desert in Namibia (Hamilton 1985; Brain 1992; Cowlishaw 1997a). They are extremely adaptable and can take to living alongside humans in rural areas developed for agriculture (Marais *et al.* 2006), but also to living in urban areas such as the chacma baboon population in the Cape Peninsula, South Africa (Hoffman & O'Riain 2011). Conflict between humans and baboons is widespread and baboons cause more crop damage than any other primate (Hill 2000; Naughton-Treves 1996; Tweheyoa *et al.* 2005) as well as all other wildlife species (Biryahwaho 2002; Naughton-Treves 1998) and may be shot as vermin (Hoffman & Taylor 2008), despite their protected status under Appendix II of CITES. Baboons are widely regarded as being among the most opportunistic feeders in African savanna mammal communities (DeVore & Hall 1965; Whiten *et al.* 1991; Jolly 2001). Their diets comprise an extremely variable mix of leaves, fruits, underground storage organs, grasses, and animal matter (DeVore & Hall 1965; Dunbar & Dunbar 1974; Moolman & Breytenbach 1976; Whiten *et al*. 1991; Byrne *et al*. 1993; Barton *et al.* 1993). Nevertheless, baboons are selective foragers, well-equipped to adapt their feeding behaviour in order to obtain maximum nutritional benefit from their immediate environment (Norton *et al.* 1987; Barton *et al.* 1992; Jolly 2001), concentrating largely on protein rich foods (Codron *et al*. 2006).

Baboons are generally not territorial (Mitani & Rodman 1979) and home ranges of neighbouring troops usually overlap, sometimes extensively (Hamilton *et al.* 1978). Northern populations of chacma baboons, however, have been reported to defend territorial boundaries in a desert habitat in Namibia and in the Okavango Delta in Botswana where population densities were relatively high (Hamilton *et al.* 1976). Chacma baboons have large home ranges and day ranges compared to other primate species in Africa (Milton & May 1976). Both home range size and day journey lengths in primates are known to be positively correlated with group size (Milton & May 1976; Clutton-Brock & Harvey 1977; Melnick & Pearl 1987), which is persistent across baboon populations (Barton 1989; Barton *et al.* 1992). Apart from group size, several other factors have been shown to affect home range size and daily ranging, such as resource density (Barton *et al*. 1992; Hoffmann & O’Riain 2011), climate (Hill 1999), the degree of predation risk (Willems *et al.* 2009; Cowlishaw 1997a, 1997b, 1997c; Hill 1999), the availability of adequate sleeping sites (Anderson 1984, 1998, 2000) and the amount of time spend on the ground (DeVore & Hall 1965). Given that baboons live in relatively large groups compare to other primate species (Melnick & Pearl 1987; Hill & Lee 1998) and they are the largest monkey species on the African continent, they make an ideal subject to study ranging patterns and spatial cognition in large-scale scale.

2.2 Research area

The study took place in the Soutpansberg or “Tha vhani ya muno” (mountain of salt), in the Limpopo Province in South Africa (Figure 2.2). The Soutpansberg is the northernmost mountain range of South Africa and spans approximately 210 km from east to west between 23° 05' S & 29° 17' E and 22° 25' S & 31° 20' E. The Lajuma Research Centre (430 ha), located in the western part of the Soutpansberg Mountains has been used as a platform for various research projects (*e.g.*, Willems 2007; Chase-Grey 2011) and was the base for this research. In recognition of the high biotic heterogeneity, Lajuma Research Centre was granted the status of Natural Heritage Site in 1997. Only very recently (May 2009) Lajuma Research Centre became part of UNESCO’s Vhembe Biosphere Reserve (30,701 km^2).

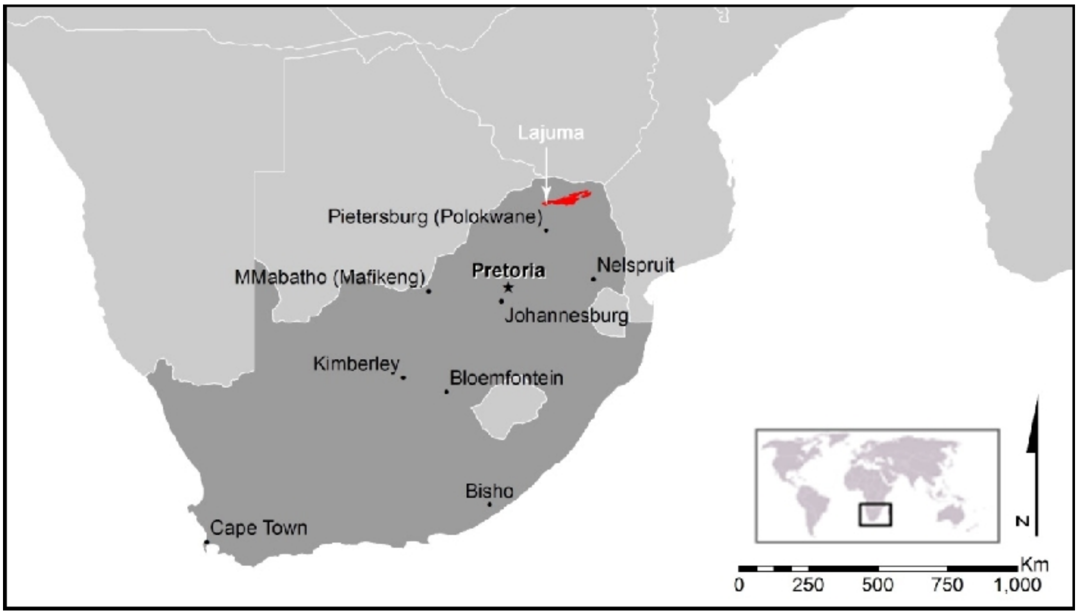

Figure 2.2 Map of South Africa (*dark grey*) showing the geographical location of the Soutpansberg mountain range (*red*) and Lajuma Research Centre is indicated (*white arrow tip*) (Willems 2007).

2.2.1 Climate and Weather

The climate of the Soutpansberg is strongly influenced by the east-west orientation of the mountain range, which forms an effective barrier between the maritime climate in the south-east and the continental climate in the north. The wind patterns created by the mountain range also play an important role in determining local climate. Due to the complex relation between topography, elevation, aspect and vegetation cover, it is difficult to fit the aggregation of regional weather conditions meaningfully into any general climatological group (Willems 2007).

To monitor key local atmospheric conditions a HOBO automated weather station was placed at Lajuma Research Centre at an elevation of 1300 m, which collected data at ½ hour intervals from 21 June 2007 to 1 November 2008. Due to a faulty data logger, data collection was impossible from 1 June 2008 – 17 August 2008. A suite of parameters encompassing air humidity, temperature, precipitation, wind speed and gust speed were recorded. All data were downloaded onto a laptop using BoxCar Pro® 4.3 software package (Onset Computer Corporation 2002). Monthly values were subsequently calculated from all available records (N=20,584) (Figure 2.3) and compared to other available short term weather data (Willems 2007) and to long term climatological data. Long term climatological conditions were based on rainfall data from a historical weather station at Lajuma Research Centre (from 1952 – 1976) and on temperature records estimated from six regional weather stations (from 1994 – 1998) made available by the South African Weather Service, Pretoria.

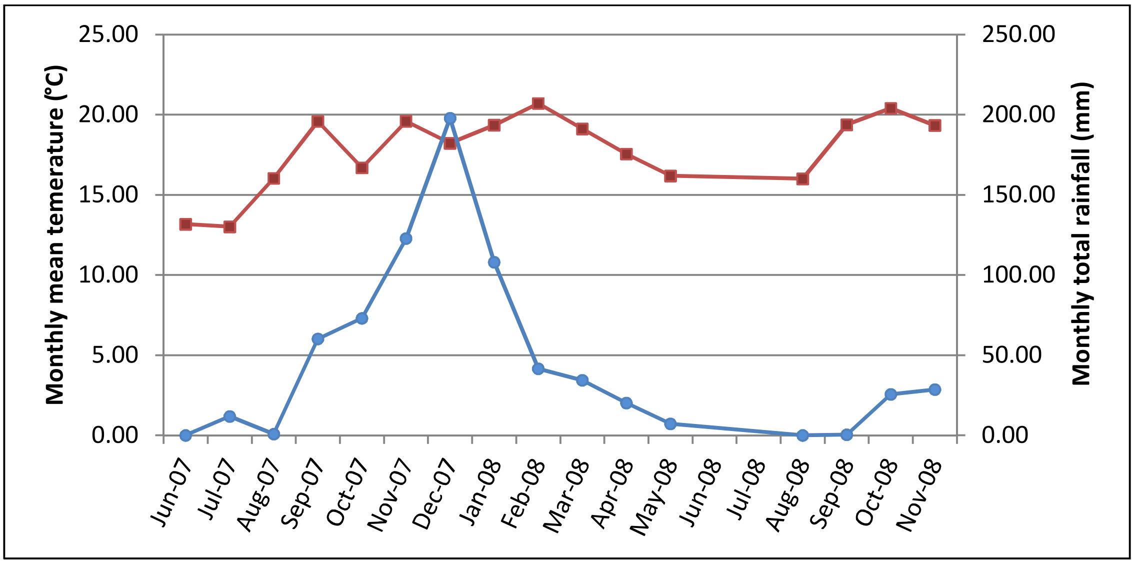

Figure 2.3 Monthly mean temperature (*red line*) and monthly total rainfall (*blue line*) over the study period. Note that values for June and July 2008 are missing due to a faulty data logger.

Table 2.1 presents resulting values of climatic conditions at the study site alongside short-term weather conditions recorded as part of research projects in 2005-2006 (Willems 2007) and 2007-2008 (this study). On basis of this, local climate could be classified as temperate/mesothermal, with a cool dry winter season from April to September and a warm wet summer season from October to March (Willems 2007), which corresponds to the Cwb-group in Köppen's climate classification (Kottek *et al*. 2006).

Table 2.1 Key atmospheric variables for long term local climate and local weather based on two short term studies.

Atmospheric variable	Local climate	Local weather (05/05-04/06)	Local weather (06/07-11/08)
T annual mean (°C)	17.1	18.3	18.0
T mean hottest month (°C)	21.2 (Jan)	21.3 (Nov 05)	20.7 (Feb 07)
T mean coldest month (°C)	10.7 (Jul)	13.4 (Jul 05)	13.2 (Jul 07)
P annual (mm)	724	594	733
P wettest month (mm)	158 (Jan)	141 (Jan 06)	198 (Dec 07)
P driest month (mm)	4 (Aug)	0.2 (Jun/Sep 05)	0.0 (Jun 07/Aug 08)

2.2.2 Flora

Although several earlier floristic surveys conducted by Hahn (1994, 1996, 1997, 1999 and 2002), Stirton (1982), Obermeyer *et al.* (1937) and Van Wyk (1984, 1996) indicated that the Soutpansberg is exceptionally diverse and species-rich for its size (Van Wyk & Smith 2001), little ecological knowledge of the area was known until recently (Anderson 2001, Berger *et al.* 2003). Recently, Mostert *et al.* (2008) provided a first approximation of the vegetation in the Soutpansberg with the aim to define and describe characteristics of the major vegetation types within the context of the Soutpansberg Conservancy to assist scientists, conservationists and land-use planners with projects conducted within area. The major vegetation types identified represent the Forest Biome, Grassland Biome, Savanna Biome and some azonal plant communities and five of the nine main vegetation types described by Mostert *et al.* (2008) were present in the research area. These are (Mostert *et al.* 2008):

- The Soutpansberg Arid Northern Bushveld, which is made up of open woodland with a sparse field layer which is confined to the northern ridges of the Soutpansberg Mountains.
- The Soutpansberg Moist Mountain Thickets, which is a mixture of plant communities and is characterised by closed thickets that show no separation between tree and shrub layers.
- The Soutpansberg Leached Sandveld, which is confined to the warmer northern slopes and arid southern slopes along the most northern ridges of the mountain range. These plant communities occur in dry areas of the mountains and are composed of a relatively homogenous group of woody and grass species.
- The Soutpansberg Cool Mistbelt, which is found 1200 m + above sea level and is confined to the mistbelt region of the mountain range. This vegetation type is diverse and includes peatlands, low open grasslands and small islands of thickets or bush clumps.
- The Soutpansberg Forest, which consists of evergreen high forests and deciduous shrub forest and is confined to the slopes of the most southern ridges of the mountain.

2.2.3 Fauna

The Soutpansberg mountain range has a notable high biodiversity of birds, insects, reptiles and mammals, which make up 60% of the total number of species that occur in South Africa (Gaigher & Stuart 2003). Potential competitors, prey and predators of chacma baboons are described.

All five southern-African representatives of the primate Order occur at the study site (chacma baboons: *Papio ursinus*, Sykes's monkey: *Cercopithecus mitis*; vervet monkey: *Cercopithecus aethiops*; thick-tailed galago: *Galago crassicaudatus*; South African lesser bushbaby: *Galago moholi*). Although scientific evidence for dietary overlap between these species is not available, the two other diurnal species are known to exploit an array of resources shared with baboons (Willems 2007; *personal observation*). Vervet and Sykes's monkeys were observed to associate with chacma baboons, but baboons appeared to have priority of access to resources. In addition to other primate taxa, various species of antelope feeding on young leaves and grass, such as bushbuck (*Tragelaphus scriptus*), red duiker (*Cephalophus natalensis*), klipspringer (*Oreotragus oreotragus*), sable antelope (*Hippotragus niger*), giraffe (*Giraffa camelopardalis*) and the common cow (*Bos taurus*), are potential competitors of baboons.

Apart from potential competition with other primate and antelope taxa, baboons are also known predators of several such species. Chacma baboons prey on vervet monkeys in the research area (3 confirmed and 2 suspected kills at the study site), but were never observed to prey on any other primate taxa. In addition, the baboons regularly prey on hare (*Lepus capensis*), the young of red duiker and bushbuck and several small unidentified bird species.

A number of carnivores in the study area are known (leopard: *Panthera pardus*) or potentially able (caracal: *Felis caracal*; serval: *Lepatailurus serval*) to pose a predation threat to at least some age-sex classes of baboons. Leopard density was particularly high around the study area with a range of 13.2 – 19.0 leopards per 100km^2 and they were frequently captured at night by camera traps within the study area (Chase-Grey 2011) and even encountered during the day (*personal observation*). Male baboons produce loud alarm wahoos while females and juveniles give distinctive alarm barks in response to mammalian carnivores like leopards (Cheney & Seyfarth 2007) and this was also observed in the study troop (*personal observation*). Broad scale faecal dietary analysis showed that species of the Primate order made up 15.8% of leopards' intake of which 4.3% baboon (Chase-Grey 2011). It is suspected that the deaths of at least two adult females in the study group during the study period were due to leopard predation, since these animals seemed to be in good condition and they had recently given birth. As such it is believed that leopards posed a considerable predation threat to baboons in the study area.

Many snake species that pose a potential threat to baboons occur in the study area. The most frequently encountered species included the African rock python (*Python sebae*), black mamba (*Dendroaspis polylepis*), Mozambican spitting cobra (*Naja mossambica*) and the puff adder (*Bitis arietans*). In addition, the boomslang (*Dispholidus typus*) is a venomous habitant that may pose a threat to baboons, but this species was never observed in the vicinity of the study group. On one occasion, when an African rock python was encountered, adult individuals elicited distinct alarm barks and alarm wahoos, while immature individuals surrounded the python, looked at the snake inquisitively, threatened the snake and elicited distinct alarm barks (*personal observation*). Fresh blood was observed on the rock next to the python, but it was impossible to determine whether this came from snake or baboon. No injuries or declining health were obvious amongst the baboons, nor did any animals die in the days following this encounter. Although baboons are known to elicit alarm calls to snakes (Cheney & Seyfarth 2007), the occasion described here was the only time during the entire study period that this was observed in the study troop. Possibly this particular snake was perceived as a threat due to the snake's large size or the circumstances of the encounter (in an exposed area in the periphery of the baboons' home range). Despite that snakes pose a potential cause of mortality, there was a notable lack of alarm calls in response to snake presence and as such it remains questionable to whether snakes at the field site should be considered predators of baboons *sensu stricto*.

Furthermore, martial eagles (*Polemaetus bellicosus*), crowned eagles (*Stephanoaetus coronatus*) and Verreaux's eagle (*Aquila verreauxi*) are big enough to pose a potential predation risk to baboons (Zinner & Peláez 1999; Cheney & Seyfarth 2007) and these three predatory species of bird are all present at the field site. During the study period a breeding pair of crowned eagles successfully raised a chick to independence within the home range of the study troop and the birds were frequently observed while follwoing the study troop. Verreaux's eagle, commonly known as the black eagle, is a known predator of hamadryas baboons (*Papio hamadryas hamadryas*) in the central highlands of Eritrea (Zinner & Peláez 1999), but no published records show that they pose a predation risk to baboons elsewhere. Hamadryas baboons were observed to elicit alarm calls in response to this avian predator’s presence (Zinner & Peláez 1999). Verreaux's eagles were in high abundance in the study area, with at least 22 breeding pairs in the extensive network of large cliffs found in the western Soutpansberg (Tarboton *et al*. 2008). Despite the abundant presence of potential avian predators at the study site, baboons were never observed to elicit any alarm calls in relation to eagle presence and attacks were never observed or suspected.

2.3 Data collection

2.3.1 Travel routes

Data were collected from April 2007 to November 2008. Baboons were followed from their morning sleeping site to their evening sleeping site during 234 days and for an additional 137 days they were followed only for part of the day. Fragments of follow days (N=49) (*e.g.*, when the baboons were located only at their sleeping site in the evening) were not included in any analysis and were considered ‘non follow days’ (Figure 2.4). A higher number of full-follow days were achieved in winter than in summer (153 and 81 respectively), but note that the total sample of 234 full-day follows is drawn from an uneven sample of winter and summer months (12 winter months and 7 summer months).

Part of the study troop’s home range was a property northeast of Lajuma Research Centre, called Sigurwana. Sigurwana is a privately owned property, where game (including sable antelope [*Hippotragus niger*] and giraffe [*Giraffa camelopardalis*]) are kept for tourism purposes, and is therefore fenced off by a 4 meter high fence. From December 2007 onwards, the study troop started ranging into Sigurwana. After the 23rd of June 2008, entrance to the property was no longer permitted, because the owners were afraid that their kept game would become distressed by the presence of observers walking around on foot. Before this date, 24 full follow days within Sigurwana were accomplished (and as such included in the full follow days in Figure 2.4). However after entrance to Sigurwana was forbidden, the study troop spend at least another 44 days (partially) ranging in Sigurwana, during which they were not followed (Figure 2.4).

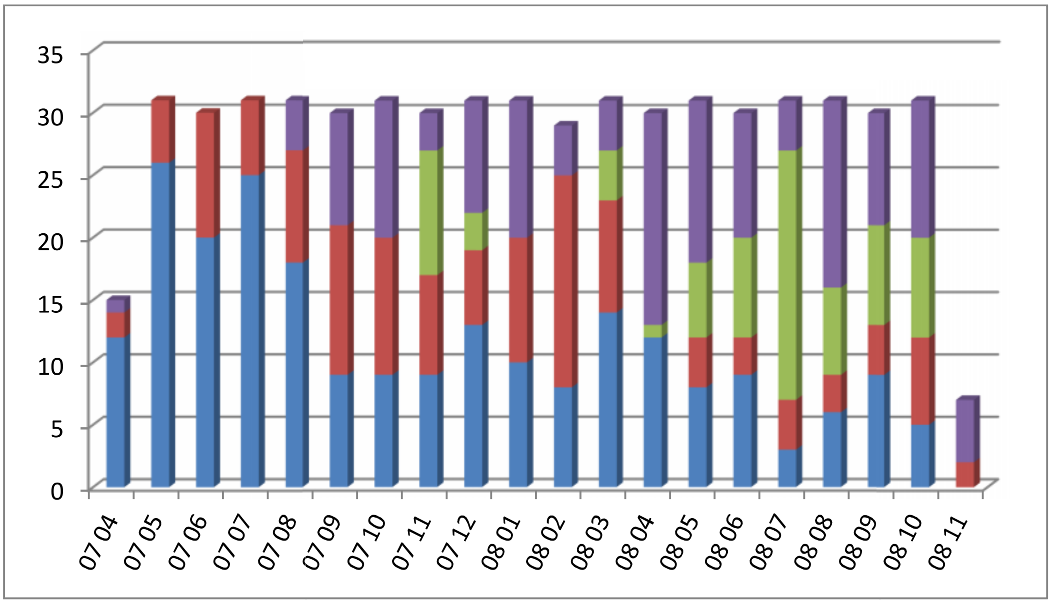

Figure 2.4 Number of full follow days (*blue*), partial follow days (between 1–11 hours) (*red*), days that HT (partially) ranged in Sigurwana and could not be followed (*green*) and non-follow days (excluding known Sigurwana days) (*purple*).

Often the troop returned to a sleeping site located on the property of Lajuma Research Centre in the evening; they did so during all 24 full follow days that were conducted in Sigurwana. However, it was clear that the study troop had at least one sleeping site of unknown location, likely to be situated within Sigurwana, since for several known "Sigurwana days" the troop could not be located at any of the known sleeping sites at Lajuma in the evening.

During follow days, track points were collected with a handheld GPS (Garmin GPSMAP60CSx) using the automatic track recording setting. GPS tracks are sequences of precise track points created by dropping a "bread crumb" trail while travelling across the landscape. Track points were recorded on average every 5.35m (±4.87m) and the average time lapse between consecutive track points was 23 seconds (N=462,556). Geographical coordinates of the track points were collected using the projected coordinate system datum WGS84 and recorded in Universal Transverse Mercator [UTM] (Zone 35S) units. GPS data were directly imported to Trip and Waypoint Manager V3 software (Garmin Ltd. 1995). Note that the observer carried the handheld GPS and as such it was in fact the movements of the observer that were recorded. Nevertheless, the locational data recorded by the observer are considered a good representation of the troop's movements since (1) the baboons could be followed from close distance (most individuals from within 10m) and as such the observer usually walked amidst the troop while recording other behavioural data; (2) in case the baboons travelled at high speeds and the observer 'lagged behind' the observer took care to catch up with the baboons using the same travel routes; (3) when the baboons travelled up or down steep cliffs that were insurmountable for the observer and the observer would have to find an alternative route to rejoin the baboons at the top or bottom of such cliffs, the location where the observer left the troop and the location where the observer rejoined the troop were both marked with a waypoint and track points in between these two waypoints were subsequently deleted; and (4) the aim in this thesis is to analyse the movements of the study troop as a whole, not those of individual baboons. Moreover, to reduce small-scale errors in the representation of baboon movements caused by observer movement within the troop while recording other behavioural data, locational data were filtered when appropriate.

2.3.2 Important Resources

Important resources (IR) were defined as resources used by 10 or more individuals for more than 5 minutes, which were recorded using *ad libitum* sampling (Altmann 1974). IR included not only locations of individual food trees (*e.g*, the common wild ficus tree species *Ficus burkei* and the waterberry tree species *Syzygium cordatum*), but also *areas* in which several of the same tree or shrub species used as a food resource were located (*e.g.*, the wild apricot species *Dovyalis zeyheri* and the flame thorn acacia species *Acacia ataxacantha*). Furthermore, IR also included drinking locations. All IR were recorded as one single waypoint with a handheld GPS (Garmin GPSMAP60CSx), and in the case that the resource covered an area; a waypoint was recorded at the centre of the area. Note that IR thus only refer to feeding and drinking resources and that additional resources that are likely to have also been of high importance to the baboons, such as those related to safety from predators (*e.g.*, resting areas and sleeping sites), were not considered in analysis presented in this thesis.

2.3.3 Behavioural observations

From September 2007 – July 2008, agonistic behaviours (Table 2.2) between individuals were recorded during 10-30 min continuous focal samples (Altmann 1974) to establish the dominance hierarchy in the troop (Section 2.4.2). Furthermore, agonistics behaviours to establish dominance hierarchy were recorded on an *ad libitum* basis (Altmann 1974), both within focal periods (of other individuals than the focal individual) and between focal periods. All behavioural data were collected on a Sony Clie PEG10SL handheld computer which was equipped with the Pendragon Forms version 4.0 (Pendragon Software Corporation 2003) and at the end of a follow day the data were directly imported into MS Access 2007.

Table 2.2 Agonistic behaviours recorded to establish dominance hierarchy.

Behaviour	Description
Supplant	One individual’s approach or movement cause another individual to move location, without direct interaction between the two individuals.
Displacement	One individual (*a*) actively causes another individual (*b*) to move location where the individual *a* may take over the action and/or location of individual *b*.
Chase	One individual follows another individual at high speed.
Attack	Aggressive physical interaction; includes biting, hitting and pinning another individual to the ground.
Fear grimace	The lips are retracted so that the teeth are shown and teeth are clenched together.
Threaten	Includes eyebrow-raising, ground slapping, lunging and head bobbing (no physical contact).

2.4 Study group

2.4.1 Composition

At least 5 groups of baboons have ranges that extend into the Lajuma area and this thesis focuses on the one referred to as the house troop (HT). HT has formed the basis of a series of unpublished university theses over the past 5 years, such that it was moderately habituated to observer presence and some of its sleeping sites were known at the start of this study in 2007. Re-habituation of HT started in January 2007, 3 months prior to the study period, by Dr. Lane as part of her PhD thesis (Lane 2008). By the start of the study period in April 2007, HT could be followed for increasingly large parts of the day and daily efforts were made to further habituate HT and to identify all the adult individuals in the troop. After 3 weeks, animal tolerance to observer presence reached a level at which complete consecutive follow days were feasible and ranging and behavioural data collection commenced. As such, data analysed in this thesis were those collected from the 23rd April 2007.

Average size of HT over the observation period was estimated around 60 individuals, although this was not verified by calculating effective mean group size from regular complete troop counts (Jarman 1974) due to the low visibility in the study area (as also experienced by Noser [2004] in the adjacent Blouberg). Data were collected on adult individuals only (see also Section 2.3.3). Females were considered adults as soon as they started cycling and included 2 females whom, based on the button like appearance of their nipples, were believed not to have given birth before (nipples of females who have nursed one or more infants tend to be much longer) and were most likely in their “adolescent sterility” phase (Altmann *et al.* 1977). Adult females were classified as lactating, pregnant or cycling, and their status was recorded during a daily census. Lactating females were defined as nursing mothers who had not yet resumed their sexual cycling. Pregnant females (from the end of their last cycle until they give birth) could be identified in the field shortly after conception when they ceased sexual cycles and their perineal skin colour changed in a few weeks to a deep magenta (Smuts 1995). The number of adult females during the study period varied from 18 – 21 and the number of adult males varied from 10 – 13 including 2 sub-adult males. The 2 sub-adult males, who were likely to have been born in the troop, remained in the troop throughout the entire study period and were included as adults because they often featured as interactants and held high ranks in the male dominance hierarchy (one even held the position of alpha male for a while) and as such were considered to play an important role in troop dynamics. An overview of the number and composition of adult group members over the observation period is shown in Table 2.3.

Table 2.3 Number of adult females (AF) and adult males (AM) in the study group over the observation period and changes in number of adult individuals due to important demographic events (*e.g.*, emigration, birth). Adult females are divided into sexual status (lactating, pregnant or cycling).

Date	Event	AF Lactating	AF Pregnant	AF Cycling	AF Total	AM Total	Adults Total
01/04/2007	**Start Study Period**	**11**	**0**	**9**	**20**	**13**	**33**
01/04/2007	Birth	11	0	9	20	13	33
20/04/2007	Pregnancy	11	1	8	20	13	33
28/04/2007	Pregnancy	11	2	7	20	13	33
03/05/2007	Pregnancy	11	3	6	20	13	33
07/05/2007	Pregnancy	11	4	5	20	13	33
14/05/2007	Pregnancy	11	5	4	20	13	33
17/05/2007	New cycling female	11	5	5	21	13	34
20/08/2007	Death AF	10	5	5	20	13	33
27/08/2007	Birth	11	4	5	20	13	33
23/09/2007	Emigration AM	11	4	5	20	12	32
25/09/2007	Pregnancy	11	5	4	20	12	32
01/10/2007	Pregnancy	11	6	3	20	12	32
03/10/2007	Disappearance AM	11	6	3	20	11	31
20/10/2007	Birth	12	5	3	20	11	31
03/11/2007	Birth	13	4	3	20	11	31
07/11/2007	Birth	14	3	3	20	11	31
10/11/2007	Cycling after birth	13	3	4	20	11	31
12/11/2007	Cycling after birth	12	3	5	20	11	31
13/11/2007	Cycling after birth	11	3	6	20	11	31
15/11/2007	Birth	12	2	6	20	11	31
20/01/2008	Pregnancy	12	3	5	20	11	31
25/01/2008	Pregnancy	12	4	4	20	11	31
28/01/2008	Birth	13	3	4	20	11	31
29/01/2008	Cycling after birth	12	3	5	20	11	31
07/02/2008	Pregnancy	12	4	4	20	11	31
21/02/2008	Emigration AM	12	4	4	20	10	30
22/02/2008	Birth	13	3	4	20	10	30
27/02/2008	Cycling after birth	12	3	5	20	10	30
23/07/2008	Death AF	11	3	5	19	10	29
28/07/2008	Birth	12	2	5	19	10	29
28/07/2008	Birth	13	1	5	19	10	29
31/07/2008	Death infant	13	1	5	19	10	29
05/08/2008	Death infant	13	1	5	19	10	29
16/08/2008	Death AF	12	1	5	18	10	28
01/09/2008	Birth	13	0	5	18	10	28
01/11/2008	**End Study Period**	**13**	**0**	**5**	**18**	**10**	**28**

Two births occurred just before the start of this study (Lane *personal communication*) and 11 births (7 males, 4 females) were observed during the study period (Figure 2.5). In addition, 3 adult females and 3 adult males disappeared as a consequence of either confirmed emigration (N=2) or suspected predatory events (N=4).

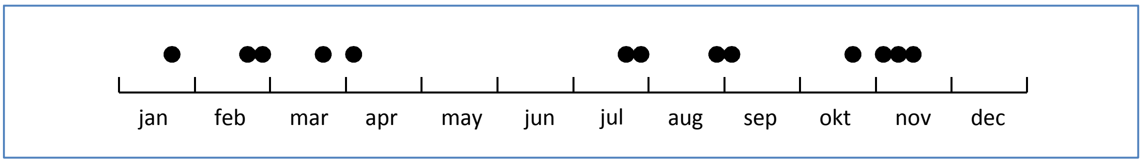

Figure 2.5 Annual distribution of births in House Troop observed from January 2007 – November 2008.

2.4.2 *Dominance Hierarchy*

Although exceptions are known (Barrett *et al.* 1999), chacma baboon groups are generally characterized by a dominance hierarchy and although a variety of concepts and definitions of dominance have been introduced over the past decades (discussed in detail by Drews 1993) it is important to emphasize that dominance does not imply leadership and as such, it is not to be conflated with control (Allee 1938; Hinde 1978; Drews 1993).

The relationship among 3 members (*triad*) can be transitive or circular. A triad (member *a*, *b* and *c*) is transitive when member *a* dominates member *c* if *a* dominates *b* and *b* does so to *c*. It is circular if the triad is not transitive. The dominance hierarchy in baboon groups is generally a linear, transitive dominance hierarchy in which all sub-adult and adult males rank above all adult females. Males form a linear, transitive dominance hierarchy, which is unambiguous over short periods of time, although rank changes occur often (Kitchen *et al.* 2003) and a male's tenure in the alpha position seldom lasts for more than a year (Cheney & Seyfarth 2007). Like males, female baboons establish linear, transitive dominance hierarchies. However, female ranks are inherited from their mothers and as such maternal kin usually occupy adjacent ranks, which are relatively stable over many years (Hausfater & Meade 1982; Walters & Seyfarth 1987; Samuels *et al.* 1987; Pereira 1995; Silk *et al.* 1999, 2002), with the exception that older mothers sometimes cede rank to mature daughters (Combes & Altmann 2001). Although rank and kinship are important determinants of female-female relationships, unrelated females of disparate ranks sometimes form close bonds and because baboon females are strongly attracted to mothers carrying young infants, all females go through periods of intense social interaction with other females (Seyfarth 1976; Smuts 1995).

To test whether HT was also characterised by a linear, transitive dominance hierarchy, frequency of agonistic behaviours (see Section 2.3.3) (N=2151) between males and females were investigated separately using frequency matrix analyses with the aid of Noldus MatMan v1.1 (de Vries *et al.* 1993). Appleby (1983) argues that a linear hierarchy in a group can only be demonstrated objectively if it can be shown that dominance in the group tends to be transitive. This condition of transitivity will be met if the proportion of triads in which relationships are circular, as opposed to linear, is less than that expected by chance. Appleby (1983) also warns that the possibility of apparently linear or near-linear hierarchies arising from purely random relationships is much greater than might be expected intuitively and is higher in small groups than in large ones.

Therefore, first the probability that a linear hierarchy in HT could be found by chance was calculated according to Appleby (1983) and the assumption that dominance in HT was generally transitive was tested (Kendall 1962). The agonistic behavioural data included interactions with adults whom disappeared or died during the study period. Three adult females disappeared or died during the study period. However, because female ranks are inherited from their mothers and as such maternal kin usually occupy adjacent ranks (Hausfater *et al.* 1982; Pereira 1995; Samuels *et al.* 1987; Silk *et al.* 1999, 2002; Walters & Seyfarth 1987), when a female is removed from the troop, the remaining females either keep their rank (if they were holding a higher rank) or ‘close the gap’ and shift one rank up (if they were holding a lower rank) and as such, no changes in relative rank occur. Female dominance rank was therefore analysed over the entire study period. To analyse the male dominance hierarchy the data were divided according to three periods (May – September 2007, October 2007 – February 2008 and March – October 2008) which correspond to the disappearance or emigration of adult males (Table 2.3). Dominance hierarchy was then analysed for each period separately, to decrease the percentage of unknown relationships.

For adult females in HT (N=21) the total number of dyadic relationships (*R*) was 210 and the number of possible combinations of relationships in the group (*C*) was 1.6455E+63 (Equation 1 and Equation 2 respectively). A linear hierarchy in any particular ordering of individuals in the group will only be produced by one particular combination of relationships out of the *C* possible and the chance of this occurring is thus 1/*C* (Appleby 1983). However the number of possible orders of individuals in the group, each of which may form a linear hierarchy, will be

$$N \times (N-1) \times (N-2) \times \ldots \times 1$$

since any of the *N* individuals may be at the top of the hierarchy, any of the remaining (N-1) in second place, and so on (Appleby 1983). The probability of a linear hierarchy occurring by chance is therefore *N* factorial (N!) divided by *C*, which was smaller than 0.0001 for both adult females (N=21) as for adult males in HT (during all three periods). It was thus concluded that the probability of finding a linear hierarchy for females or males by chance ($p<0.0001$) is negligible.

Equation 1:

$$R = \frac{N \times (N - 1)}{2}$$

Equation 2:

$$C = 2^{R}$$

Interaction frequency matrices (*e.g.*, Table 2.4) of agonistic behaviours (see Table 2.2 in Section 2.3.3) were created separately for adult females and adult males (and for adult males for the three periods separately). Hierarchical rank order analyses of agonistic ranks were carried out with the aid of MatMan (de Vries *et al*. 1993). The behavioural interactions were evaluated as an expression of a dominance relationship by determining their linearity and unidirectionality. Kendall's index of linearity (*K*) was calculated to test for linearity of the dominance hierarchy and its significance tested (Kendall 1962; Appleby 1983). Kendall's coefficient was calculated differently for odd values of *N* (Equation 3) than for even values of *N* (Equation 4) according to the procedure described in Appleby (1983), where *N* is group size and *d* is the number of circular triads. The directional consistency index (DC) gives the frequency with which the behaviour occurred in its more frequent direction relative to the total number of times the behaviour occurred (van Hooff & Wensing 1987) and was calculated across all female and male dyads. The total number of times the behaviour was performed in the main direction within each dyad (H) minus the number of times the behaviour occurred in the less frequent direction within each dyad (L) divided by the total number of times the behaviour was performed by all individuals (H+L): DC = (H-L)/(H+L). This DC-index ranges from 0 (completely equal exchange: 'biodirectional') to 1 (complete unequal exchange: 'unidirectional') (Van Hooff & Wensing 1987). To qualify as a strongly linear hierarchy, the index of linearity should be ≥0.90 (Martin & Bateson 1993).

Equation 3:

$$K = \frac{1 - 24d}{N^{3} - N}$$

Equation 4:

$$K = \frac{1 - 24d}{N^{3} - 4N}$$

Table 2.4 Example of a frequency matrix of behaviours (for adult females of whom names are abbreviated in the first column and first row) with receivers on columns and actors on rows.

	al	**an**	**be**	**co**	**di**	**ed**	**he**	**ju**	**la**	**li**	**ma**	**me**	**op**	**rh**	**rh2**	**sc**	**sh**	**st**	**ti**	**tu**	**wh**
al	0	0	3	0	0	11	0	0	1	1	0	0	0	19	0	0	7	16	3	3	0
an	3	0	1	0	4	4	6	0	3	4	0	0	0	4	3	5	3	6	4	2	0
be	10	0	0	0	9	3	18	0	1	24	0	0	2	10	0	0	5	8	5	3	1
co	5	10	9	0	15	6	6	0	9	5	0	0	5	5	7	15	4	3	5	1	11
di	6	0	0	2	0	9	3	0	0	5	0	0	0	6	0	0	6	13	4	4	0
ed	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	9	5	0	0	0
he	2	0	0	0	0	3	0	0	0	0	0	0	0	4	0	0	8	3	5	9	0
ju	7	7	4	9	8	5	5	0	2	7	1	1	3	1	6	4	1	2	5	4	11
la	9	0	9	0	5	6	4	0	0	7	0	0	0	3	9	1	5	3	3	1	0
li	5	0	0	0	1	3	2	0	0	0	0	0	1	12	0	0	5	4	1	7	0
ma	1	1	0	3	3	1	0	3	2	1	0	4	1	1	1	0	2	3	0	2	0
me	3	3	5	5	2	4	6	9	3	5	0	0	0	2	4	4	2	2	2	2	5
op	0	0	1	0	0	2	0	0	0	1	0	0	0	1	0	0	2	4	0	3	0
rh	0	0	0	0	1	4	0	0	0	0	0	0	0	0	0	1	9	18	4	3	0
rh2	8	0	9	0	4	7	3	0	2	5	0	0	2	7	0	0	2	6	0	4	0
sc	10	1	14	0	12	5	6	1	10	9	0	0	3	10	10	0	11	8	8	5	2
sh	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	5	0	0
st	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0
ti	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
tu	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	8	10	1	0	0
wh	4	0	4	1	4	4	1	0	3	5	0	0	1	7	4	4	0	1	1	1	0

For adult females the value of Kendall's linearity index *K* equalled 0.865, which was significant (χ^2=159.848, df=27.612 and p<0.0001), and the DC-index was 0.94. For adult males, Kendall's index was 0.986 (χ^2=67.06, df=20.20 and p=0.0001), 0.605 (χ^2=43.06, df=20.20 and p=0.0072) and 0.825 (χ^2=51.33, df=20.00 and p=0.0003) and the values of the DC-indices were 0.81, 0.88 and 0.77, for the three respective periods. It can thus be concluded that dominance relationships in the study troop were not randomly distributed, but instead HT females were characterised by a very strong linear hierarchy and also the males in HT showed a significant, linear dominance hierarchy with a high unidirectionality throughout the study period.

2.5 Software

Data analyses in this thesis were conducted using several different software packages, versions and references as follows: ArcGIS Desktop version 9.3 (ESRI 2008), BIOTAS version 2.0a 3.8 (Ecological Software Soluations 2005), CrimeStat III update version 3.2a (Levine 2009), R version 2.13.0 (R Development Core Team 2011), Trip and Waypoint Manager V3 (Garmin Ltd. 1995), PASW Statistics 17 version 17.0.1 (SPSS Inc. 2008), Oriana (Kovach Computing Services 2009), MS Office Excel (2007), Topofusion Basic version 4.2 (Morris & Morris 2011). Specialised add-ins, toolboxes or packages used within these software are described where relevant in the methodology section of each chapter.

CHAPTER 3

HOME RANGE

3.1 Introduction

An understanding of the way animals move through their habitat can help to more fully comprehend the manner in which they conceive and perceive their world (Powell 2000). In an effort to quantify ranging behaviour, studies typically focus on two measurements: home range and daily path lengths, which vary widely within and between animal species (*e.g.*, Turner *et al.* 1969; Horne *et al.* 2008; van Beest 2011). Understanding why home range size varies between and within species remains a fundamental issue in socio-ecological research (*e.g.*, Krebs & Davies 1984; McLoughlin & Ferguson 2000; Börger *et al.* 2008).

McNab (1963) was the first to plot body size against home range size for a variety of mammal species and to conclude that home range size is determined by an animal's energetic needs. Since then, similar positive correlation between body size and home range size have been shown in other taxa (*e.g.*, birds: Schoener 1968, Armstrong 1965; Mace & Harvey 1983 lizards: Turner *et al.* 1969, primates: Milton & May 1976; Terborgh 1983; Clutton-Brock & Harvey 1977, 1979; Harvey & Clutton-Brock 1981, other mammals: Gittleman & Harvey 1982; Harestad & Bunnell 1979; Mace & Harvey 1983). It is now well-known that interspecific variation in home range size is largely driven by body-size-dependent metabolic requirements (Harestad & Bunnell 1979; Lindstedt *et al.* 1986; Carbone *et al.* 2005) and as a result, larger animals generally have larger annual home ranges than smaller animals or alternatively have access to richer habitats (Harvey & Clutton-Brock 1981; Swihart *et al.* 1988; Bassett 1995; Leonard & Robertson 2000).

Many of the social and environmental conditions that affect daily path lengths also affect home range. For example, both home range size and day journey lengths in primates are positively correlated with group size (Milton & May 1976; Clutton-Brock & Harvey 1977; Melnik & Pearl 1987). Larger groups need to travel further than small groups to meet the energetic and nutritional requirement of all group members because they deplete resources quicker (Melnik & Pearl 1987; Chapman & Chapman 2000). However, patch depletion may occur only sporadically in some species, or not at all, depending on a species diet (Chapman & Chapman 2000; Isbell 1991). An alternative explanation to account for further travel in large groups may be through the process of avoidance of search field overlap, referred to as the 'pushing forward' mechanism by Chapman & Chapman (2000).

Papio spp. are relatively large primates that live in large social group (Milton & May 1976; Swedell 2011). They are one of the best studied primate taxa, as they are mostly terrestrial and many populations range in open environments, it is easier to observe them in comparison to many other primate species, especially arboreal ones (Henzi & Barrett 2003). Because of their broad geographic distribution, baboons range in different habitat types with variable ecological conditions, and their adaptability and wide habitat tolerance are accompanied by striking variations in social organization (Kummer 1968, 1984; Altmann & Altmann 1970; Anderson 1982, 1983; Byrne *et al.* 1987, 1990), which makes them particularly interesting for primate socio-ecology (Byrne *et al.* 1993). Consequently, their ranging has been extensively studied from an ecological and socio-ecological point of view (*e.g.*, Barton 1989; Hill 1999; Henzi & Barrett 2003; Hill *et al*. 2003).

The positive correlations between home range size and day journey length with group size are persistent across baboon populations (Barton 1989; Barton *et al.* 1992; Dunbar 1992; Hill 1999). Several other factors have been demonstrated to play a role in baboon ranging, including climate (Hill 1999), day length (Hill *et al*. 2003), predation risk (Byrne 1981; Cowlishaw 1997a, b, c; Hill 1999; Bidner 2009), surface water availability (Barton *et al.* 1992), distribution of sleeping sites (Altmann & Altmann 1970; Post 1978; Barton *et al*. 1992), thermal costs (Stelzner & Hausfater 1986; Stelzner 1988) and resource density (Barton 1989; Barton *et al*. 1992).

Together, these factors illustrate the complex relationships between ranging behaviour and an animal’s physiology, habitat, social conditions, life history traits, and ecology. This chapter does not, however, attempt to reveal the behavioural or ecological determinants of baboons’ ranging, but instead, home range size of the study troop is identified to contribute towards a comprehensive body of baboon ranging with relevant data from a new study site, and to lay the foundation for following chapters that build on the concepts of home range and core area. First, a review of the home range concept and home range estimation methods are provided. Methodological issues related to home range estimations, particularly those of the potential effects of sample size, are discussed in more detail and two different methods to estimate home ranges are compared.

3.1.1 Home Range concept

For decades, ecologists have been studying the dynamics of animal movements in relation to social and ecological factors (Börger *et al*. 2006) and the notion that individual animals restrict their movements to finite areas known as home ranges is perhaps as old as ecology itself (Darwin 1859). Hence animal movements are often defined using the home range concept, which is most commonly described by the definition given by Burt (1943: 351) as “… that area traversed by the individual in its normal activities of food gathering, mating, and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered as in part of the home range.” Although this is a concise description of the biological phenomenon, it does not give any indication of how this area should be estimated from observations of the animal (Worton 1995), nor does it recognize the importance of variations in the intensity of space use within the home range (Kie *et al*. 2010). Home ranges were typically estimated by non-statistical polygon procedures based on estimators derived from the peripheral points of the range, such as minimum area convex polygons (MCP) (Mohr 1947) and the distance between the furthest points (Clutton-Brock *et al*. 1982), or non-statistical grid cell occupancy methods (Voigt & Tinline 1980). These methods were appealing because they allowed comparison with previous studies and they do not define a model, but by virtue of their simplicity they do have many undesirable properties and often over-estimate home range size (Getz *et al*. 2007). For example for the MCP method, home range estimates are highly correlated with the number of observations used and often includes large areas of land which are never visited (Getz *et al.* 2007). Furthermore, the MCP makes strong and usually inadequate biological assumptions, such as a convex from of the home range determined only by the position of the outermost locations (Worton 1995). Börger *et al*. (2006) went as far as stating that ‘the MCP method should not be used at all for estimating home range size and the results of studies employing MCP should be treated with caution’ (p. 1402). Methods such as the MCP also only give the extent of the animal’s home range and so provide no information on the intensity of range use.

Although Burt’s (1943) definition of a home range is still widely accepted and cited more than any other, the need for performing statistical analyses on home ranges has led to more explicit definitions (Seaman & Powell 1996). The home range concept was formalised by a probabilistic model that assumes an animal has a fixed, but unknown, utilisation distribution over the plane (Calhoun & Casby 1958) for some specified time period. The term *utilisation distribution* (UD) has been defined by Van Winkle (1975, pp: 118) as “the two-dimensional relative frequency distribution for the points of location of an animal over a period of time” and is thus a probabilistic model of home range that describes the relative amount of time that an animal spends in any place (Seaman & Powell 1996). Using this model, one can then define the home range as the minimum area in which an animal has some specified probability, *p*, of being located (*i.e.*, the smallest sub-region which accounts for a specified proportion of its total utilisation) (Jennrich & Turner 1969): this is the area within the specified probability density contour of the utilisation distribution (Worton 1995).

Earlier research in the field of home range estimations focussed on the development, evaluation and comparison of different home range methods including the popular MCP method (Mohr 1947), harmonic mean method (Dixon & Chapman 1980), Fourier series method (Anderson 1982), the (modified) bivariate normal model 95% ellipse method (Jennrich & Turner 1969; Koeppl *et al*. 1975) and the kernel density method (Worton 1989) (for method reviews see Van Winkle 1975; Worton 1987; Boulanger & White 1995; Worton 1995; Seaman & Powell 1996). Nowadays the kernel density estimator (KDE) function, introduced to ecologists as a home range estimator by Worton (1989), has become one of the best known and most widely applied nonparametric statistical methods for estimating UD in animal ecology (Strickland & McDonald 2006) and seems to be increasingly favoured over other methods (although the MCP method is still used in some comparative studies despite its well known shortcomings) (Worton 1987; Börger *et al*. 2006; Lichti & Swihart 2011). As a result, the methodological issues surrounding kernel density estimators, those of autocorrelation of animal movements, the concept of time-to-independence and the effects of sampling regime, have been the focus of discussion in more recent publications in the field of home range estimation (*e.g.*, Otis & White 1999; Börger *et al*. 2006; Katajisto & Moilanen 2006; Fieberg 2007a,b; Kie *et al*. 2010). Nevertheless, many recent studies investigating home range and habitat use in primates still use more traditional methods such as grid cell occupancy and minimum convex polygon (*e.g.*, orangutans (*Pongo pygmaeus*): Wartmann *et al.* 2010; mountain gorilla (*Gorilla beringei beringei*): Robbins & McNeilage 2003; western gorillas (*Gorilla g. gorilla*): Bermejo 2004; lemurs (*Indri indri*): Glessner & Britt 2005; black-faced black spider monkey (*Ateles chamek*): Wallace 2006; black-and-white snub-nosed monkeys (*Rhinopithecus bieti*): Grueter 2008; baboons (*Papio hamadryas ursinus*): Henzi *et al*. 2011).

One of the latest additions to home range estimation methods is a method called the Local Convex Hull (LoCoH) (Getz & Wilmers 2004), which has been proposed for estimating the area of home ranges and constructing bounded UD from spatial data. This method has been shown to outperform the kernel density estimator in accuracy and precision of home range estimates from simulated and empirical data (Getz *et al.* 2007). This is especially the case when constructing home ranges and UD that include hard boundaries, corridors and internal structures from which animals are excluded and when dealing with a large number of stacked data points (Getz *et al.* 2007). The LoCoH has been widely applied in the last couple of years to estimate home ranges of a wide variety of species (*e.g.*, deer (*Dama dama L.*): Morse *et al.* 2009; spotted hyena (*Crocuta crocuta*) Stratford & Stratford 2011; Asian houbara bustards (*Chlamydotis undulate macqueenii*): Combreau *et al.* 2011; Andean bear (*Tremarctos ornatus*): Castellanos 2011; eastern kingsnake (*Lampropeltis getula getula*): Linehan 2010); black-necked cranes (*Grus nigricollis*) Liu *et al.* 2010); white-faced capuchins (*Cebus capucinus*) Campos & Fedigan 2009).

The popularity of the new LoCoH method may be attributed in part to the ease of use. The method is relatively easy to understand and a LoCoH web application (http://locoh.cnr.berkeley.edu/) provides users with a comprehensible tutorial and the option to analyse data directly online (for data sets with N<1000), while for large data sets, users are presented with scripts to run the LoCoH method in R software or with a toolbox to run the LoCoH method in ArcGIS, all making the LoCoH method relatively easy to implement. Studies that included both the new LoCoH method and earlier methods to estimate home range from empirical data showed that the LoCoH method performed better than the KDE and MCP method (*e.g.*, Ryan *et al.* 2006; van Beest *et al.* 2011; Getz *et al.* 2007) for a variety of reasons. Foremost, the LoCoH method accommodates user knowledge of known physical barriers and is more adept than the KDE at excluding geographical features such as rivers, lakes, inhospitable terrain, and so on (Ryan *et al*. 2006; Getz & Wilmers 2004). A second reason why the LoCoH method is preferred over the KDE method involves the user-specified parameter that determines the shape of the UD estimate produced by a given dataset (Campos & Fedigan 2009). The adaptive LoCoH method (see Section 3.1.3) is relatively robust against suboptimal choices of this parameter and against changes in sample size (Getz *et al.* 2007), whereas the home range estimates generated by KDE methods are heavily affected by the choice of the user-specified parameter, called the 'smoothing parameter' for the KDE. Despite a large body of literature on the many methods for selecting the optimal smoothing parameter (*e.g.*, cross-validation, "plug-in" methods and "n-root bandwidth" method) (*e.g.*, Seaman & Powell 1996; Seaman 1999; Blundell *et al*. 2001; Gitzen & Millspaugh 2003; Hemson *et al*. 2005; Gitzen *et al.* 2006; Horne & Garton 2006) there is no universally accepted method for choosing a value of the smoothing parameter that is biologically relevant for a given data set of ranging points.

When applied to simulated data, the LoCoH had a clear advantage for applications that strongly prioritised excluding completely unused areas, but the KDE method was found to produce a better volume of overlap between the true and estimated UD than the LoCoH method and was generally considered to outperform the LoCoH method (Lichti & Swihart 2011).

In the next two sections the kernel density and the LoCoH method are described in more detail (largely drawn from Silverman [1986] and Getz *et al.* [2007] respectively) and the main methodological issues associated with the estimation of home range size are briefly discussed. Then, both the KDE method and the LoCoH method are used to estimate the home range and core area (see Section 3.2.2 for definitions) of the study troop. Home range area is known to increase with sample size (*e.g.*, Ostro *et al*. 1999) to converge towards an asymptote (Getz *et al*. 2007), whereby sample size is influenced both by the time interval between consecutive data points (*i.e.*, the smaller the time interval, the larger the sample size) and the length of the study period (*i.e.*, the longer the study period, the larger number of follow days and thus the larger the sample size). Therefore, potential effects of the study period and the time interval on home range estimations were investigated also.

3.1.2 Kernel Density Estimator (KDE)

3.1.2.1 Kernel methods

The KDE relies on non-parametric algorithms to provide a probabilistic measure of animal space use in which the density at any location is an estimate of the amount of time an animal spent there (Silverman 1986; Worton 1989; Seaman & Powell 1996; Horne & Garton 2006). A home range can then be defined as the smallest area of the utilisation distribution that accounts for a certain percentage of the animal's total space use whereby the boundary of the home range is delimited by a certain percentage volume isopleths (see also Section 3.1.2.3) from the utilisation distribution of the animals (Jenrich & Turner 1969; Anderson 1982; Gitzen *et al.* 2006).

There are a number of kernel methods which produce subtle differences in the shape of the interpolated surface or contour. The *normal* (Gaussian) distribution (bell shaped) weights all points in the study area, though near points are weighted more heavily than distant points. The normal distribution can cause some edge effects to occur, particularly if there are many points near one of the boundaries of the study area. Other techniques use a restricted circle around the points. The *uniform* distribution (flat shaped) weights all points within the circle equally. The *quartic* distribution (spherical shaped) weights near points more than far points, but the fall off is gradual. The *triangular* distribution (conical shaped) weights near points more than far points within the circle, but the fall off is more rapid. Finally, the *negative exponential* distribution (peaked shaped) weights near points much more highly than far points within the circle. The use of any one of these depends on how much the user wants to weight near points relative to far points. Using a kernel function which has a big difference in the weights of near versus far points (*e.g.*, the negative exponential or the triangular) tends to produce finer variations within the surface than functions which are weight more evenly (*e.g.*, the normal distribution, the quartic or the uniform); these latter ones tend to *smooth* the distribution more. There are thus several kernel methods to choose from, although it is generally accepted that the choice of the kernel method is not as important as the choice of the smoothing parameter, since all kernel methods give essentially equivalent results (Worton 1987, Seaman & Powell 1996).

3.1.2.2 Smoothing parameter

In the kernel density literature, the bandwidth or smoothing parameter (h) refers essentially to the width of the kernel, which can be varied by the user. Figure 3.1 shows how the smoothness of the resulting density function is a consequence of the bandwidth size. Generally, bandwidth falls under either *fixed* or *adaptive* choices.

Depending on the type of kernel estimate used, the fixed interval has a slightly different meaning. For the normal kernel function, the bandwidth is the standard deviation of the normal distribution. For the uniform, quartic, triangular and negative exponential kernels, the bandwidth is the radius of the search area to be interpolated. Typically, a small bandwidth value will allow the fine detail of the data to be observed, it will lead to a finer mesh density with many little peaks and valleys, while a larger bandwidth value obscures all but the most prominent features, leading to a smoother distribution and less variability between areas (Worton 1989). If the sample size is not very large, then a smaller bandwidth may lead to statistical imprecision in the estimates and the peaks and valleys may represent nothing more than random variation in the data (Levine 2009).

An adaptive bandwidth adjusts the bandwidth interval so that a minimum number of points are found. This has the advantage of providing constant precision of the estimate over the entire study area. Thus, in areas that have a high concentration of data points, the bandwidth is narrow whereas in areas where the concentration of data points is sparser, the bandwidth will be larger. The degree of precision is generally dependent of the sample size of the bandwidth interval. The estimate is made finer grained by selecting a smaller number of points, or made more smooth, by selecting a larger number of points. Adaptive kernels tend to perform poorly, often over-estimating home range areas (of known home range areas in simulation studies) and as such, fixed kernel density analyses have been recommended in ecological studies (Powell 2000; Kernohan *et al*. 2001).

There have been variations of the shape and size of the bandwidth recommended with various formulae and criteria (Silverman 1986; Härdle 1991; Venables & Riply 1997) and also different solutions have been proposed to counteract possible edge effects that may occur (Venables & Riply 1997). Since statistical properties of kernel density estimators depend heavily on the level of smoothing used, objectivity in selecting the value of the smoothing parameter is highly desirable (Worton 1995). Many different methods for choosing an optimal smoothing parameter in the context of independent data have been suggested in the literature (*e.g.*, Seaman & Powell 1996; Seaman 1999; Blundell *et al*. 2001; Gitzen & Millspaugh 2003; Hemson *et al*. 2005; Gitzen *et al.* 2006; Fieberg 2007b), which included cross-validation methods, plug-in methods, the ‘n-root’ bandwidth method, smoothed boot-strap methods and solve-the-equation methods. There is still a major dispute about how to assess the quality of the estimate and which choice of smoothing parameter is optimal. The main argument is on whether to use the *Integrated Squared Error* (ISE) or the *Mean Integrated Squared Error* (MISE) (see Jones [1991] for discussion on the roles of ISE and MISE in kernel density estimation) (Turlach 1993). Not only is there no consensus on which is best method to select the value of the smoothing parameter, the number of methods available is still growing.

Until recently, ecological studies and most home range estimation software recommended the fixed kernel density analysis with the least squares cross-validation (LSCV) (proposed by Rudemo 1982 and Bowman 1984) as the default selector of smoothing parameter (*e.g.*, Seaman & Powell 1996; Horne & Garton 2006; Fieberg 2007b). However, LSCV has several drawbacks, including high variability, a tendency to undersmooth data, and a disability to handle ‘stacked’ data points (*i.e.*, data points at the same location) (*e.g.*, Marron 1987; Wand & Jones 1995; Jones *et al*. 1996; Amstrup *et al*. 2004; Hemson *et al.* 2005; Horne & Garton 2006; Gitzen *et al*. 2006; Getz *et al*. 2007; Lichti & Swihart 2011). As such, the LSCV method is no longer recommended to select the smoothing parameter value. Instead, the newer methods for selecting the optimal value of the smoothing parameter (*e.g.*, plug-in methods, solve-the-equation methods and smoothed boot-strap techniques), are considered superior over “first generation” methods such as the LSCV and biased cross-validation (Jones *et al.* 1996; Gitzen *et al*. 2006; Lichti & Swihart 2011).

An extremely large body of literature exists on bandwidth selection for kernel density estimation (see for instance Marron 1987; Park 1991; Jones *et al*. 1992, 1996; Gitzen *et al*. 2006 for reviews) and it is by no means an aim of this chapter to provide an overview or description of all the methods available. Two main points are that the sensitivity of kernel methods to the smoothing parameter is a major drawback to the kernel estimation method and that there is currently no consensus for choosing the optimal value of the smoothing parameter in the context of home range and UD estimation, although the plug-in method and solve-the-equation method are currently recommended methods (Jones *et al.* 1996; Gitzen *et al*. 2006).

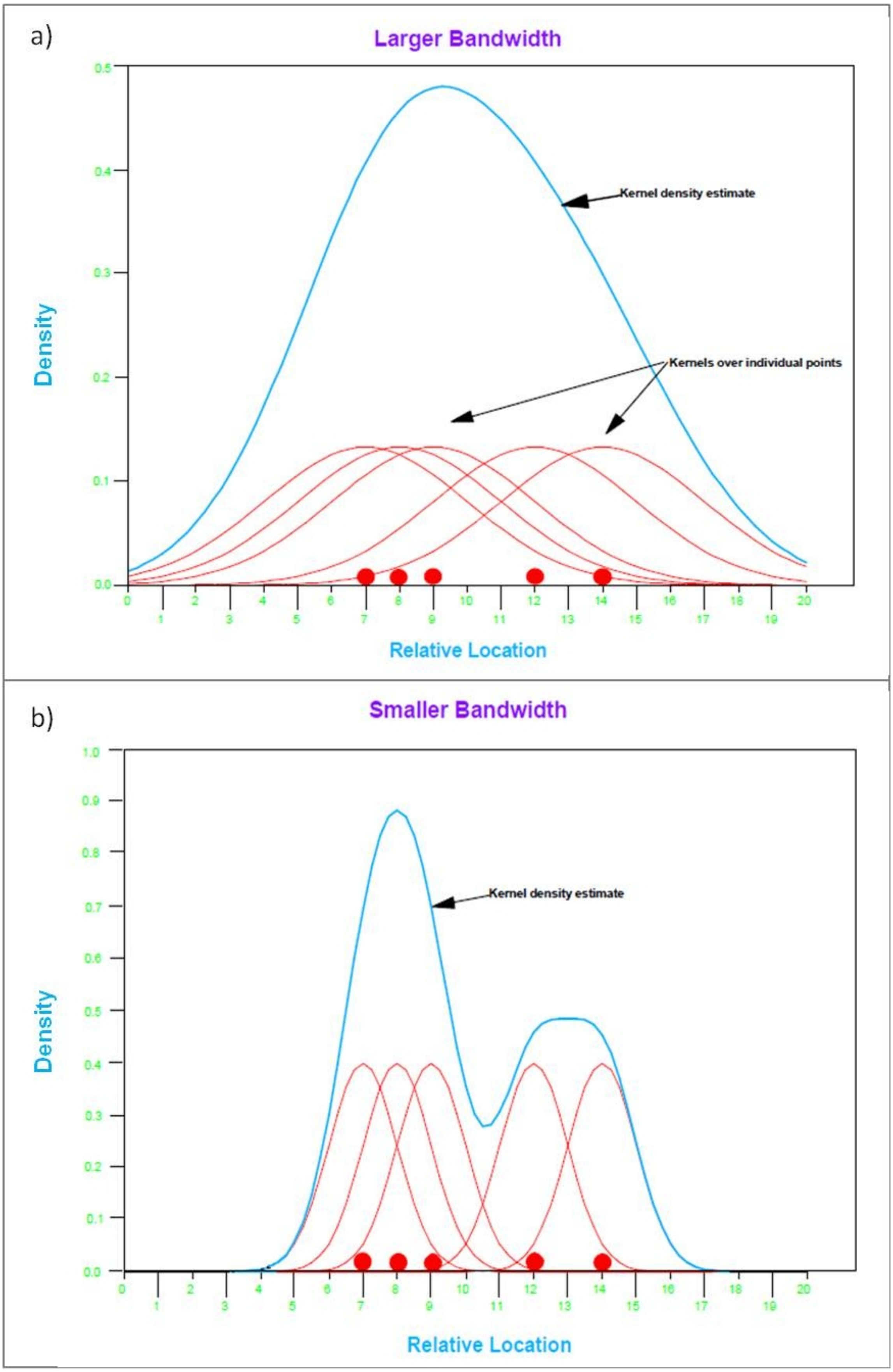

Figure 3.1 Two kernels with (a) a larger bandwidth and (b) a smaller bandwidth placed over the same five points. The smoothness of the resulting density function is a consequence of the bandwidth size.

3.1.2.3 Further methodological issues KDE

The kernel method implicitly assumes statistical independence among the observations and to this end researchers have often re-sampled data with an appropriate time interval (*i.e.*, “time-to-independence”) (*e.g.*, Harris *et al.* 1990; Rooney *et al.* 1998; Kenward *et al.* 2001) as suggested originally by Swihart & Slade (1985a). However, recent studies have shown that re-sampling data often results in severe reduction of the data and consequently a decrease in the precision of home range and UD estimates (Rooney *et al*. 1998; Kernohan *et al*. 2001; Dahle & Swenson 2003; Katajisto & Moilanen 2006; Fieberg 2007b) and that removing autocorrelation removes the biological signal of interest (De Solla 1999; Blundell *et al*. 2001). Furthermore, Otis &White (1999) showed that the conclusions of the analyses of Swihart & Slade (1985a) were based on a methodological error. Overall, current studies have concluded that the concept of ‘time-to-independence’ or ‘distance-to-independence’ is mistaken (*e.g.*, Fortin & Dale 2005).

A second issue concerns delineating home range boundary. Since a Gaussian kernel yields an infinite distribution, strictly speaking a 100% isopleth does not exist. The boundary of the home range is commonly delimited using the 95% - 99% isopleths of an unbounded UD (*e.g.*, Silverman 1986; Worton 1987, 1989, 1995; Seaman & Powell 1996). A recent study of Börger *et al.* (2006) demonstrated that using isopleths in this range, produces area estimates that are biased by sample size and they recommend using isopleths in the range of 50% - 90% to estimate home range size instead. This recommendation of lowering the number of points in estimating home range size, is mainly relevant for (1) data collected with the use of radio/vhf collars, when locations may be based on relatively inaccurate triangulation of radio collars leading to imprecise location estimates and (2) home range estimators using MCP and parametric kernel construction methods which are very sensitive to outlying points (Börger *et al*. 2006) which may reflect exploratory animal movements rather than those necessary for survival and reproduction (Getz *et al*. 2007).

3.1.3 Local Convex Hull Estimator (LoCoH)

3.1.3.1 LoCoH methods

More recently, the Local Convex Hull (LoCoH) method has been proposed for estimating the area of home ranges and for constructing bounded UD from spatial data (Getz & Wilmers 2004) and two modifications have been presented since (Getz *et al.* 2007). The LoCoH method is both a generalisation of the MCP method and essentially a non-parametric kernel method (Getz *et al*. 2007). The LoCoH method applies the MCP construction to a subset of data localised in space, and the local convex polygon (*i.e.*, local hull) is constructed using the *k*-1 nearest neighbours for each data point, thereby producing a set of nonparametric kernels whose union is the UD (Getz *et al*. 2007) and as such the LoCoH uses kernels with forms arising directly out of the data.

The original “fixed *k*” LoCoH method (Getz *et al.* 2007) presented as “k-NNCH” in Getz & Wilmers (2004) begins by constructing a UD from the union of convex hulls associated with each point and its *k* – 1 nearest neighbours and as such requires only the selection of the value *k* (the number of points). The area covered by the finite union of all these convex hulls is referred to as a *k*-NNCH covering (*k* nearest neighbour convex hull), while the subcovering obtained from a union of the smallest of these convex hulls covering x% of points provides for the construction of the x% isopleths (Getz & Wilmers 2004). The first modification is a “fixed radius” (*r*-LoCoH) method, in which all the points in a fixed “sphere of influence” of radius *r* (selected by the user) around each root point are used to construct the local hulls (Getz *et al*. 2007). The second modification is an adaptive (*a*-LoCoH) method, in which all points within a variable sphere around a root point are used to construct the local hulls such that the sum of the distances between nearby points and the root point is less than or equal to *a* (Getz *et al*. 2007).

In selecting the optimal parameter *a*, an initial value equal to the maximum distance between any two points in the data set is proposed (Getz *et al.* 2007). For home ranges with known topologies (*i.e.*, where the number of holes that the UD should contain is known ahead of time) the “minimum spurious hole covering” (MSHC) rule (Getz & Wilmers 2004) may be used to select the smallest value of parameter *a* that produces a covering that has the same topology as the given set (Getz *et al.* 2007). If topology is unknown, differences between real and spurious holes in LoCoH constructions may be evident in plots of area covered by the UD against the value of the parameter *a*: with an increase in parameter value the estimated area may level off once all spurious holes are covered (Getz & Wilmers 2004; Ryan *et al.* 2006), but should increase again when one or more real holes become totally or partially spuriously covered and these plateaus in UD construction thus determine which parameter value to use (Getz *et al.* 2007). The optimal parameter *a*, can thus be identified by adjusting the initial value of *a* until small lacunae are removed and large unused areas remain outside of the 100% UD (Getz *et al.* 2007; Campos & Fedigan 2009).

Getz *et al*. (2007) concluded that *a*-LoCoH method performed the best of the three LoCoH methods, unless there is a particular motive to either have all the kernels constructed from the same number of points (*k*-LoCoH) or for all to be of the same size (*r*-LoCoH). The reasons why the *a*-LoCoH method was found superior to the *k*-LoCoH and *r*-LoCoH methods are threefold: (1) the *a*-LoCoH adapts the size of the kernel elements resulting in smaller kernels in regions with a higher density of locations, (2) the *a*-LoCoH is relatively insensitive to suboptimal value choices for the parameter *a*, and (3) the heuristic rule proposed for the initial selection of *a* (maximum distance between any two points in the data set) provided values close to the optimal value of *a* and seemed much less affected by changes to sample size than was the case for *r* and *k*.

Provided that the value of parameter *a* exceeds the sum of the two greatest distances between points in a data set, the construction will always produce the 100% isopleths while keeping the radius of LoCoH elements small in high density regions of the data (Getz *et al.* 2007). Although there is no guarantee that every point will be included in a hull, this can be required by the user. Duplicate points (*i.e.*, multiple data points at the same location) can cause problems when constructing local hulls because at least three unique points are needed to create a hull and there are three options to handle duplicate points. Duplicated points can be displaced in a random direction by a user-specified distance, or duplicate points can be included when searching for the k-1 nearest neighbours. In the latter case a hull might be formed with less than three unique points, resulting in a zero-area hull. The third option is to simply exclude duplicate points from hull creation and nearest neighbour searches.

3.1.3.2 Methodological issues LoCoH

One major limitation of the LoCoH is the number of point locations that can be analysed. The web version of LoCoH is limited to analysing approximately 1000 points, although a larger number of points can be analysed in R. Ultimately, the maximum number of points depends on the amount of memory of the machine analysing it, but analysing 4000 points in R takes 4 hours on a PC with a 3 GHz processor and 1 GB of RAM (http://locoh.cnr.berkeley.edu/). Developments in GPS tracking are increasing the ability to obtain accurate and precise information on individual(s) movements trajectories (Tomkiewicz *et al.* 2010; Urbano *et al.* 2010) and in recent primate studies the location of the study animal(s) has often been recorded at 5 minute time interval (*e.g.*, Noser 2004; Valero & Byrne 2007; Di Fiore & Suarez 2007; Presotto & Izar 2010), while some have used even smaller time intervals (*e.g.*, Asensio *et al.* 2011). The recording of locational data every 5 minutes already results in over 4000 data points, after as few as 34 full-day follow (based on only 10 hour follow days). For locational data recorded at small intervals this thus means that the LoCoH method is likely only to be functional when a subsample of the data is analysed.

3.2 Methodology

3.2.1 Home range estimates

Home ranges were estimated with (1) the fixed Gaussian kernel (KDE) method (Worton 1987) using a plug-in method for selecting the smoothing parameter of the kernel density estimate as proposed by Sheather & Jones (1991) and described in detail in Section 3.6 of Wand & Jones (1995) and (2) the nonparametric local convex hull (LoCoH) method (Getz 2004; Getz *et al.* 2007). The LoCoH script was downloaded from http://locoh.cnr.berkeley.edu (accessed 1st August 2011). To apply the KDE with the plug-in method to determine the smoothing parameter, ACCRU Tools (Nielsen 2010) was downloaded from http://www.biology.ualberta.ca (accessed 15th August 2011). The ACCRU Tools toolbox is compatible with ArcGIS version 9.3, however, the KDE Tool is “currently being tested for public consumption” (Nielsen 2010). Therefore, the R script that is automatically downloaded as part of ACCRU Tools was modified and directly applied in R software. Analyses were conducted in R and using packages ‘ks’ (Wand & Jones 1995) for the KDE method and ‘adehabitatHR’ (Calenge 2006), ‘gpclib’ (Peng 2007) and ‘ade4’ (Chessel *et al*. 2004) for the LoCoH method.

The adaptive Local Convex Hull method (*a*-LoCoH) (Getz *et al.* 2007) was employed and values of *a* ranging from 500 to 6000 were investigated. When the value of *a* was plotted against the home range size it showed that home range size increases exponentially with value *a*, with big jumps for a values between 500 and 1500 (Figure 3.2). As *a* increases further, the home range converges toward the Minimum Convex Polygon (as long as *a* is larger than the maximum distance between any two points in the data set the home range is the MCP). Important values are those just after big jumps (Getz *et al*. 2007) and therefore results of values of *a* between 1500 and 3500 were investigated in more detail. Based on a visual review of the home range estimations with different values of *a*, a value of 3000 was selected. Although this introduces a degree of arbitrariness, the *a*-LoCoH method is relatively robust against suboptimal choices of *a* (Getz *et al.* 2007; Campos & Fedigan 2009; Lichti & Swihart 2011). This is confirmed by the small differences in home range area (estimated by 75%, 95% and 99% volume isopleths) using different values of *a* (Figure 3.3). Prior to the analysis, duplicate points were shifted randomly by 1 meter.

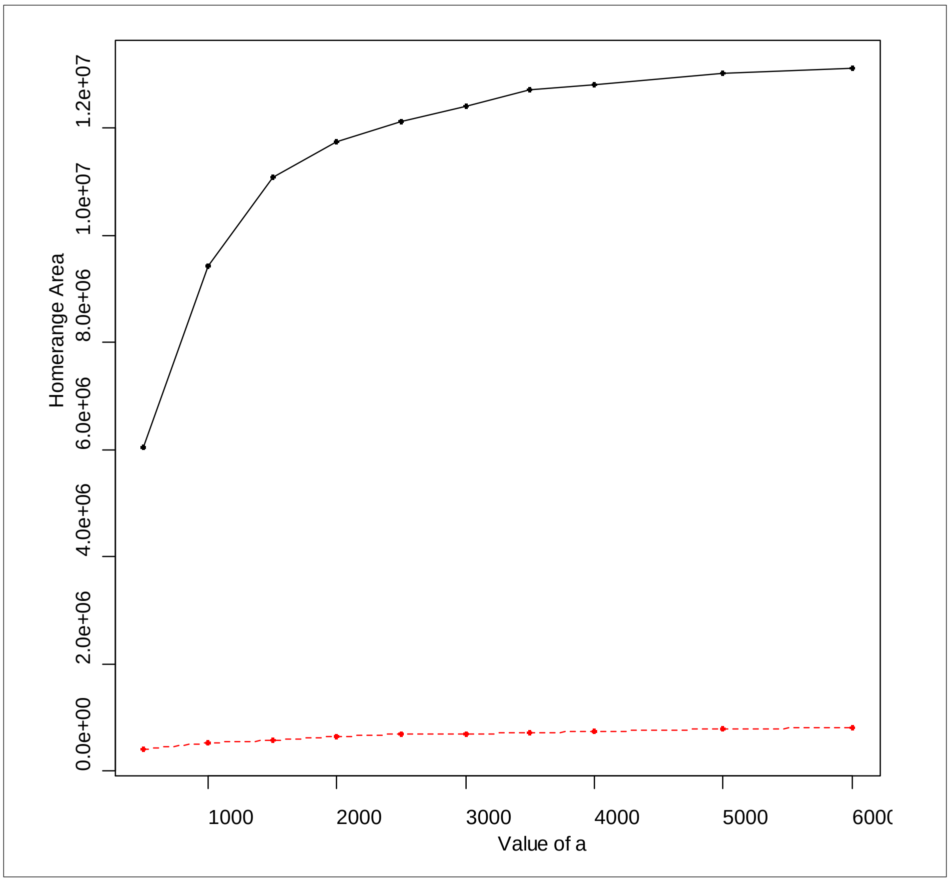

Figure 3.2 Shows how the home range area (in m^2) estimated by the *a*-LoCoH method changes with different values of *a*. The top line (*black continuous*) shows the 99% isopleth and the bottom line shows the 50% isopleth (*red dashed*).

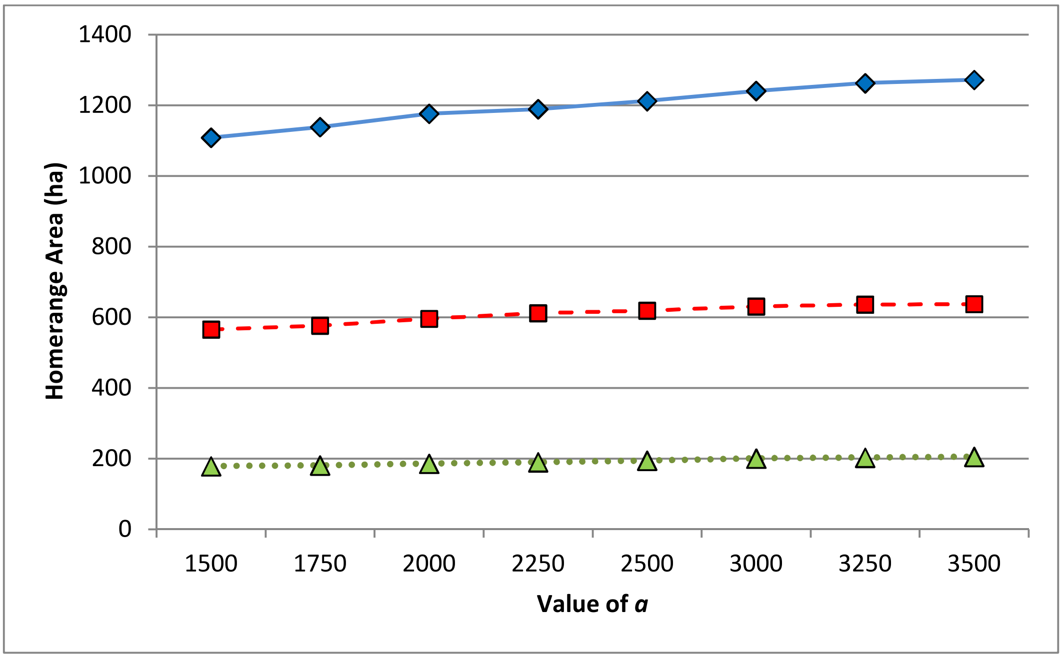

Figure 3.3 Values of *a* between 1500 and 3500 were investigated further, but showed little differences in home range area for the 75% isopleth (*green dotted line with triangles*), 95% isopleth (*red squared line with squares*) and 99% isopleth (*blue line with diamonds*).

3.2.2 *Data manipulation: time interval*

Location records (N=462,556 over 371 full and partial follow days) were collected from late April 2007 to November 2008 using the automatic track recording setting of the handheld GPS device, which recorded track points at an irregular time interval (see Chapter 2 Section 2.3.1 for more details on data collection). For the purpose of analysis and to reduce errors in the representation of baboon movements caused by observer movement within the troop while recording other behavioural data, new waypoints were created spaced at regular time intervals (manually adjustable) using an automated script in R (Appendix I).

Due to the relatively small time interval between consecutive waypoints in the original data (31 ±55 seconds), it was assumed that the baboons travelled at constant speed in a straight line. The locations of new waypoints (WP_N) were therefore based on the relative time to the previous track point (TP_{N-1}) and the time duration between the two surrounding track points (TP_{N-1} and TP_{N+1}) (Equation 1and Equation 2).

Equation 1:

$$X_{WP\,N} = X_{(N-1)} + ((X_{(N+1)} - X_{(N-1)}) * ((\text{time interval} - \text{duration}_{(N-1)}) / (\text{duration}_{(N+1)} - \text{duration}_{(N-1)})))$$

Equation 2:

$$Y_{WP\,N} = Y_{(N-1)} + ((Y_{(N+1)} - Y_{(N-1)}) * ((\text{time interval} - \text{duration}_{(N-1)}) / (\text{duration}_{(N+1)} - \text{duration}_{(N-1)})))$$

To illustrate the creation of a data set with regular time intervals between consecutive waypoints, some original data are presented in Table 3.1 to which a 5 min time filter is applied. In the new 5 min data set, TP_1 will become the first waypoint [WP_1], and a second waypoint will be created between TP_7 and TP_8. The duration between WP_2 and TP_7 is (300-290) 10 seconds, whilst the total duration between TP_7 and TP_8 is (330-290) 40 seconds. WP_2 will therefore be located a quarter of the way (10/40=0.25) between TP_7 and TP_8. The ‘remaining’ 30 seconds between WP_2 and TP_8 (330-300) are added to the next interval, so that the sum duration at TP_8 is 30 seconds, at TP_9 is 100 seconds (30+70) and the sum duration at TP_{10} is 186 seconds (100+86), etc. When the duration between two track points was larger than the pre-determined time interval, then multiple new waypoints were created between the two track points, again assuming a continuous movement throughout the interval.

Table 3.1 Data set of 10 recorded track points [TP] (based on real data), time of recording (hh:dd:ss), the duration (sec) from the previous TP (*e.g.* duration at TP_2 represents the time interval between TP_1 and TP_2) and the summed duration (sec). A new 5 min time interval data set includes TP_1 (is WP_1), after which a waypoint is created between TP_7 and TP_8. Summed duration starts at zero again at WP_2, but includes 'remaining' time from WP_2 to TP_8.

TP	Time	Duration	Sum Duration
1 (WP_1)	07:52:00		
2	07:52:26	26	26
3	07:53:10	44	70
4	07:54:20	70	140
5	07:54:43	23	163
6	07:55:26	43	206
7	07:56:50	84	290
WP_2			(300)/(0)
8	07:57:30	40	30
9	07:58:40	70	100
10	08:00:06	86	186

Data gaps occurred when the baboons travelled up or down steep cliffs that were insurmountable for the observer and the observer would have to find an alternative route to rejoin the baboons at the top or bottom of such cliffs. The location where the observer left the troop and the location where the observer rejoined the troop were both marked with a waypoint and track points in between these two waypoints were subsequently deleted. The resulting gaps in the data set are referred to as 'cliff gaps'. To prevent home range estimators to systematically exclude steep cliff areas that were in fact used by the baboons, waypoints were created within the cliff gaps at the required time interval as described above. Occasionally the baboons were lost for short periods of time due to high travel speed, low visibility or otherwise rough terrain. This also resulted in gaps in the data, referred to as 'lost gaps', but such 'lost gaps' were not filled with new waypoints, but instead the first track point after such a period, was considered a new waypoint and time intervals were started afresh (thus sum duration would start at zero seconds).

In first instance, the aim was to estimate home ranges using data with a relatively small time interval of 5 minutes. However, due to computer memory limitations neither method (KDE and LoCoH) managed to analyse the large number of data points (N=35,880) with a 5 min time interval. Therefore, home ranges were estimated using data points re-sampled to 30 minute time intervals; the time interval resulting in the largest sample size (N=6175) that did not result in errors indicating lack of computer memory.

3.2.3 Sample size

In this study data were collected over a 19-month period (Chapter 2 Section 2.3.1) rather than a 12-month period and subsequently re-sampled to a 30-min time interval (Chapter 3 Section 3.2.2). The potential effects of this prolonged study period and relatively large time interval on home range estimations were investigated in several ways.

The KDE method is widely available in a range of software programs and extensions (*e.g.*, ArcGIS, BIOTAS, GRASS, Hawth's Tool Extension, Home Ranger), but in these applications the smoothing parameter selection methods are limited to a few older "first-generation" methods (*e.g.*, LSCV, reference bandwidth, ad-hoc method, biased cross-validation) (Jones *et al.* 1996; Gitzen *et al*. 2006; Lichti & Swihart 2011). Nevertheless, these applications are able to analyse large data sets, which was not possible using either the KDE plug-in method or the LoCoH method. To investigate the potential effect of a 19-month rather than a 12-month study period, home ranges were estimated using the KDE method, using the 'ad-hoc' smoothing parameter selection method in BIOTAS and home range areas were subsequently plotted against the number of sample months to explore the point at which (if any) an asymptote was reached. Next, to assess whether the larger 30-min interval resulted in significantly smaller home ranges two approaches were used. First, the same KDE ad-hoc method was applied to the data re-sampled to different time intervals. Since this involved comparison between sampling intervals for only one method, the concern of the effects of smoothing parameter selection method, which may have been sub-optimal, was disregarded. The KDE ad-hoc method was applied to data re-sampled to 5-min to 120-min intervals in BIOTAS software. Second, the KDE plug-in method and *a*-LoCoH method (using value a=3000) were applied to data re-sampled to 60 minute intervals (N=3184). If differences in home range estimations between the 30-min data set and 60-min data set were small then it was assumed that adding more data points to the analysis (*i.e.*, analysing the data at a smaller than 30 minute time interval) would not have significantly improved the home range estimates presented in this chapter.

Locational data in this thesis are spatially very precise (See Chapter 2 section 2.3.1) and no stray points were visually detected (*i.e.*, all points are part of travel paths), although it may be argued that travel to far outer regions were exploratory and should not be included in the home range estimation. Therefore, home range boundaries were delimited by 95% and 99% volume isopleths. The core area was defined as that area in which the animals spend 75% of the time (Normand & Boesch 2009).

3.3 Results

3.3.1 Sample size

After applying a 30-min time interval to all location data collected during the 19-month study period, a total of 6175 location records remained (480 tracks with an average of 12.9 waypoints per track). After a 12-month period 81.4% of these points (N=5025) were collected and thus the addition of 7 months more data (from May 2008 – November 2008) resulted in another 1150 data points to be added to the analyses (Figure 3.4)

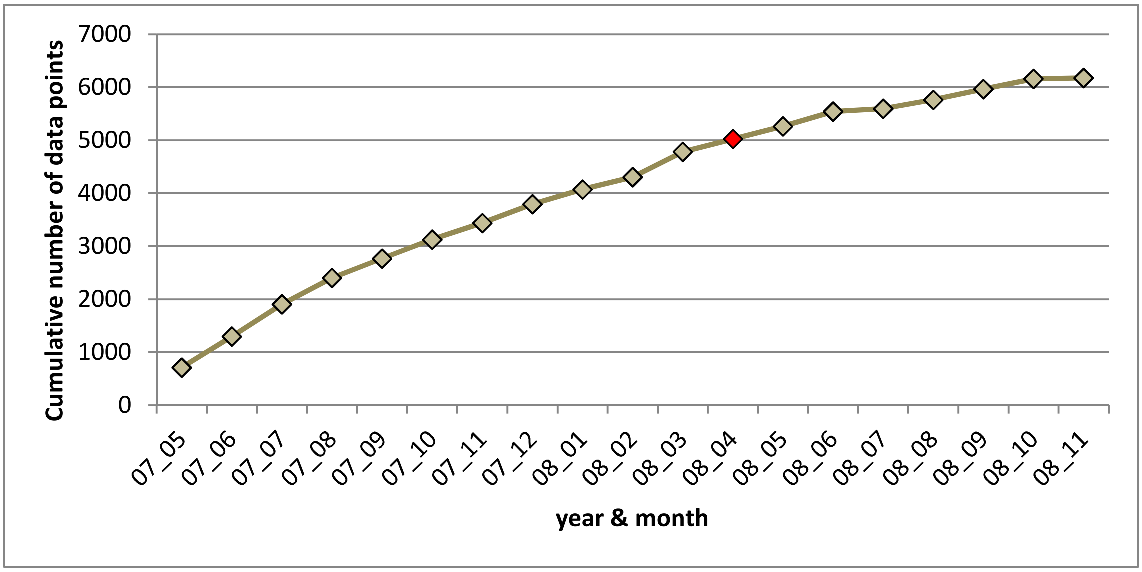

Figure 3.4 Cumulative number of data points in the course of the 19-month study period (*red marker* shows the number of data points after a 12-month period) after applying a 30-min time interval to the data.

The addition of 7 months more data (from May 2008 – November 2008) to a 12-month period has very little effect on home range area estimations when home range area is delineated by 75% or 95% isopleths, but has a somewhat larger effect when the home range size is delineated by the 99% isopleth (Table 3.2 and Figure 3.5). When delineated by the 99% isopleth the home range area converges to a first asymptote after 7 months of data collection (November 2007), but then there is another increase of home range area after 11 months of data collection (March 2008) after which the home range area converges to a second asymptote after a 14 month period (June 2008) (Figure 3.5). A similar trend can be observed when home range area is delineated by 75% or 95% isopleths, although the home range expansion is only minor (25 and 53 ha respectively) (Table 3.2).

Table 3.2 Home range areas (ha) delineated by 75%, 95% and 99% isopleth for a 12-month and 19-month study period (estimated using the KDE ad-hoc method).

	75%	95%	99%
12-month period	206	547	1037
19-month period	231	600	1210

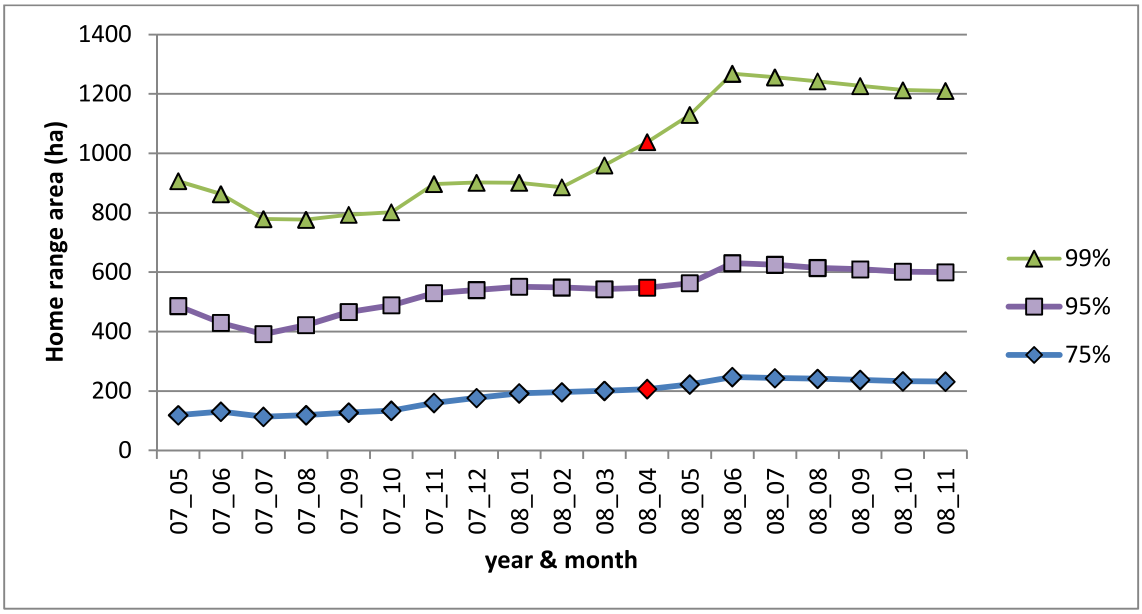

Figure 3.5 Cumulative home range area (ha) delineated by 99% (*green triangles*), 95% (*purple squares*) and 75% (*blue diamonds*) isopleths in the course of the 19-month study period (estimated using KDE ad-hoc method). Data markers after a 12-month period (April 2008) are coloured *red*.

Home ranges were estimated after the data was re-sampled to different time intervals ranging from 5-min (N=35882) to 120-min (N=1653). This showed that home range estimates at all three isopleth levels (75%, 95% and 99%) increased for 5-min to 30-min time intervals, after which home range estimations steadily decreased for larger time intervals (Figure 3.6). The 30-min interval thus did not result in smaller home range estimations compared to smaller time intervals, but instead resulted in larger home range estimations.

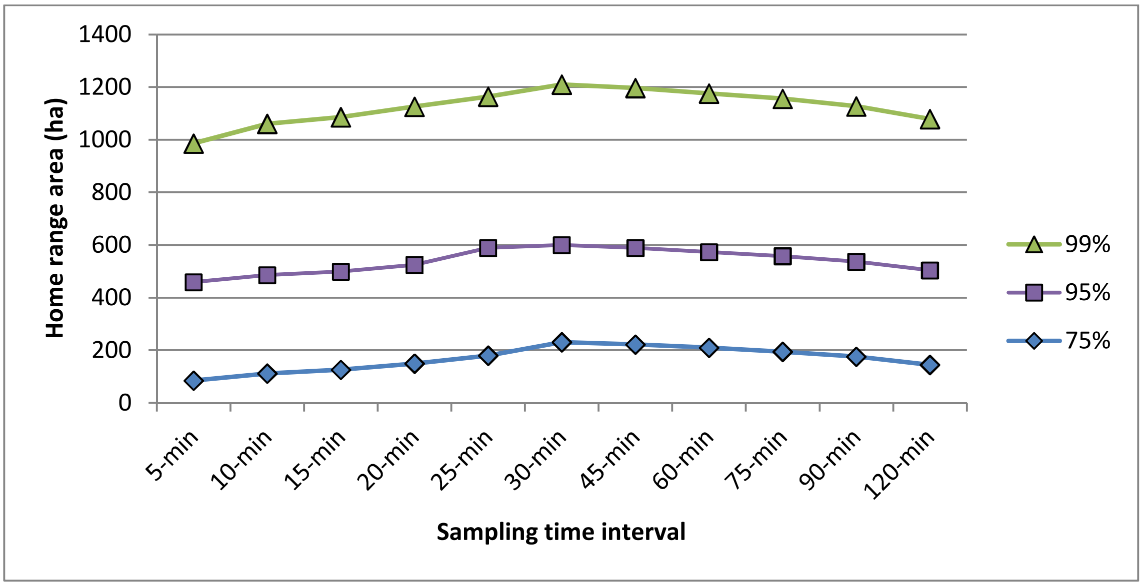

Figure 3.6 Home range area (ha) delineated by 99% (*green triangles*), 95% (*purple squares*) and 75% (*blue diamonds*) isopleths in the course of the 19-month study period (estimated using KDE ad-hoc method).

To assess whether the relatively large sampling interval of 30-min resulted in significantly smaller home range estimates both the KDE plug-in method and the *a*-LoCoH method were applied additionally to data re-sampled to 60 minute intervals (N=3184). The differences in home range estimations between the 30-min and 60-min sampling interval were largest at the 99% isopleth level (<14%) and smallest at the 75% isopleth level (<5%) (Table 3.3). Total difference in home range size between 30-min and 60-min sampling interval was 271 ha for the KDE plug-in method and 150ha for the LoCoH method. So although both methods showed only small differences in home range estimation, the *a*-LoCoH seemed more robust to sample size.

Table 3.3 Comparison of home range areas (ha) estimated for the baboons data set re-sampled at 30 minutes (N=6034) and at 60 minutes (N=3184) intervals, determined by the 75%, 95% and 99% isopleths for the adaptive a-LoCoH method and the KDE plug-in method.

Isopleth	30 min (KDE plug-in)	60 min (KDE plug-in)	30 min (*a*-LoCoH)	60 min (*a*-LoCoH)
75%	248	229	200	192
95%	692	600	631	598
99%	1189	1029	1241	1032

The analyses above show that sample size has a very limited effect on home range estimations in this study. The additional data obtained by a 19-month instead of a 12-month study period did increase the home range estimation, but for the 75% and 95% isopleth this increase was only minor. Moreover, the relatively large 30-min time interval used due to computer limitations was shown unlikely lead to smaller home range estimations. Furthermore, these analyses showed that home range estimates by the KDE ad-hoc method (1210 ha, 600 ha and 231 ha at 99%, 95% and 75% isopleths respectively) were very similar to the home range estimates by the KDE plug-in method and the *a*-LoCoH method at a 30-min time interval (Table 3.3).

3.3.2 Home range estimations

The results of the home range estimations using the KDE plug-in method and the a-LoCoH method are shown in Figure 3.7. Furthermore, to allow evaluation of overlap in home range estimations, the two methods are plotted together at different isopleths levels (Figure 3.8).

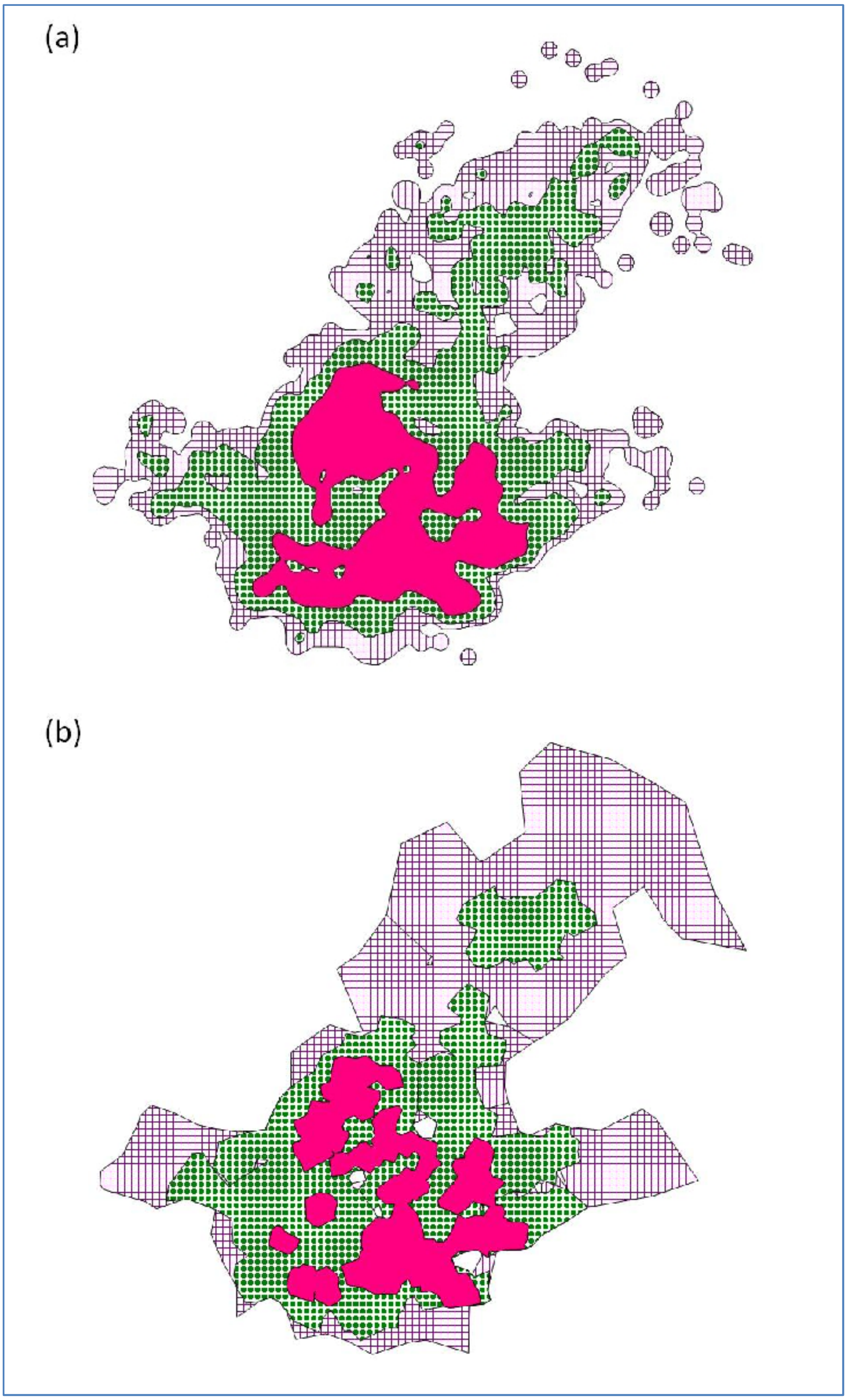

Figure 3.7 Home range estimations using (a) the KDE plug-in method and (b) the *a*-LoCoH method. Boundaries are delineated by 75% isopleth (*pink area*), 95% isopleth (*green dotted area*) and the 99% isopleth (*purple checked area*)

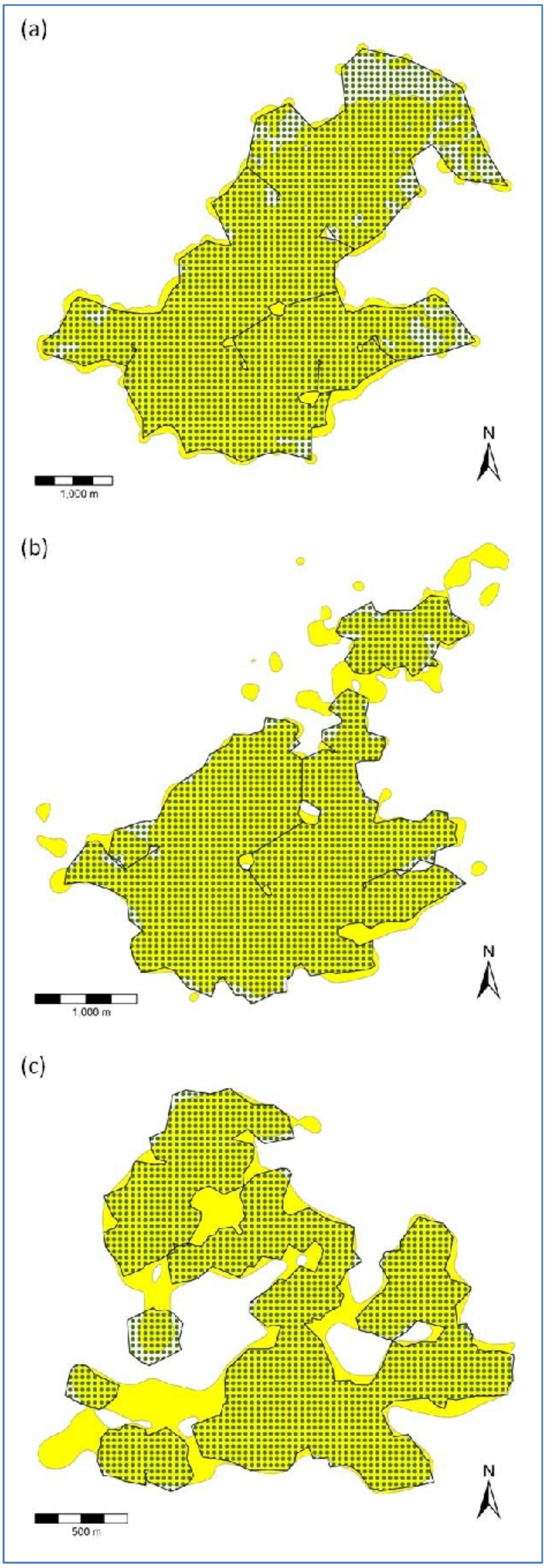

Figure 3.8 Overlap in home range area between the KDE plug-in method (*yellow polygons*) and the *a*-LoCoH method (*green dotted polygons*) at the (a) 99% isopleth (b) 95% isopleth and (c) 75% isopleth level.

At the 75% and 95% isopleth level the KDE plug-in method produces larger home range estimates than the *a*-LoCoH method, but at the 99% isopleth level the KDE produces a slightly smaller home range estimate (Table 3.4). The KDE plug-in method produces several "islands" at the edge of the home range (Figure 3.7a) at the 99% isopleth level, which is in contrast with the LoCoH method that has a hard boundary (Figure 3.7b). Overlapping home range estimates of the two methods at the 99% level shows that the *a*-LoCoH method "bridges" the gaps at the edge of the boundary, to also include the island areas produced using the KDE plug-in method (Figure 3.8b). This tendency of the KDE plug-in method to produce islands at the home range border becomes even clearer at the 95% isopleth level, especially in the most northern range and the most eastern range of the baboons (Figure 3.7, Figure 3.8c). The opposite is true however at the 75% isopleth level (Figure 3.8c). Here the *a*-LoCoH produces a core range estimate consisting of several separate core areas (although not such small islands as the KDE plug-in method at larger isopleths levels), whereas the KDE plug-in method results in a more continuous core area (Figure 3.8c). At all isopleths levels the boundary of the home range area is smoother (*i.e.*, more curved) when using the KDE plug-in method than the *a*-LoCoH method.

Table 3.4 Comparison of home range areas (ha) estimated for the baboons data set (N=6174) by the 75%, 95% and 99% isopleths for the adaptive *a*-LoCoH method and the KDE plug-in method.

Isopleths	*a*-LoCoH	KDE plug-in	Overlap
75%	200	248	200
95%	631	692	631
99%	1241	1189	1080

Previous studies showed that the *a*-LoCoH method performed better than the KDE plug-in method, primarily because the *a*-LoCoH method accommodates user knowledge of known physical barriers and is more adept than the KDE plug-in method at excluding geographical features such as rivers, lakes, inhospitable terrain, and so on (*e.g.*, Ryan *et al*. 2006; Getz & Wilmers 2004). The study site did not include obvious physical barriers such as lakes or rivers. Although the study area is mountainous, this did not seem to limit baboon range and corrections were made to the data to compensate for observer inability to follow baboons over some cliffs (see Section 3.2.2). Therefore, no obvious 'holes' in the home range were expected due to topology. Nevertheless, both methods contained several small holes (N=10 for both methods) in the main home range area (not including areas between the 'islands' on the edge of the home range for the KDE plug-in method) (Figure 3.9). The size of the holes did not differ significantly between the KDE plug-in method (1.14 ±1.25 ha) and the *a*-LoCoH method (1.04 ±1.10) (t-test: t=1.82, df=18, p=0.858). Indeed there were no locational records at these excluded locations (*i.e.*, 'in the holes') in the 30 minute data set, however, overlaying the original data (N=462,556) shows that some of the holes in fact did contain data points and are thus not impassable (or unused) areas (*e.g.*, holes 5, 7 and 8 in Figure 3.10).

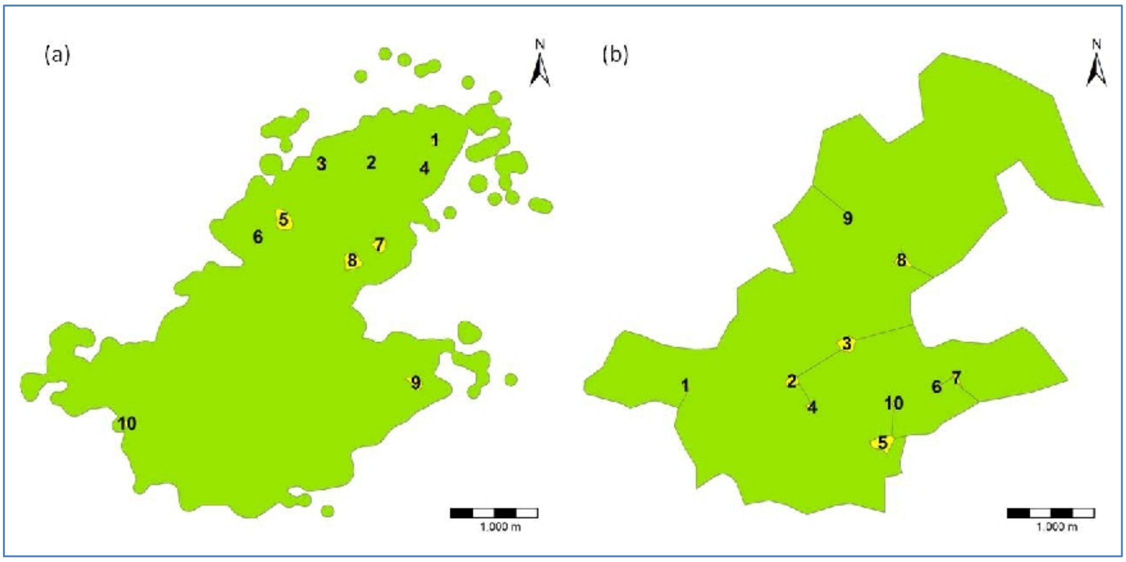

Figure 3.9 'Holes' in the home range at 99% isopleth levels for (a) the KDE plug-in method and (b) the *a*-LoCoH method.

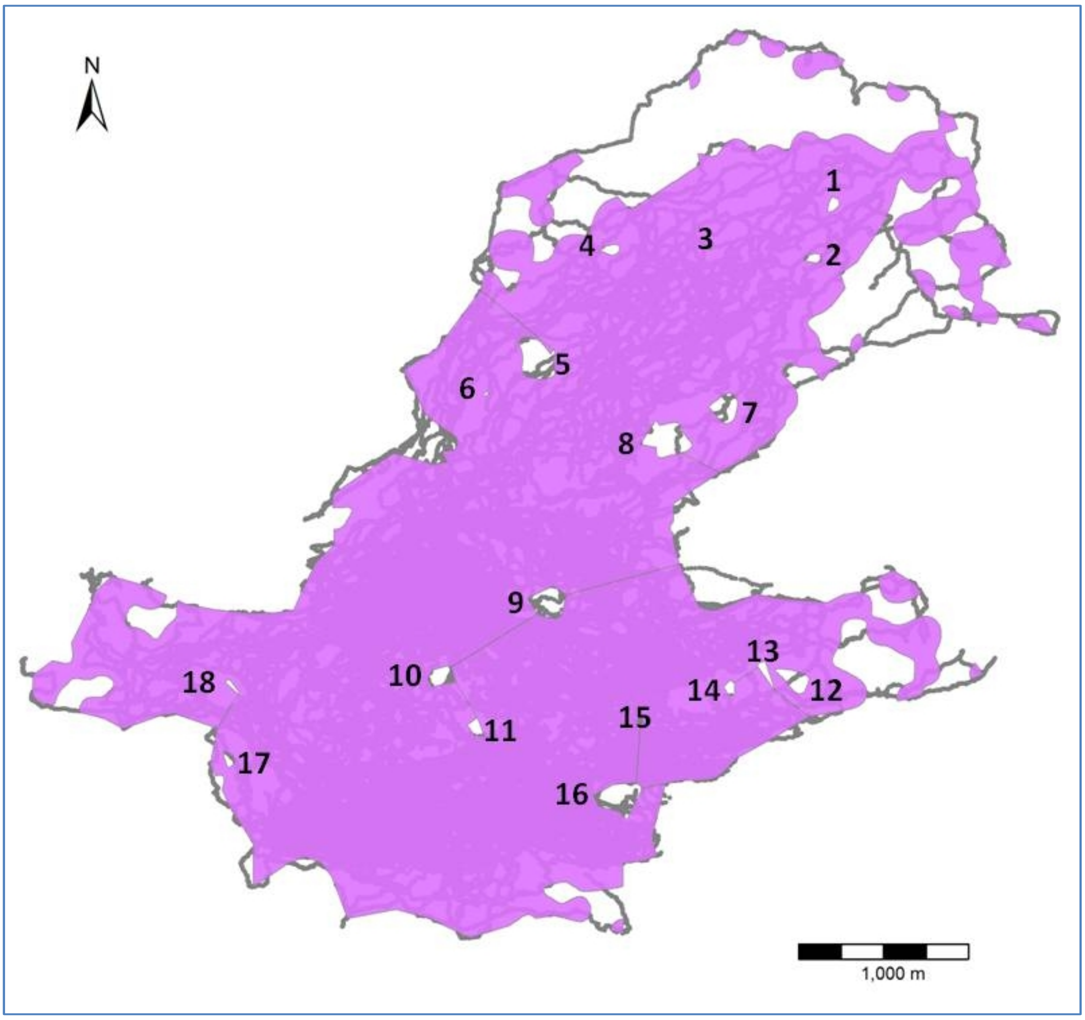

Figure 3.10 Home range area (*purple polygons*) where the KDE plug-in method and *a*-LoCoH method overlapped (based on 30-min interval data set and 99% isopleths) includes small lacunae (*i.e.*, holes). However, original location records (*grey dots*) show that some of these excluded areas (*e.g.*, holes 5, 7 and 8) were used.

In total 18 areas were excluded by the two methods, however, there was only little overlap in the location of the holes: holes 5, 8 and 12 were excluded by both the KDE plug-in method and the *a*-LoCoH method (Figure 3.10). Of the 18 small areas excluded, only for 2 holes can an explanation for the exclusion be readily provided. Holes number 9 and 18 in Figure 3.10 were located at swamp areas, which were circumvented by the observer when possible. Since this involved only very small detours and the baboons were not out of sight during the detour, generally the travel route was not adjusted afterwards as was the case for larger detours due to cliffs (see Section 3.2.2). Since no obvious holes were expected due to the lack of large physical features such as lakes, the performance of the home range estimators could not be assessed by evaluating holes in the home range. Note that for the *a*-LoCoH method however, the value of *a* can be adjusted as to limit the number of holes in the home range, which is not possible for the KDE plug-in method. Had a larger value of *a* been selected for the *a*-LoCoH, the number of holes in the estimated home range estimated would have been smaller and vice versa.

3.4 Discussion

3.4.1 Sample size

Sampling recommendations have been often made based on the minimum necessary number of data points to calculate home range size (*e.g.*, Hansteen *et al*.1997; Girard *et al*. 2002), although some studies have investigated the effect of sampling interval between data points (*e.g*., Börger *et al*. 1996; DeSolla 1999). These studies concern locational data from radio tagged animals with the aim to estimate home ranges at population level for which there is often a trade-off between the number of locations sampled per individual animal and the number of animals monitored (Otis & White 1999; Börger *et al*. 1996). It was concluded that for such studies that variation in home range estimation is largely due to differences between individuals and study areas (Hurlbert 1984; Börger *et al*. 1996; DeSolla 1999) and therefore, resources should be allocated towards collecting data on as many individuals possible, instead of collected as many data per individual possible (Börger *et al*. 1996).

In the present study, location data from one baboon troop is analysed and the troop was regarded as one unit. It has been suggested that as long as the data are collected at a regular time interval, the number of observation should be maximised to obtain better parameters, such as accuracy and precision of home range size estimations, regardless of the estimation method used (DeSolla 1999). When the number of data points is restricted, the number of (partial) day ranges is more relevant than the sampling interval between data points (Otis & White 1999; Börger *et al*. 1996). In other words, it is expected that home range estimates of a baboon troop will be more accurate when 100 data points are collected over 10 days then when 100 data points are collected in 1 day.

Home range size generally increases with sample size (*e.g.*, Ostro *et al*. 1999) to converge towards an asymptote (Getz *et al*. 2007), whereby sample size is influenced both by the time interval between consecutive data points (*i.e.*, the smaller the time interval, the larger the sample size) and the length of the study period (*i.e.*, the longer the study period, the larger number of follow days and thus the larger the sample size). In this study, data were collected over a 19-month period rather than a 12-month period to estimate annual home range size (*e.g.*, Hamilton *et al.* 1976; Bidner 2009; Henzi *et al*. 2010; Hoffman & O'Riain 2011), which could have led to an increased annual home range area estimation. However, it was shown that the increased sample size due to the prolonged study period had a very limited effect on home range estimations since the asymptote was reached well before even a 12-month period when home ranges were delineated by 75% and 95% isopleths.

Furthermore, data were re-sampled to relatively large 30-min time interval due to computer limitations, which could have led to a decreased annual home range area estimation. However, the number of data points analysed to estimate home was still very high (N=6,175) due to the large number of follow days. It was therefore expected that including more data points (by decreasing sampling interval) would not significantly increase the accuracy or size of the home range estimation. This notion was confirmed when the KDE ad-hoc method was applied to the data re-sampled to time intervals from 5-min (N=35882) to 120-min (N=1653), which showed that the 30-min interval did not result in smaller home range estimations compared to smaller time intervals, but instead resulted in larger home range estimations. In addition, the KDE plug-in method and the LoCoH method were used to estimate home range size after the data were re-sampled at an even larger time interval (60-min) and thus to estimate home range area based on a smaller sample size (N=3184). For both the KDE method and the LoCoH method the differences in home range estimations between the 30-min and 60-min sampling interval were relatively small, although the LoCoH seemed more robust to differences in sample size. It must be noted that that home range estimations by the LoCoH can be further influenced by adjusting the value of *a* (although this was not done in this comparison). Home range estimated based on the data re-sampled to a 30-min time interval therefore provides home range area estimates as precise as if the data were analysed at a smaller time interval (*e.g.*, 5 minutes).

It is therefore concluded that neither the prolonged study period nor the relatively large time interval greatly influenced home range estimations in this chapter. The very minor effects that sample size had on home range estimations in this study are likely to be explained by the relative high number of (partial) follow days (371 of which 234 full follow days) analysed compared to other studies. For example, Hill (2009) collected location data for 45 and 53 full-day follows at 30-min interval for his two study troops during a 10-month period, Noser (2004) collected location data over 224 days (of which 96 full-day follows) at 5-min intervals over a 16-month study period and Hoffman & O'Riain (2011) collected data over 137 days (of which 74 full-day follows) at 20-min intervals over a 12-month period. Both Hill (2009) and Noser (2004) show that the final estimates of home range size for their study troops are near asymptotic values, suggesting that their numbers of observation days, which were still significantly smaller than those in this study, were sufficiently high to yield reliable estimates of the ranging area of the troops.

3.4.2 Home range estimation method

Home ranges were estimated using kernel density estimation (KDE) and adaptive local nearest-neighbour convex-hull (LoCoH) methods and were delineated by 99% and 95% isopleths. Overall, the KDE and LoCoH produced very similar results. Nevertheless, two main differences were that at larger isopleths levels, the KDE had a tendency to produce 'islands' at the border of the home range and that the KDE produced smoother boundaries than the LoCoH method (Figure 3.7, Figure 3.8b). The islands produced by the KDE method seemed unrealistic as part of the home range estimate of one baboon troop, since the baboons would have to use the areas surrounding the islands to get to these areas in the first place. The areas connecting the islands produced by the KDE method to the 'main' home range area were indeed included in the home range estimation by the LoCoH method (Figure 3.8a-b). The core of activity, delineated by 75% isopleths was very similar in size (248ha and 200ha for the KDE and LoCoH method respectively), although more patchy for the LoCoH method than for the KDE method (Figure 3.8c). The main reason why the two methods evaluated in this chapter showed little differences in home range estimations is likely to be the large number of data points analysed.

To assess any method's performance in home range size estimation some notion must exist of 'true' home range size. Only in this way can a method be assessed as to whether it is 'underestimating' or 'overestimating' home range size and compared to other methods. Although this is feasible for simulation studies, for studies analysing empirical data the 'true' home range cannot be known and is likely to depend on the research question under investigation and the time scale of interest (Börger *et al.* 2006). One method that has been suggested for estimating 'true' home range size from empirical data is to create continuous travel routes from unfiltered locational data (*i.e.*, connect successive points into lines) and subsequently buffer the routes with a biological meaningful buffer (*e.g.*, based on troop spread) (Ostro *et al.* 1999). However, this method is highly dependent on what is considered a biological meaningful distance area and even small variations result in large differences of 'true' home range estimates. For instance, when this method was applied to the baboon travel routes with a 15m buffer, a 'true' home range area of 862 hectares was obtained whereas when a 20m, 25m and 30m buffer were applied, 'true' home range areas of 955, 1027 and 1123 hectares were obtained respectively. Furthermore, this method uses a subjective ad-hoc criterion to fill resulting holes (≤ 1% of the area of associated MCP with the data) (Ostro *et al*. 1999). As such, differences in 'true' home range size due to the selection of buffer distance and ad-hoc criterion are much greater than differences in home range estimations between the two methods applied to estimate home ranges in this chapter (1189ha and 1241ha for KDE and LoCoH respectively for 99% volume isopleths). It would therefore be unjust to make statements about whether the methods used in this chapter, underestimated or overestimated home range using this notion of baboons' 'true' home range.

The use of the KDE method and the LoCoH method are both challenging due to limitations of software packages. Although newer methods to select the optimal smoothing parameter in kernel density estimations (*e.g.*, plug-in methods and solve-the-equation methods) are considered superior over "first generation" methods (reference bandwidth [*href*], LSCV and biased cross-validation) (*e.g*., Jones *et al*. 1996; Gitzen *et al*. 2006; Lichti & Swihart 2011), these new methods are not yet readily available in many software packages. The new methods can be applied in R, but there seems to be a severe limitation in the amount of data that can be analysed. For instance, when locational data were re-sampled to 15-min intervals (N=12,114), home range estimations in R failed despite the use of typical modern computer capacity (3GB RAM, AMD Athlon ™ II X3 445 Processor 3.11 Ghz). Moreover, in contrast to more user-friendly software, R requires detailed knowledge on R programming language, which further complicates the application of these new methods in home range estimations. It is thus imperative that widely used software packages, such as ArcGIS and extensions, such as Home Ranger (Hovey 2000) are updated to include new methods to select the optimal smoothing parameter, if these methods are to be more commonly used in future home range studies and to allow comparison with other methods. Until that time, the limited availability and relative complicated use in R are two major limitations to the application of these new methods, including the plug-in method used in this study.

It is thus difficult to assess which method performed better than the other having used empirical data obtained in a study area that lacks large geographical features that should have evidently been excluded from the home range estimation. Nevertheless, the LoCoH was considered a better, but also the more convenient method to estimate home range, because (1) the KDE produced unrealistic patchy home range estimates 'islands' that the LoCoH did not (2) the KDE requires selection of an optimal smoothing parameter value and there is no consensus on what is the best method to do so (3) the value *a* in the LoCoH is robust to sub-optimal choices compared to the smoothing parameter in the KDE method (4) the LoCoH has the potential to exclude physical barriers and (5) the LoCoH was relatively easy to use with a user-friendly web-interface, user instructions and readily available scripts to use in R.

CHAPTER 4

CHANGE-POINT TEST

4.1 Introduction

Despite huge diversity in morphology, ecology and behaviour, all animals have the need to navigate towards specific places to reach food sources. Animals navigating through large-scale space (*i.e.*, an area that cannot be seen entirely from a single vantage point, *sensu* Byrne 2000) face a complex environment with a high number of resources randomly distributed. Possessing some kind of spatial memory and planning in advance which resources to visit, would thus be highly advantageous (Normand & Boesch 2009).

In studies on spatial cognition, linear travel paths to out-of-sight resources have 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 (*e.g*., Janmaat *et al*. 2006; Janson & Di Bitetti 1997; Noser & Byrne 2007b; Valero & Byrne 2007). Nevertheless, such an approach does not account for the potential effects of non-visual sensory cues, such as olfactory or vocal cues, which may be picked up from further away. In addition, 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 (Asensio *et al.* 2011). As such, a major challenge faced by researchers is to objectively identify the travel goal (if any) for an animal as well as the points at which they supposedly decided to move towards a goal (Byrne *et al.* 2009).

Recently, Byrne *et al*. (2009) developed a method based on the statistical characteristics of a subject's travel route, to circumvent the problem that researchers cannot know what the goal is in the mind of the subject whose ranging behaviour is being recorded. This novel statistical method, termed the change-point test (CPT), has been shown to successfully identify locations at which animals start orienting towards the next goal, which in the great majority of cases can be readily interpreted in biological terms (Byrne *et al*. 2009; Asensio *et al*. 2011). The CPT offers the chance to identify such locations at which animals significantly change their travel direction, so-called 'change-points', independent of the possible reasons for the change, such as the animal's demeanour at the change-point, or any resources to which the travel led (Byrne *et al.* 2009). As a consequence, the test removes much of the subjectivity and circularity inherent in more traditional methods of determining when an animal began heading in a particular direction or oriented towards a particular goal. Using the CPT to systematically identify change-points has thus been suggested as a first step to understanding how animals navigate their environment, and ultimately, how they represent and store spatial information of their home range in the brain (Byrne *et al.* 2009).

This chapter first provides a detailed description of the CPT followed by an evaluation of the effect of the type of data sampling protocol on the CPT results. Then an extensive sensitivity analysis is conducted with the aim to determine the optimal parameter values, which are considered crucial to the successful application of the CPT (Byrne *et al.* 2009), in order to identify those locations in baboon travel routes at which the baboons started orienting towards new goals (*i.e.*, change-points) (Chapter 5) to provide inside into their spatial abilities.

4.2 The change-point test (CPT)

4.2.1 General operating of the CPT

Direct observation of individuals in the field and recording their travel paths through time and space is a very powerful empirical method for quantifying movement (Turchin 1998). To analyse movement patterns using the CPT, travel paths have to be represented as a series of physical locations, called waypoints, and travel between each consecutive pair of waypoints is represented as a vector (Byrne *et al.* 2009). Two distinct features of the CPT are (1) that the test is sequentially applied to segments of travel "*backwards in time*" and so the test starts at the end of the travel path, and (2) that once a waypoint is identified as a change-point, this location then becomes the starting point for the second iteration of the CPT and the process repeats iteratively (*i.e.*, the CPT must be re-applied each time after a change-point is identified in a travel route) (Byrne *et al.* 2009).

The CPT operates by comparing a set of k vectors, describing travel *after* a potential change-point to a set of q vectors describing travel *before* the potential change-point (*after* and *before* are from the "travel direction point of view", not the "test direction point of view"). The k vectors are labelled $\overline{v}_1$, …, $\overline{v}_k$, with vector $\overline{v}_1$ leading from the potential change-point location, $\overline{v}_2$ leading to $\overline{v}_1$ and so on, whereas the q vectors are labelled $\overline{v}_{k+1}$,…, $\overline{v}_{k+q}$, with $\overline{v}_{k+1}$ leading to the potential change-point, $\overline{v}_{k+2}$ leading to $\overline{v}_{k+1}$ and so on. The value of parameter q has to be determined by the user in advance and remains the same throughout the use of the CPT. Figure 4.1 shows the first iteration of the CPT for a hypothetical travel route of 10 waypoints with a change-point occurring between $\overline{v}_4$ and $\overline{v}_5$. In this example the value of q has been randomly set to 4. Variable t is used to count the waypoint 'backwards in time' so that t=0 is the last waypoint of the travel path (here located as the rightmost waypoint), which in this study represents the baboons' evening sleeping site. The CPT assesses waypoint locations one by one, starting the first iteration at the end of a travel day at t=0. For this first iteration, k will equal t at the first potential change-point considered by the CPT (since the CPT works backwards in time it is the first potential change-point seen from the end of the travel path). The possibility of a change-point between two vectors is examined by comparing the distances of vectors $\bar{R}_k$ and $\bar{R}_q$ with the length of the resultant vector $\bar{R}_{(k+q)}$ (see Section 4.2.2). In this example a change-points occurs at *t*=4 (which thus equals *k*=4) between vector $\bar{v}_4$ and $\bar{v}_5$. After the CPT identifies this waypoint as a change-point, the second iteration of the CPT starts at that location, which then becomes *k*=0, but remains labelled as *t*=4 (Figure 4.2).

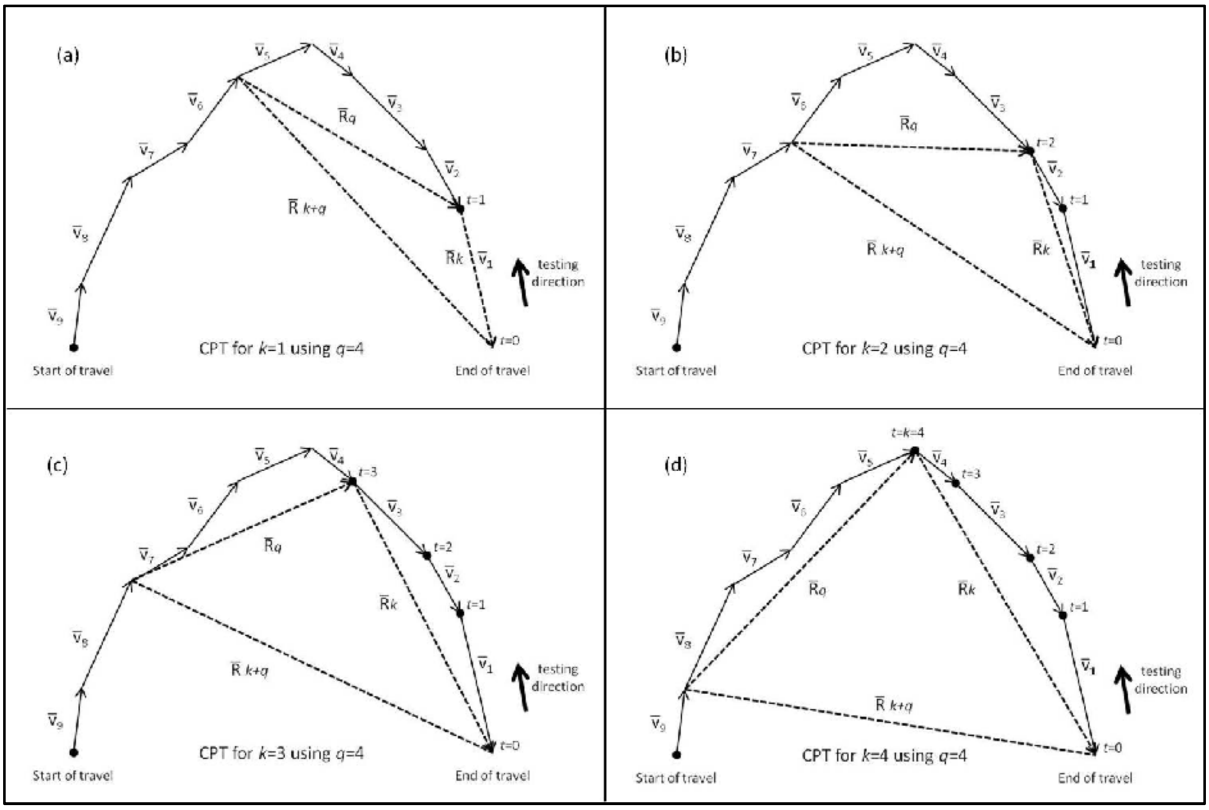

Figure 4.1 Application of the first iteration of the CPT in a hypothetical route, using q=4, at (a) k=t=1, with a testing direction backwards along the travel path (b-d) until a change-point is identified. Potential change-points between two vectors are examined by comparing the distances of $\bar{R}_k$ and $\bar{R}_q$ with the length of the resultant $\bar{R}_{(k+q)}$ (see Section 4.2.2).

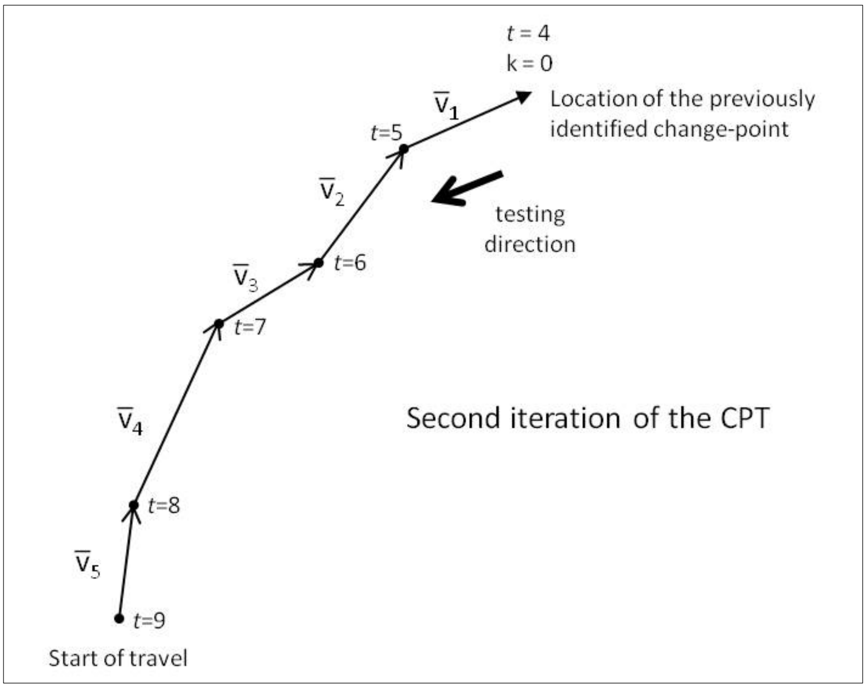

Figure 4.2 If the change-point at *t*=4 (Figure 4.1) is identified, this location becomes the starting point (*k*=0) for the second iteration of the CPT.

4.2.2 Identification of waypoints as change-points

The CPT first calculates the length of vectors $\bar{R}_k$ (Equation 1), $\bar{R}_q$ (Equation 2) and the resultant vector $\bar{R}_{(k+q)}$ (Equation 3). If $\bar{R}_k + \bar{R}_q - \bar{R}_{(k+q)}$ is “large” then the waypoint in question is more likely to be a change-point than if $\bar{R}_k + \bar{R}_q - \bar{R}_{(k+q)}$ is “small” as illustrated by an example in Figure 4.3.

Equation 1:

$$\bar{R_k} = ||\bar{v_k} + \cdots + \bar{v_1}|| = \surd\,((\bar{v}_{1x} + \cdots + \bar{v}_{kx})^2 + (\bar{v}_{1y} + \cdots + \bar{v}_{ky})^2$$

Equation 2:

$$\bar{R_q} = \left|\left|\bar{v}_{(k+q)} + \cdots + \bar{v}_{(k+1)}\right|\right| = \surd\,(\bar{v}_{(k+1)x} + \cdots + \bar{v}_{(k+q)x})^2 + (\bar{v}_{(k+1)y} + \cdots + \bar{v}_{(k+q)y})^2$$

Equation 3:

$$\bar{R}_{(k+q)} = ||\bar{v}_{(k+q)} + \cdots + \bar{v}_1||$$

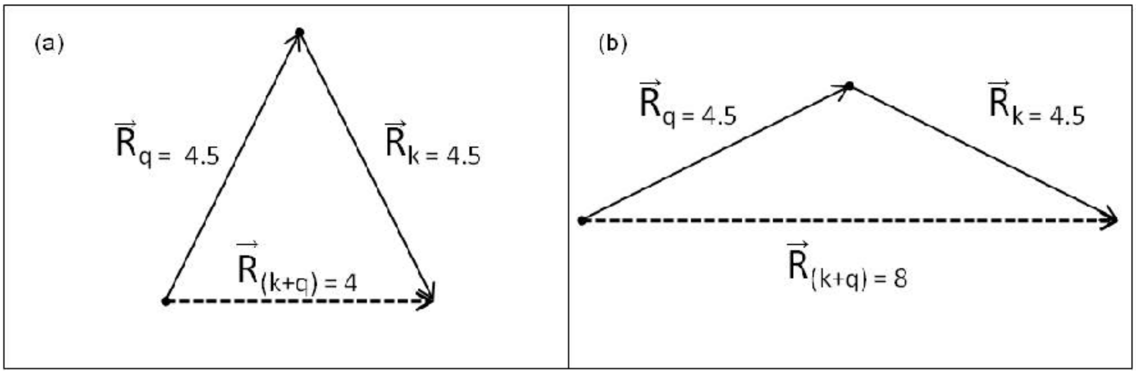

Figure 4.3 Simple example to show that if $\bar{R}_k + \bar{R}_q - \bar{R}_{(k+q)}$ is (a) "large" (4.5 + 4.5 – 4 = 5), it is more likely to be a change-point than if it is (b) "small" (4.5 +4.5 – 8 = 1).

To assess the significance of $\bar{R}_k + \bar{R}_q - \bar{R}_{(k+q)}$ (*i.e.*, the 'largeness') a permutation test is used with a random set of N permutations. This test permutes $\bar{R}_k$, $\bar{R}_q$ and $\bar{R}_{(k+q)}$, in other words it changes the order of the vectors of $\bar{R}_k$ and $\bar{R}_q$ and the order of the vectors within $\bar{R}_{(k+q)}$ so that:

- $\bar{R}_k(\sigma) = ||\bar{v}_{\sigma(k)} + \ldots + \bar{v}_{\sigma(1)}||$
- $\bar{R}_q(\sigma) = ||\bar{v}_{\sigma(k+q)} + \ldots + \bar{v}_{\sigma(k+1)}||$
- $\bar{R}_{(k+q)}(\sigma) = ||\bar{v}_{\sigma(k+q)} + \ldots + \bar{v}_{\sigma(1)}||$

The obtained values by permutation of $\bar{R}_k(\sigma) + \bar{R}_q(\sigma) - \bar{R}_{(k+q)}(\sigma)$ are arranged in numerical order and if the observed value of $\bar{R}_k + \bar{R}_q - \bar{R}_{(k+q)}$ is the r^{th} largest, the p value is $(\bar{R}_k(\sigma) + \bar{R}_q(\sigma) - \bar{R}_{(k+q)}(\sigma) \geq \bar{R}_k + \bar{R}_q - \bar{R}_{(k+q)}) / N$). Fundamental to trigonometry however is that even though the order of vectors may change, the resultant vector will remain the same (Figure 4.4), and so $\bar{R}_{(k+q)}(\sigma) = \bar{R}_{(k+q)}$. Because the value of $\bar{R}_{(k+q)}(\sigma)$ is the same as the value of $\bar{R}_{(k+q)}$, these vectors may be taken out of the equation, resulting in the *p* value being equal to $(\bar{R}_k(\sigma) + \bar{R}_q(\sigma) \geq \bar{R}_k + \bar{R}_q) / N$. $\bar{R}_k + \bar{R}_q - \bar{R}_{(k+q)}$ is considered to be significant (*i.e.*, a change of direction to occur) at $p \leq 0.01$.

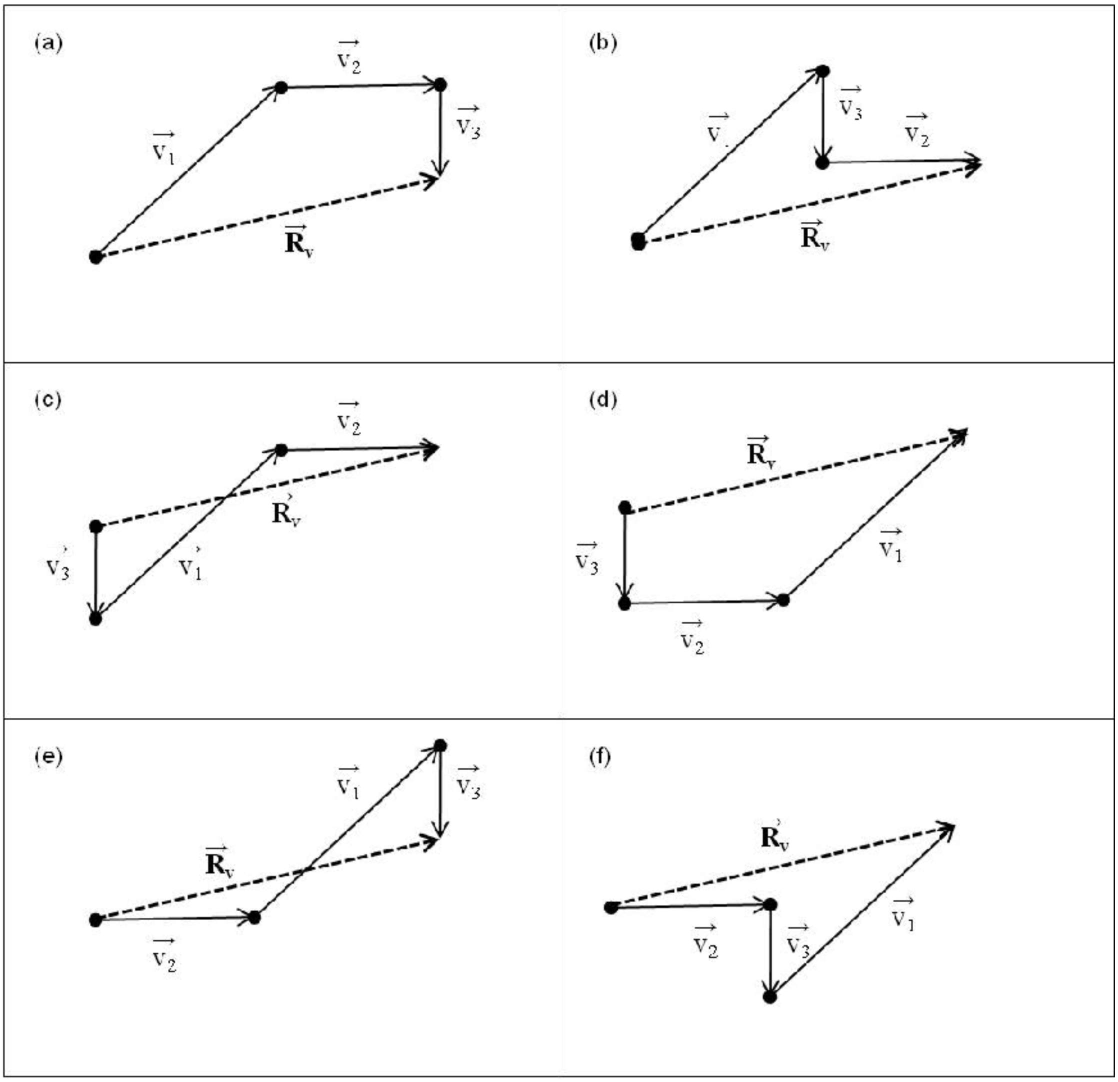

Figure 4.4 Six permutations of ($\overline{v}_1$+ $\overline{v}_2$+ $\overline{v}_3$)! with (a) $\overline{v}_1$, $\overline{v}_2$, $\overline{v}_3$ (b) $\overline{v}_1$, $\overline{v}_3$, $\overline{v}_2$, (c) $\overline{v}_3$, $\overline{v}_1$, $\overline{v}_2$, (d) $\overline{v}_3$, $\overline{v}_2$, $\overline{v}_1$, (e) $\overline{v}_2$, $\overline{v}_1$, $\overline{v}_3$ and (f) $\overline{v}_2$, $\overline{v}_3$, $\overline{v}_1$. The resultant vector $\overline{R}_v$ has the same start and end point and the same length for all iterations.

4.2.3 The CPT: An empirical example

To show how the CPT works in practise, the CPT is applied to a single travel route represented by 122 waypoints (Figure 4.5). Variable t was used to count the waypoints backwards in time, with $k = t = 0$ at the end of a day's travel, $t = k$ at the first change-point, and for all subsequent iterations, the value of t at a potential change-point is $t = t_0 + k$, where t_0 is the value of t at the start of that iteration (at k=0). The q value (*i.e.*, the number of vectors leading *towards* a potential change-point [from the "travel direction point of view"]) was set to 3.

Figure 4.5 Baboons' travel route on the 24th April 2007 represented by 122 waypoints with a total distance of 5.7 km (average ±SD step length of 47.2m ± 8.0m and average step duration 5:07 minutes) with travel direction (*thin black arrow*) from the morning sleeping site to the evening sleeping site (*i.e.*, from right to left). The variable *t* is used to label waypoints starting at the end of the day (t=0 is the evening sleeping site).

The output of the CPT is shown in Figure 4.6 where the X axes show the waypoint locations (k) at which the test statistic was computed, the Y axes show probability p, using a logarithmic scale to aid visual inspection, and points connected with a solid line show p values of the CPT at k=1,…,t+1. Critical values of the CPT are shown as straight horizontal lines, for α=0.1 (bottom), 0.05 (middle) and 0.01 (top). The waypoint is considered to be a change-point if $p < \alpha$, that is, if the plot of –log p at k lies above the horizontal line corresponding to –log α. When several consecutive values of –log p in a row exceed their critical values, the value of k giving the largest of these values (thus forming the peak of the line) can be viewed as the 'true' change-point (Byrne *et al.* 2009) (*e.g.*, Figure 4.6 iteration 2 where values for k = 8, 9 and 10 all exceed –log p and k = 10 is therefore considered the 'true' change-point). When this 'peak rule' and a level of significance of α=0.01 are applied, change-points were identified at t=40 (k=40 in 1st iteration), t=50 (k=10 in 2nd iteration), t=68 (k=18 in 3rd iteration and t=101 (k=33 in 4th iteration) (Figure 4.6). The final 5th iteration did not show any significant change-points (no waypoints were located above the horizontal line corresponding to –log 0.01) and is therefore not shown. It is important to realise that only one change-point is identified per iteration and thus that the CPT has to be applied several times to each travel route, until all change-points are identified. For a clearer visual presentation of these results, the change-points were transferred onto the baboons' travel route in Figure 4.7

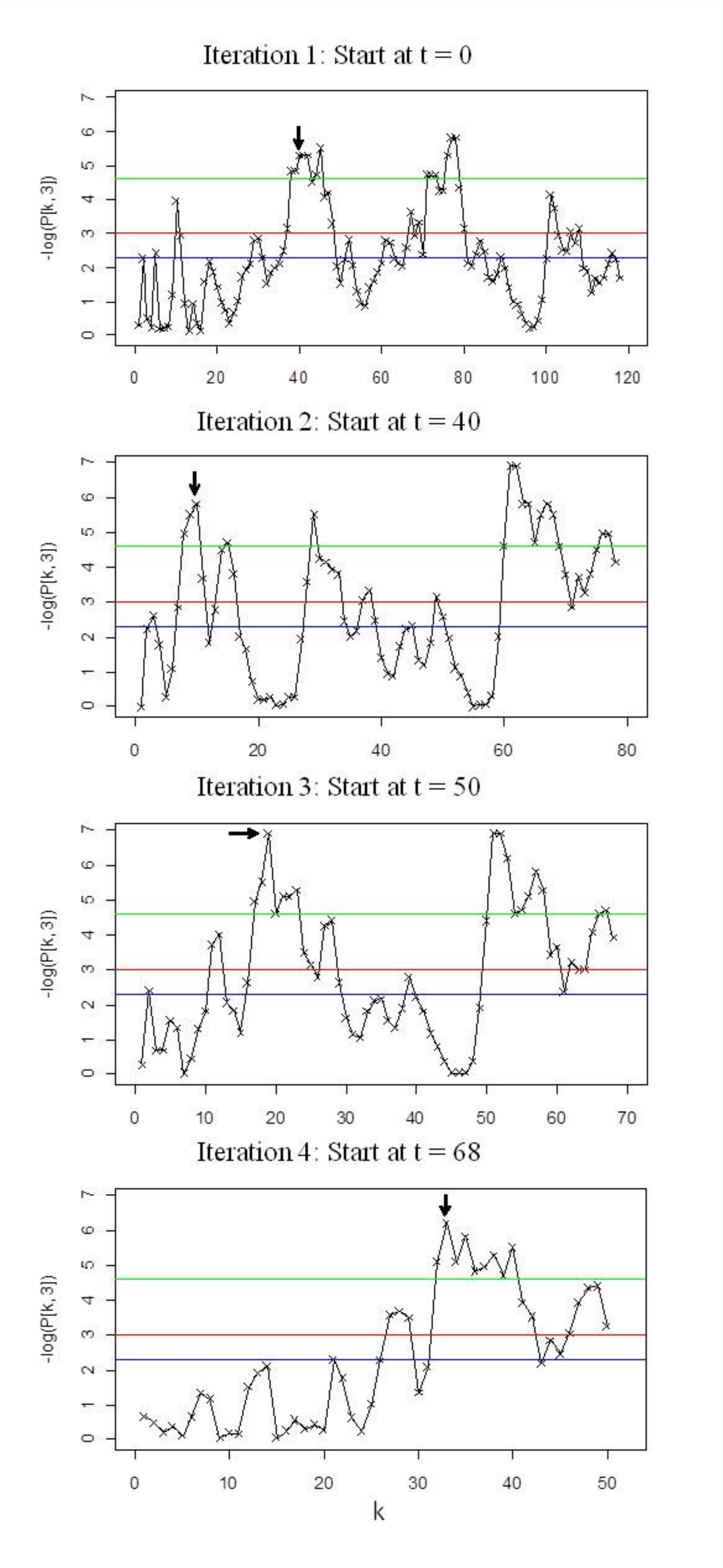

Figure 4.6 CPT output using *q*=3. Iterations started at *k*=*t*=0; the baboons' evening sleeping site. The X axes show the locations (*k*) at which the test statistic was computed; the Y axes show probability P, using a logarithmic scale to aid visual inspection, and points connected with a solid line show P values of the CPT at k=1,…,t+1. Critical values of the CPT are shown as straight horizontal lines, for α=0.1 (bottom), 0.05 (middle) and 0.01 (top). Using α=0.01, change-points are identified at t=40 (k=40 in 1st iteration), t=50 (k=10 in 2nd iteration), t=68 (k=18 in 3rd iteration) and t=101 (k=33 in 4th iteration), as indicated by *black arrows*.

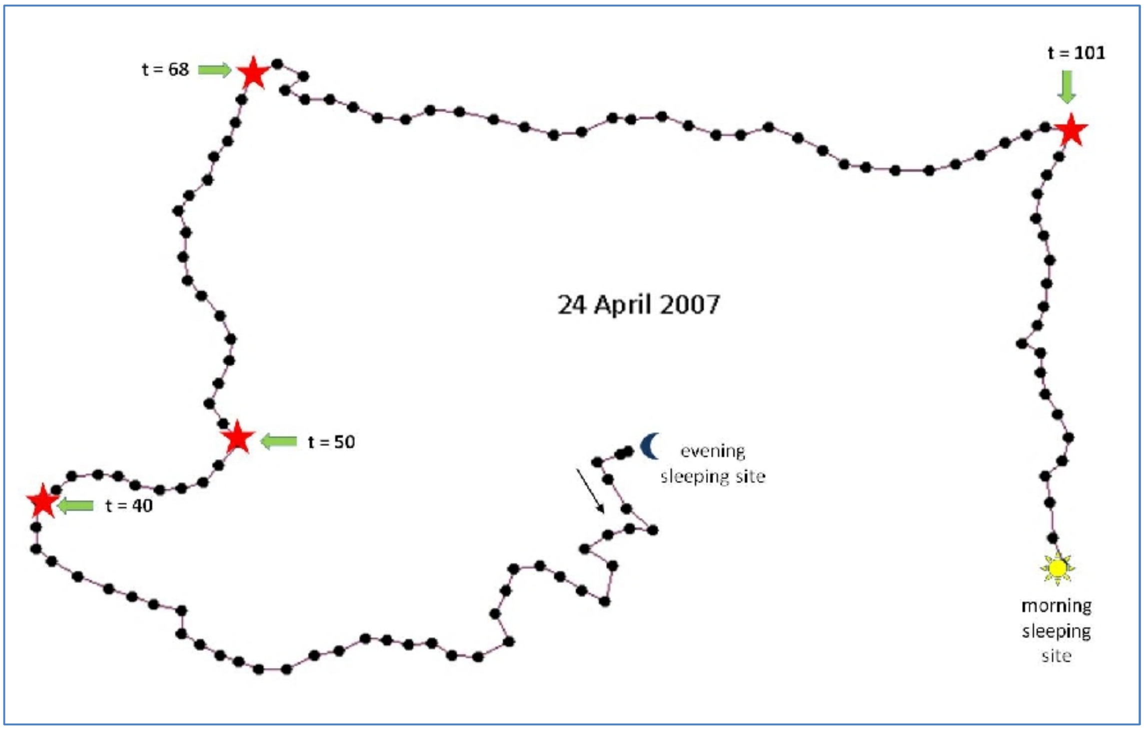

Figure 4.7 Baboons travel route on the 24th of April 2007 represented by 122 waypoints (*black dots*). The evening sleeping site was the location where the first iteration of the CPT started (*t*=0). Note that the direction of testing (*thin black arrow*) is opposite to the direction of travel. Significant directional changes (*i.e.*, change-points) (*red stars*) were identified by the CPT using $q = 3$ and $p < 0.01$ (see text above for further explanation).

4.2.4 Considerations of the CPT

4.2.4.1 Selection of the type of sampling protocol

As explained in Section 4.2.2, the CPT compares the lengths of R_k (set of vectors k representing travel after a potential change-point) and R_q (set of vectors q representing travel before a potential change-point) to the length of the resulting vector R_{k+q}. Vector lengths, represented by the distance between waypoints (*i.e.*, step length), and the variation therein is therefore expected to affect the results of the CPT. Different sampling protocol types will result in different step lengths and different variation in step length (for example a protocol in which waypoints are collected every 20 meters is likely to have smaller step lengths and smaller variation in step length than a protocol in which waypoints are collected every hour). Since some sampling protocol types will have higher variation in step length than others, the type of sampling protocol is expected to affect the success of the CPT. The first aim of this chapter was to evaluate the sensitivity of the CPT to different types of sampling protocols, in order to select the appropriate post-hoc data filter that would give the most reliable output and to make recommendations for future studies which aim to incorporate the CPT. Three types of sampling were investigated; timed sampling, distance sampling and a combination of timed and distance sampling. It was expected that the sampling protocol type with most similar vector lengths throughout the travel route (*i.e.*, with the lowest variation in step length) would allow the CPT to give the best results (following Byrne *et al.* 2009).

4.2.4.2 The value of q

The number of *q* vectors included in v_{k+1}, ..., v_{k+q} will also change the test's sensitivity (*i.e.*, its power). The test will be relatively insensitive even to pronounced directional changes when using very low values of *q*, whereas when *q* gets very large, the corresponding segments are likely to include more and more conflicting directional changes and as a result, the sensitivity to detect a significant difference to the segment based on the *k* vectors, decreases. Also, the larger *q* is, the further away from the journey's start are the locations that can be tested at all. Byrne *et al.* (2009) point out that there is a trade-off between statistical robustness of the results on the one hand and the number of locations identified as change-points on the other and therefore recommend applying a sensitivity analysis to the CPT to determine the optimal value for *q*. To determine which mechanisms underlie the selection of the value of *q* and the appropriate significance level an extensive sensitivity test should therefore be conducted.

4.2.4.3 Scale and sampling interval

For decades researchers in the field of ecology and animal behaviour have been recording animal's travel routes to study a range of topics such as habitat use (*e.g.*, Watts 1998), home-range (*e.g.*, Takasaki 1981), optimal foraging (*e.g.*, Cramer & Gallistel 1997) and spatial cognition (*e.g.*, Garber & Jelink 2006). Most often, information on travel routes is collected by direct observation of individuals in the field. With current technical advances it is possible to collect data points representing a travel route at a very small scale, much smaller perhaps than may be relevant for the research question to be studied. For instance in this study data points were obtained roughly every 5 meters, enabling travel routes to be mapped almost continuously. This fine scale may not always be necessary or even appropriate for the topic under study.

It is recommended to use the value of *q* at which the CPT is most sensitive to directional changes and thus results in the identification of the highest number of change-points (Byrne *et al.* 2009), which is referred to in this thesis as the '*q* rule'. However, it seems that this *q* rule is only applicable when the appropriate sampling interval has been selected. In this chapter, sixteen different sampling intervals are evaluated to assess the appropriate scale at which to analyse baboon travel routes so that the *q* rule may be applied.

4.3 Methodology

4.3.1 Sampling protocol

Seven follow days were selected from the entire data set (see Chapter 2) based on the criteria that the route represented the baboons' travel from sunrise to sunset (*i.e.*, a full follow day) and that the baboons were never out of the observer's sight. Geographical coordinates were collected by the observer using a handheld GPS (Garmin GPSMAP60CSx) using the automatic track recording setting. The data were filtered to represent different types of sampling protocol in order to evaluate the sensitivity of the CPT to different sampling protocols.

Trip and Waypoint Manager software allows four types of data filters or a combination thereof; 1) time filter – set by the user in seconds 2) distance filter – set by the user in meters 3) automatic filter set by the user using a slide bar from fewer points to more points and 4) max waypoint filter – set by the user as a maximum total number of waypoints. When a filter is applied, for example a 20m distance filter, this does not mean that the resulting route contains a waypoint exactly every 20m, but instead waypoints are located at a minimum distance of 20m from one another. The software filters out any existing (original) waypoint that is closer than 20m to the previous one and so the filter needs to be applied several times as illustrated by Figure 4.8. In this example, 7 waypoints were recorded at 5, 7, 12, 45, 71, 85 and 100m. When applying a 20m distance filter for the first time, waypoints at 5, 12, 45, 71 and 100m will remain and when applying the filter a second time, waypoints at 5, 45, 71 and 100m remain. Applying the filter a third time will not change the total number of remaining waypoints, which means that each waypoint is now located at least 20m away from the previous one. After applying a time filter, for example a 5 minute filter, waypoints are not exactly 5 minutes apart, instead waypoints are filtered out so that each consecutive waypoint is located at a minimum of 5 minutes apart. Time filters, however, only have to be applied once.

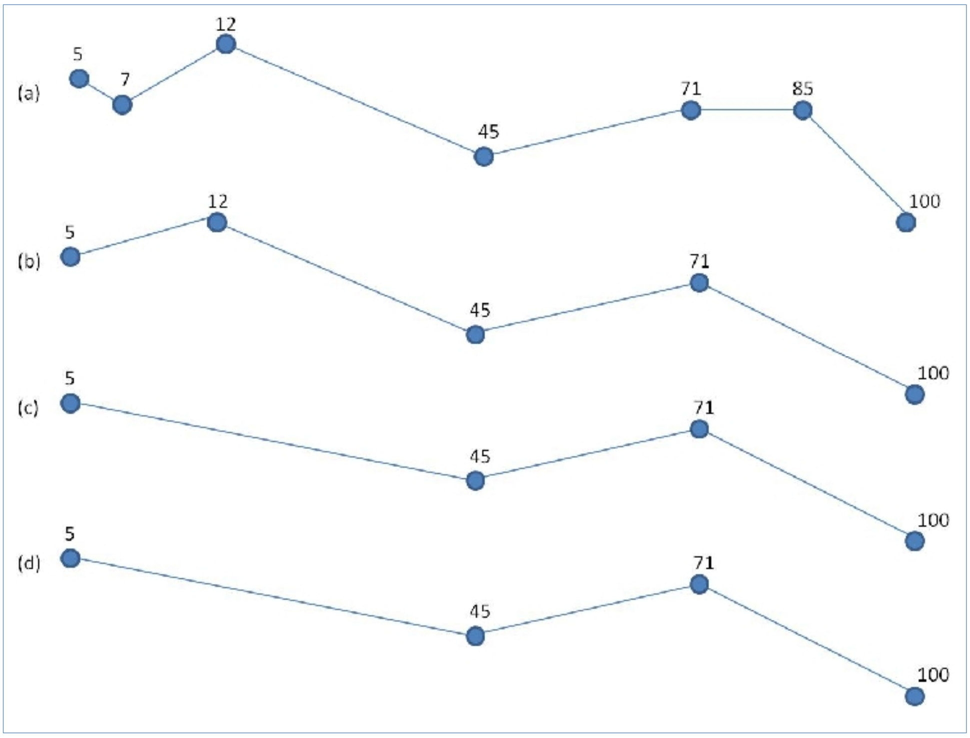

Figure 4.8 Example of the application of a 20 meter distance filter in Trip and Waypoint Manager V3 software (Garmin Ltd. 1995) showing (a) original data points (b) points after the first (c) points after the second and (d) points after the third application of the 20m filter.

Of the four filter type options that the Trip and Waypoint Manager offers, only the time filter and the distance filter were included in the evaluation because these are the most common types of sampling protocol used for recording travel routes. In addition, a combination of a time and distance filter, as used by Byrne *et al.* (2009), was included. These three filters thus represent different types of sampling protocol based on a timed interval, a distance interval and a combination of the two.

The data were filtered using a 5 minute time filter (T), a 20 meter distance filter (D) and a combination thereof (T/D) (*i.e.*, 5 minute time filter followed by a 20 meter distance filter) and average step length (*i.e.*, average distance between two consecutive waypoints) and the variation in step length (standard deviation) was determined for each of these three data filters. Note that with the distance filter, the *minimum* distance between consecutive waypoints was 20m (but not exactly 20m) and that therefore that the average step length is expected to be larger than 20m. The effect of the three filter types, representing different sampling protocols, on step length variation was investigated.

Different sampling protocols (time sampling, distance sampling or a combination of the two) result in different average step lengths and in different variation in step length, both of which might affect the results of the CPT independently. To further investigate how the variation in step length may affect the results of the CPT, two additional distance filters (D-F1 and D-F2) were selected to match the average step length of the time filter (T) and time/distance filter (T/D) respectively. In this way, the average step lengths of D-F1 and T and of D-F2 and T/D were similar, but the variation in step length was expected to be significantly different between the distance filters and the time and time/distance filter. Thus the effect of variation in step length on the results of the CPT was further investigated while average step length was kept constant.

The original code for performing the CPT was downloaded from http://www.mcs.st-andrews.ac.uk/wpej/CPT.html (accessed 10 April 2010). The code was modified to automate the process of identifying all change-points within a single daily travel route based on the peak rule (Byrne *et al.* 2009) and to enable the user to select a series of parameters values. The automated CPT (Appendix II) was run in R and change-points were identified using a significance level of α = 0.01 unless stated otherwise. The resulting change-point data sets were imported into ArcMap in which maps of the spatial distribution of the identified change-points were produced.

4.3.2 Sensitivity Test

Sixteen different sampling intervals were simulated by applying distance filters ranging from 20 to 100m with a 5m interval to the data. The CPT was carried out for each distance filter using *q* values 1 to 12 for all 7 test days, so that 1344 separate tests were performed using the automated version of the CPT script.

4.4 Results

4.4.1 Sampling Protocol

Follow days (N=7) were represented by an average of 1689 (range 1062-2547) waypoints, with an average step length (distance between consecutive waypoints) of 5.16 (± 4.49) meters and an average step duration (travel time between consecutive waypoints) of 23 (range 17-39) seconds (Table 4.1).

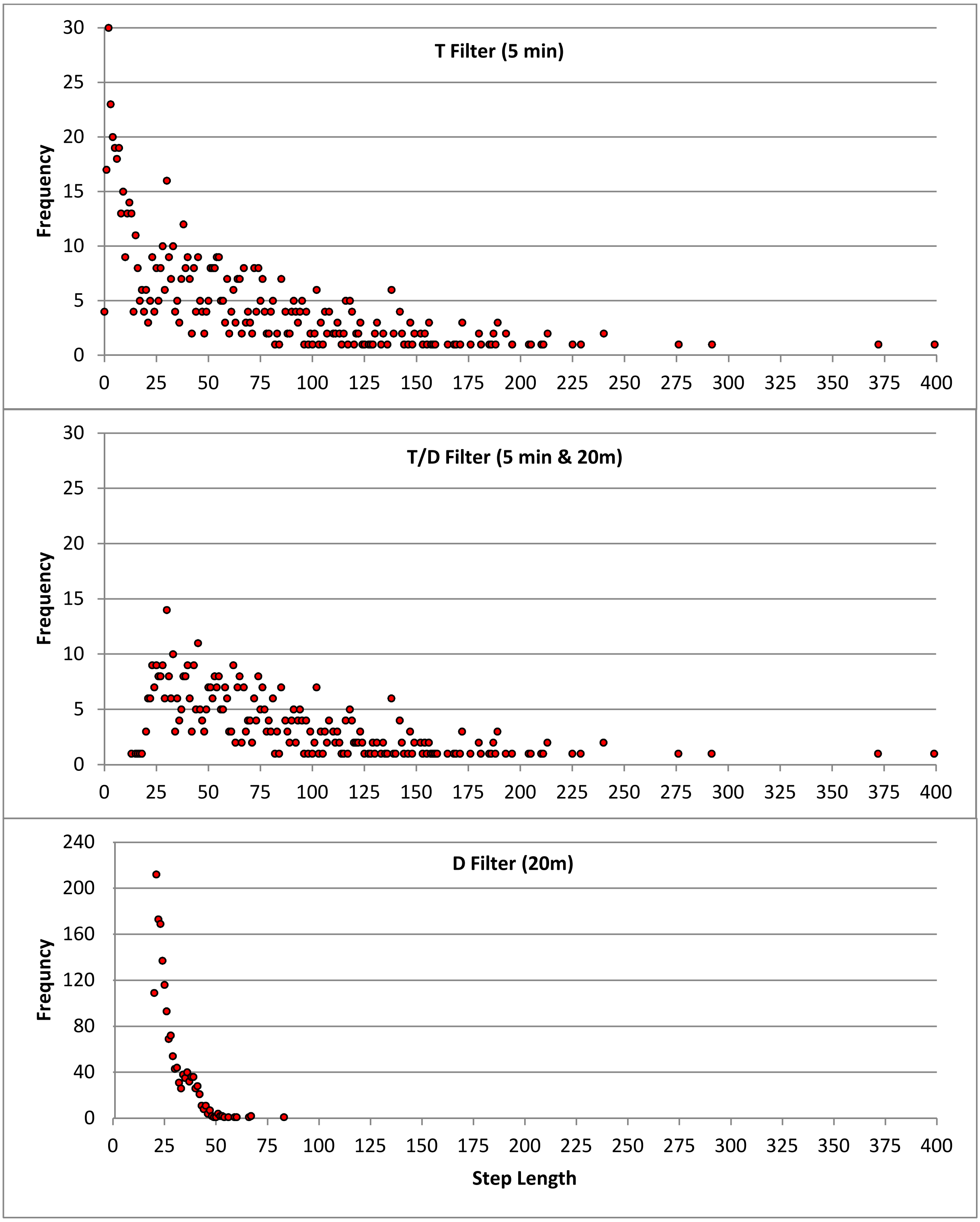

Figure 4.9 Step lengths after applying three different filters (time (T), time/distance (T/D) and distance (D). Note the different scale of the Y-axis for the 20 meter distance filter indicating higher frequencies.

Table 4.1 Description of unfiltered travel routes including the date, average step length (SL) ± standard deviation (SD) (in meters), average step duration (Duration) (in seconds) and total number of waypoints (WP) for each travel route separately as well as the average (last row) per travel route.

Date	SL (m)	±SD (m)	Duration (sec)	WP
24-Apr-07	5.84	4.24	30	1246
25-May-07	5.38	3.82	32	1277
26-May-07	5.44	4.36	39	1062
23-Nov-07	4.39	3.57	18	2547
12-Dec-07	5.58	4.31	17	2398
29-Apr-07	5.82	5.20	32	1124
01-Mar-08	3.68	5.89	19	2168
Average	**5.16**	**4.49**	**27**	**1689**

Figure 4.9 shows the step length frequencies for each of the three filter types. It shows that the range in step length is smaller for the distance filter (range: 78m) than for both the time (range: 399m) and time/distance (range: 384m) filter. Average step length (measured over the 7 days) using the distance filter (27.4m, N=1706) is significantly smaller than when using a time filter (54.5m, N=826) (Mann-Whitney test: U=543005.5, Z= -9.416, p<0.001) or a time/distance filter (76.1m, N=576) (Mann-Whitney test: U=5101117.5, Z= -28.590, p<0.001).

Table 4.2 summarises mean step length, step length standard deviation (SD), range, minimum and maximum step length values for the 20m distance filter (D), the 5 min time filter (T) and the 5min & 20m time/distance filter (T/D). The standard deviation is significantly smaller for the distance filter than for the time and the time/distance filter (Kruskall Wallis χ^2= 695, p<0.001). Note that if a larger distance filter had been selected, for example 50m instead of 20m, values for the mean, minimum and maximum step length would have been higher, but the range and standard deviation would have stayed similarly small.

Table 4.2 Mean, standard deviation (SD), range, minimum (Min) and maximum (Max) step length of different filter types averaged over all seven test days.

Filter	Mean	SD	Range	Min	Max
D	27.4	7.3	78	20	83
T	54.5	52.9	399	0	399
T/D	76.1	50.5	384	20	399

To investigate the effect of variation in step length on the results of the CPT whilst keeping average step lengths constant, two additional distance filters (D-F1 and D-F2) were applied. The D-F1 distance filter has an average step length similar to the time filter (54.04m versus 53.96m), whereas the D-F2 distance filter has an average step length similar to the time/distance filter (both 74.8m) (respectively highlighted in orange and blue in Table 4.3). As expected on the basis of the previous analysis, step length standard deviation was significantly different between the time filter and the F1 distance filter (paired T-test, t=8.206, df=6, P<0.001) and between the time/distance filter and the F2 distance filter (paired T-test, t=6.387, df=6, P=0.001). This confirms that the variation in step length is significantly smaller for sampling protocols based on distance intervals than for sampling protocols based on a timed interval or based on a combination of time and distance intervals.

Table 4.3 Comparison between a time filter and a time/distance filter to distance filters D-F1 and D-F2 respectively, which have similar average step length (Step length). Step length standard deviation (SD) is significantly smaller for the distance filters (D-F1 and D-F2) compared to both the time and time/distance filter.

			Time filter (T)		
Date	**Waypoints**	**Step length**	**±SD**	**Step duration**	**Filter**
24-Apr-07	103	55.6	49.9	00:06:01	5 min
29-Apr-07	96	53.3	64.5	00:06:16	5 min
25-May-07	116	46.1	42	00:05:53	5 min
26-May-07	125	27.7	29	00:05:37	5 min
23-Nov-07	138	68.8	47.3	00:05:34	5 min
12-Dec-07	129	77.3	67.4	00:05:15	5 min
01-Mar-08	121	49.5	47.7	00:05:48	5 min
Average	**118.29**	**54.04**	**49.68**	**00:05:46**	
			Distance filter 1 (D-F1)		
Date	**Waypoints**	**Step length**	**±SD**	**Step duration**	**Filter (m)**
24-Apr-07	100	55.7	16.9	00:06:12	40
29-Apr-07	100	52.5	14	00:05:50	37
25-May-07	111	47.3	13.2	00:05:59	33
26-May-07	130	27.1	7.5	00:05:22	19
23-Nov-07	136	68.3	17.7	00:05:39	47
12-Dec-07	130	76.2	19.3	00:05:15	50
01-Mar-08	114	50.8	20.7	00:06:09	35
Average	**117.29**	**53.96**	**15.6**	**00:05:46**	
			Time/Distance filter (T/D)		
Date	**Waypoints**	**Step length**	**±SD**	**Step duration**	**Filter**
24-Apr-07	75	76.1	45.2	00:08:22	5min20m
29-Apr-07	62	81.7	66.8	00:09:33	5min20m
25-May-07	79	64.9	38.8	00:08:26	5min20m
26-May-07	69	45.9	30.6	00:10:10	5min20m
23-Nov-07	122	78	43.8	00:06:21	5min20m
12-Dec-07	93	106.4	59.3	00:07:22	5min20m
01-Mar-08	84	70.6	44.8	00:08:27	5min20m
Average	**83.4**	**74.8**	**47**	**00:08:23**	
			Distance filter 2 (D-F2)		
Date	**Waypoints**	**Step length**	**±SD**	**Step duration**	**Filter (m)**
24-Apr-07	70	77.2	19.6	00:08:51	54
29-Apr-07	63	81.3	22	00:09:15	55
25-May-07	78	64.1	18.7	00:08:26	45
26-May-07	68	46.4	13.5	00:10:19	32
23-Nov-07	114	79.8	17.9	00:06:44	50
12-Dec-07	91	104.1	26.4	00:07:22	70
01-Mar-08	80	70.5	30.9	00:08:46	47
Average	**80.6**	**74.8**	**21.3**	**00:08:32**	

To assess the effect of step length variation on the results of the CPT three example travel routes are presented below, each represented by three different sampling protocols: 1) a sampling protocol based on a combination of time and distance (using the TD filter); 2) a sampling protocol based on time (using the T filter); 3) a sampling protocol based on distance (using the D-F1 and D-F2 filters).

The first example shows the baboons' travel route on the 24th April 2007 (Figure 4.10 a-d). An interesting result is that the larger 54m D-F1 filter the CPT fails to identify a change-point (CP2 in Figure 4.10 a-b-d), which is identified by the smaller 40m D-F2 filter and both the T filter and TD filter. Change-points can only be identified at the locations of data points and after applying the different filters the resulting routes will usually have data points at slightly different locations. As a consequence, there will be small shifts in the precise location where the change-points are identified (*e.g.*, CP1 Figure 4.10 c-d). However, it is also possible that the CPT identifies the location of change-point at a slightly different location (*e.g.*, CP4 Figure 4.10 a-b). The variation in average step length is, as expected, much larger for the TD and T filter than for the D filters. This is particularly evident for instance, in the horizontal top part of the travel route when comparing the TD or T filter to the D filters. With the TD and the T filters, the data points are sparse and unevenly spaced, while using the D filters the data points are evenly distributed and more frequent. The same is true for the part of the travel route that goes down from change-point number 4 in Figure 4.10a, b and d, which is change-point number 3 in Figure 4.10c. Despite this obvious variation in step length, there seems to be little effect on the output of the CPT. This example therewith illustrates that the larger variation in step length of the TD and T filter compared to both the D filters, does not affect the results of the CPT when the travel route is relatively straight and furthermore that a smaller distance filter appears to identify seemingly important changes of direction that are missed by a larger distance filter.

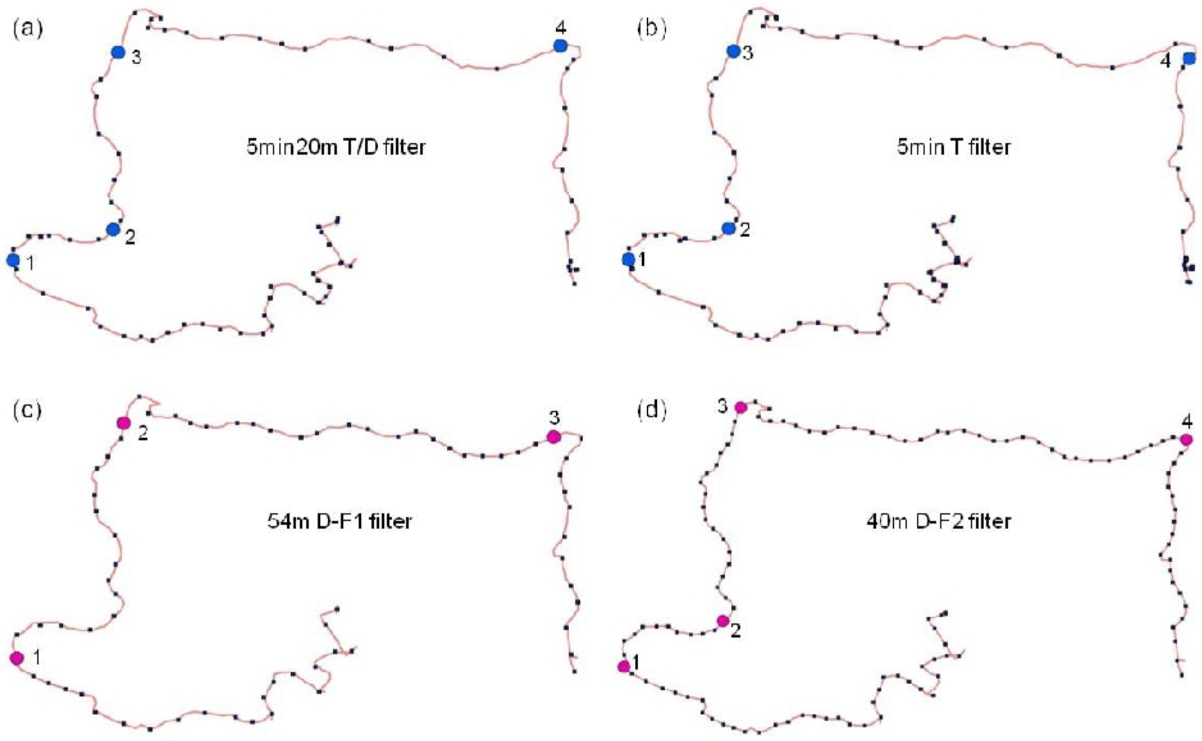

Figure 4.10 Travel route on the 24th April 2007 with (a) 5min20m time/distance filter (av. SL 76.1m ± 45.2m) (b) 5min time filter (av. SL length 55.6m ± 49.9m) (c) 54m distance filter (av. SL 77.2m ± 19.6m) and (d) 40m distance filter (av. SL 55.7m ± 16.9m). The *red line* represents the original travel route more continuously based on a 20m filter. The CPT (using *q*=3) identified 4 change-points (*blue circles*) for the TD and the T filter and 3 and 4 change-points (*pink circles*) for the 54m and 40m D filter respectively.

A second example (Figure 4.11 a-d) illustrates the baboons' travel route on the 29th April 2007. Again, there is a large variation in step length for the TD and T filter compared to the D filters, particularly in the travel section between CP1 and CP2 in Figure 4.11 a-b, which equals the route section between CP1 and CP3 in Figure 4.11 c-d. Figure 4.11 a-b shows that for the TD and the D filter this route section contains two waypoints located close together, followed by very widely spaced points. Due to this variability in step length, the CPT fails to identify a change-point for the TD and D filter, which is identified for both D filters (change-point 2 in Figure 4.11 c-d). Also, CP1 and CP4 of the TD filter (Figure 4.11a) do not seem to be located very accurately compared to the other filter types. This example illustrates that the larger variation in step length of the TD and T filter compared to both the D filters, can affect the results of the CPT when travel routes are less straight and furthermore that the TD filter identifies some change-points "too early" (*i.e*., before the actual change of direction).

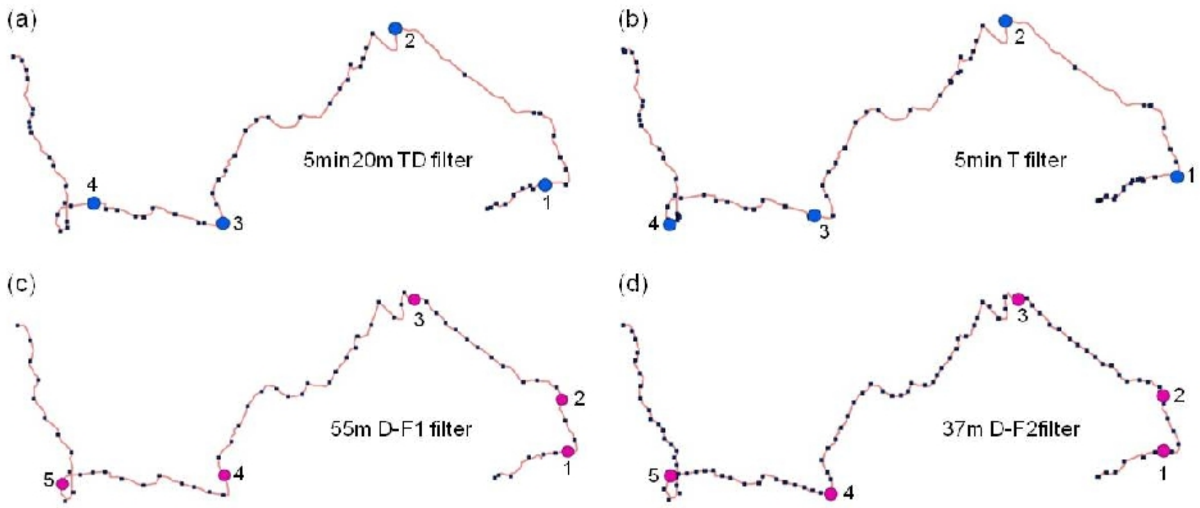

Figure 4.11 Travel route on the 29th April 2007 with (a) 5min20m time/distance filter (av. SL 81.7m ± 66.8m) (b) 5min time filter (av. SL length 53.3m ± 64.5m) (c) 55m distance filter (av. SL 81.3m ± 22.0m) and (d) 37m distance filter (av. SL 52.2m ± 14.0m). The *red line* represents the original travel route more continuously based on a 20m filter. The CPT identified 4 change-points (*blue circles*) (using *q*=3) for the TD and the T filter and 5 change-points (using *q*=6) (*pink circles*) for both D filters.

The third example is shown in Figure 4.12 a-d, which illustrates the baboons' travel route on the 25th May. As in the previous two examples there is a large variation in step length for both the TD and the T filter and here it affects the results of the CPT even more severely, since the TD and T filter both fail to identify two seemingly important changes of direction (CP3 and CP6 in Figure 4.12c which are CP4 and CP7 in Figure 4.12d). When first comparing Figure 4.12a with Figure 4.12c there are 2 change-points detected by the D filter that were missed by the T filter, despite having the same average step length. It is the variability in step length, the unevenly spaced waypoints of the T filter that results in these change-points being missed by the CPT when using a T filter. Secondly, comparing Figure 4.12b with Figure 4.12d these same two change-points (CP4 and CP7 in Figure 4.12d) have not been detected using the TD filter due to the large variability in step length. Furthermore, when comparing the two D filters, the 33m D filter detects an additional change-point (CP2 in Figure 4.12d) due to its smaller step length. It can thus be concluded that variation in step length has a negative effect on the CPT output and that smaller step lengths give the CPT resolution to also pick up smaller, less significant, changes in direction.

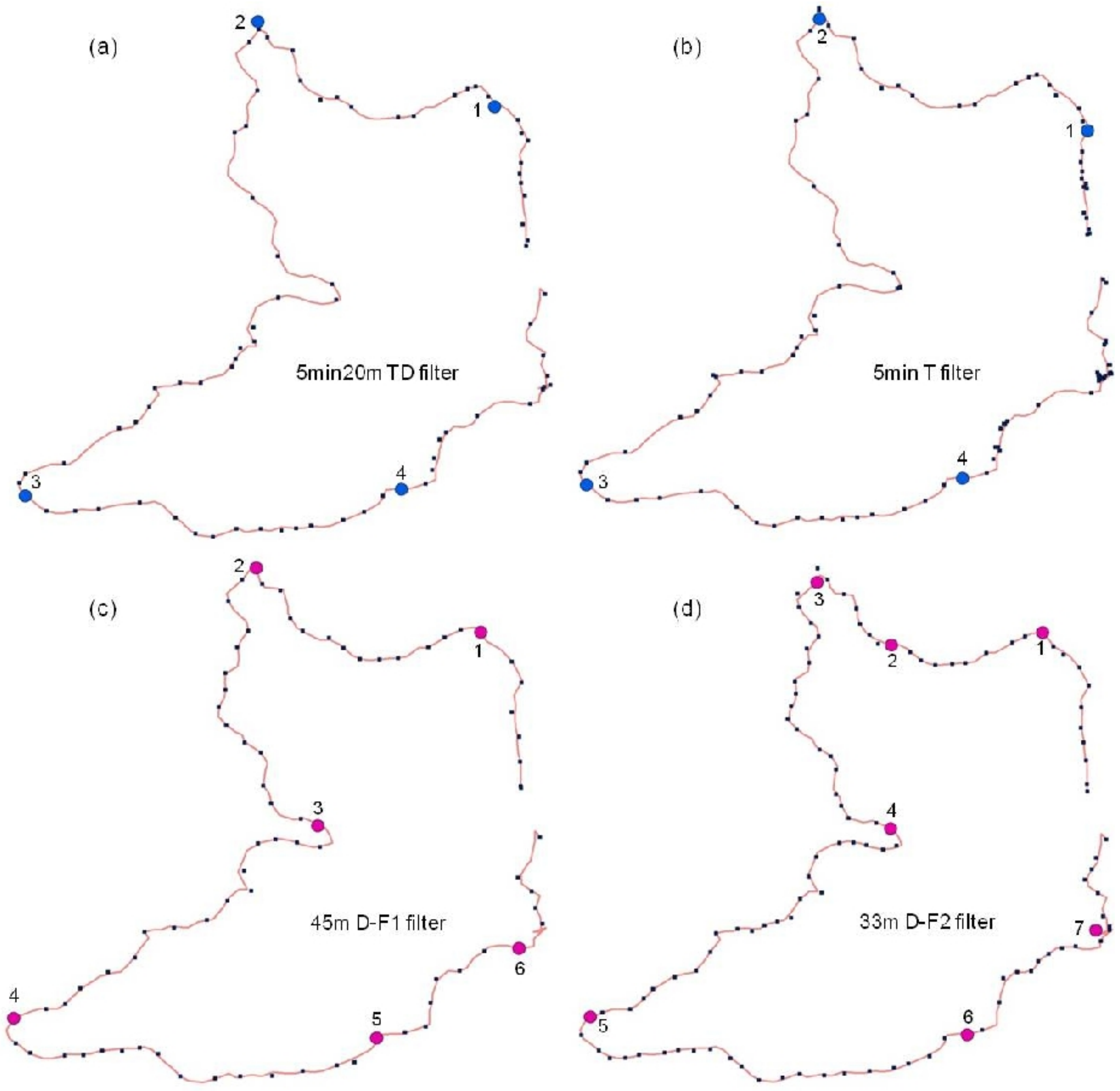

Figure 4.12 Travel route on the 25th May 2007 with (a) 5min20m time/distance filter (av. SL 64.9m ± 33.8m) (b) 5min time filter (av. SL length 46.12m ± 42.0m) (c) 45m distance filter (av. SL 64.1m ± 18.7m) and (d) 33m distance filter (av. SL 47.3 ± 13.2m). The *red line* represents the original travel route more continuously based on a 20m filter. The CPT (using *q*=3) identified 4 change-points (*blue circles*) for the TD and the T filter and 6 and 7 change-points (*pink circles*) for the 45m and 33m D filters respectively.

The analyses so far have shown that sampling protocols based on a time or time/distance interval both have significantly larger variability in step length than sampling protocols based on a distance interval, even when the average step length was kept constant. The effect of variation in step length on the results of the CPT was illustrated by three examples, which showed that when a travel route is relatively straight, this variation in step length does not necessarily influence the results of the CPT, but when seemingly important changes of travel direction did occur, sampling protocols based on a time interval and based on time/distance interval often failed to identify these locations as change-points due very unevenly spaced waypoints. Furthermore, for distance based sampling protocols, smaller intervals allowed the CPT to detected changes of direction at locations that were not identified as change-points when using larger distance intervals. In conclusion, variation in step length was shown to have a negative effect on the results of the CPT and smaller average step lengths appears to give the CPT the resolution to also pick up more subtle changes in direction. Accordingly, distance based sampling protocols are preferred over sampling protocols based on time intervals or a combination of time and distance intervals with the preferred distance interval depending on the scale of interest.

4.4.2 Selection of the value of q and α

Sampling intervals were simulated by applying 17 distance filters ranging from 20m to 100m to the travel routes, resulting in an average number of waypoints representing each follow day ranging from 245 (20m filter) to 39 (100m filter). The number of waypoints representing travel routes decreased exponentially with increasing intervals of the distance filter (Figure 4.13).

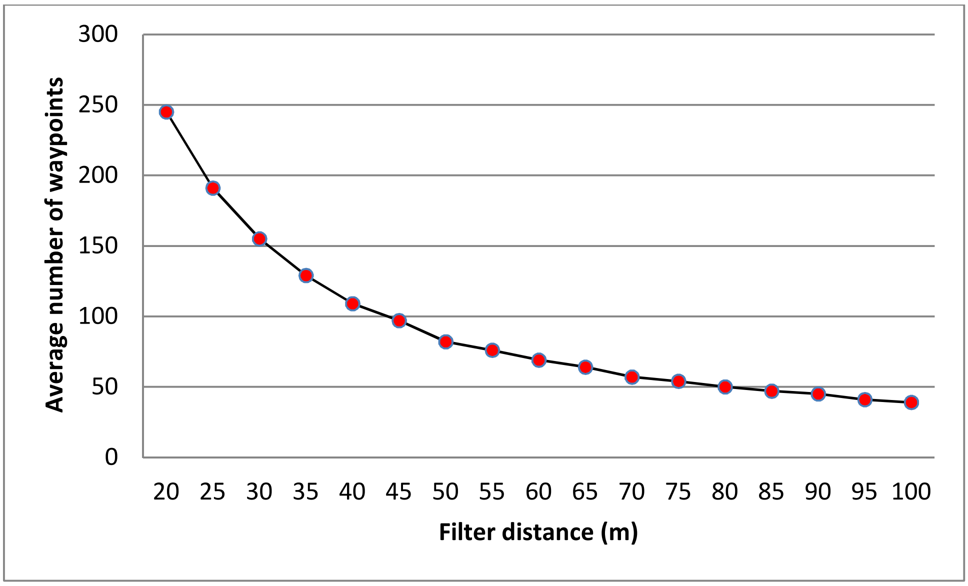

Figure 4.13 The average number of waypoints per travel route (N=7) for the different filter distances.

The CPT was subsequently applied using *q* values 1 to 12 for each distance filter, so that 1344 separate tests were performed using the automated script. The number of change-points identified by the CPT increased with increasing values of *q* from 1 to 5 to peak at *q* = 5 (20m, 35m, 45m distance filter), *q* = 6 (25m, 35m, 40m, 60m, 65m, 70m, 75m, 80m, 90m and100m), *q* = 7 (30m and 95m) or *q* = 8 (50m, 55m and 85m) (Figure 4.14). After this first peak the number of identified change-points more or less stabilises, showing for some distance filters, a distinct second peak. For example, the 35m distance filter peaks at *q* = 5 with 56 change-points detected, followed by a more or less stable number of change-points (56 for *q* = 6, 55 for *q* =7), to then show a second peak at *q* = 11 with 68 identified change-points (Figure 4.14). The value of *q* at which the CPT is most sensitive to directional change thus varies for different filter distances and therewith for different sampling intervals.

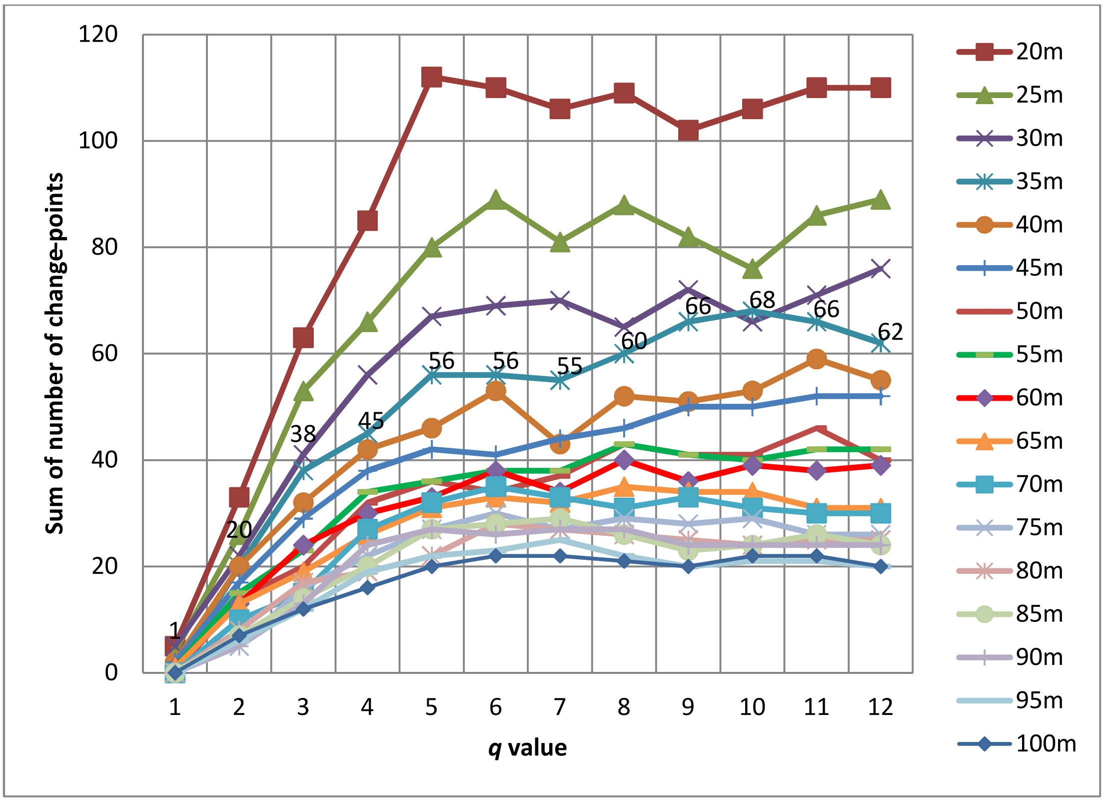

Figure 4.14 The number of change-points identified by the CPT (summed for the 7 travel routes) using different *q* values and $p < 0.01$. Data labels are shown for the 35m distance filter.

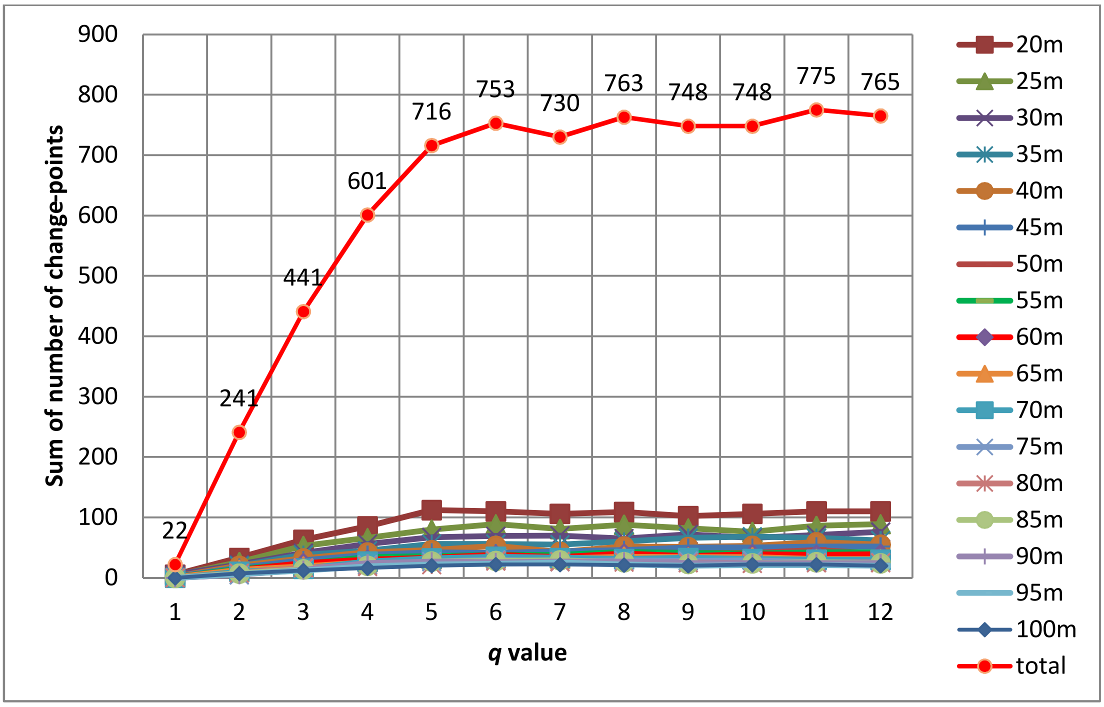

Figure 4.15 The number of change-points identified by the CPT (summed over the 7 travel routes) using *q* values 1 – 12 and $p < 0.01$. The top red line with data labels shows the number of change-points detected cumulated over the 17 distance filters.

When the number of identified change-points was summed over all 17 distance filters, an increase was observed for *q* 1 to 6 after which the summed number of identified change-points more or less stabilizes (Figure 4.15). A significant positive correlation was found between the value of *q* and the total number of change-points identified for all filter distances together (Spearman's Rho correlation coefficient = 0.475, p<0.01) as well as for each filter distance separately (Spearman's Rho correlation coefficient ranged from 0.473 – 0.602, all significant at the 0.01 level).

The numbers of change-points identified by the CPT using *q* values from 1 to 12 were summed over the 7 travel routes. For each value of *q*, the summed number of identified change-points decreased for larger sampling intervals (Figure 4.15), which were found to be highly significant negative correlations (Table 4.4). The negative correlation between sampling interval and the number of identified change-points remains highly significant when controlling for the value of *q* (Spearman's Rho correlation coefficient = -0.524, p<0.01 for all *q* values together).

Table 4.4 Significant negative correlations were found between sampling interval and the number of identified change-points for each value of *q* and for each follow day. Spearman's Rho correlation coefficients (two-tailed and all highly significant p<0.01) are shown for the 12 different q values for each follow day separate and summed for the 7 follow days (All) in the last row. On three days no change-points were identified using q=1 (No output: n/o).

Day	q=1	q=2	q=3	q=4	q=5	q=6	q=7	q=8	q=9	q=10	q=11	q=12
1	n/o	-0.661	-0.835	-0.920	-0.837	-0.816	-0.854	-0.808	-0.945	-0.945	-0.955	-0.975
2	n/o	-0.866	-0.677	-0.843	-0.862	-0.934	-0.876	-0.948	-0.954	-0.965	-0.952	-0.946
3	-0.559	-0.954	-0.973	-0.919	-0.919	-0.837	-0.953	-0.971	-0.968	-0.944	-0.954	-0.981
4	n/o	-0.910	-0.959	-0.774	-0.779	-0.856	-0.924	-0.934	-0.906	-0.874	-0.852	-0.849
5	-0.819	-0.684	-0.940	-0.946	-0.946	-0.951	-0.920	-0.904	-0.913	-0.932	-0.956	-0.939
6	-0.708	-0.783	-0.881	-0.958	-0.954	-0.974	-0.956	-0.955	-0.982	-0.968	-0.968	-0.977
7	-0.661	-0.729	-0.726	-0.848	-0.817	-0.935	-0.911	-0.918	-0.920	-0.940	-0.923	-0.982
All	**-0.457**	**-0.727**	**-0.729**	**-0.666**	**-0.624**	**-0.622**	**-0.610**	**-0.694**	**-0.737**	**-0.733**	**-0.744**	**-0.752**

Results showed that not only the average of the number of identified change-points decreases with larger sampling intervals, but also the variation in the number of identified change-points between *q* values decreases with larger sampling intervals (Table 4.5). This indicates that the CPT results may be more consistent (*i.e.*, there were fewer fluctuations in the number of identified change-points) to the selection of *q* value at larger distance filters.

Table 4.5 The number of identified change-points (summed over the 7 travel routes) averaged over the 12 different *q* values for each filter distance. This average and the standard deviation are summarized per distance filter (for each distance filter N=84).

Filter distance	Number of Change-Points	Standard Deviation
20m	87.6	35.5
25m	68.3	27.4
30m	56.7	22.4
35m	49.4	20.5
40m	42.3	16.7
45m	38.6	15.4
50m	32.0	13.8
55m	32.8	13.1
60m	30.4	12.1
65m	26.7	10.5
70m	25.6	11.1
75m	22.1	9.9
80m	20.5	8.5
85m	20.7	9.1
90m	20.4	9.2
95m	17.6	7.6
100m	17.0	7.1

The sampling interval thus affects the maximum number of change-points that can be identified in the first place (irrespective of the value of *q*), and sampling interval also affects the value of *q* at which the CPT identifies the highest number of change-points. When using the *q* value found to be most effective in detecting change-points (*q*=6) at a significance level of α = 0.01, “too few change-points were identified for evaluation” for the chimpanzees’ travel routes (Byrne *et al.* 2009 pp 627). To be able to interpret the results of Byrne *et al.* (2009), which were based on a time/distance sampling protocol with a sampling interval of 5min/20m (Noser and Bates *personal communication*), average step lengths (SL) were calculated for each sampling interval (*i.e.*, distance filter) presented in this chapter (Table 4.6). Byrne *et al.* (2009) presented four chimpanzee (*Pan troglodytes*) routes with average SL of 92, 104, 108 and 177 meters (Bates *personal communication*) (Table 4.7). Average SL of the first chimpanzee route (92m) is similar to the average SL resulting from a 60m distance filter (87.8m), while for the second and third chimpanzee travel routes average SL (104m and 108m) are similar to those resulting from a 70m or 75m distance filter (102.9m and 112.7m respectively). The average SL of the fourth chimpanzee route (177m) would require a distance filter larger those presented in this chapter (*i.e.*, larger than 100m) to give a similar average SL (hence > 150.1). Since it was shown here that sampling interval limits the maximum number of change-points that can be identified, and does so more at larger sampling intervals (*i.e.*, when average SL are larger) (Figure 4.14 and Table 4.5), it is not surprising that the relative large step lengths of the chimpanzee routes presented by Byrne *et al.* (2009) resulted in a relative low number of change-points (“too few”) being identified by the CPT. Although the reason why the number of identified change-points at a significance level of α = 0.01 was considered “too few for evaluation” was not discussed in more detail, this shows that when the sampling interval is large compared to the scale of interest, the ‘*q* rule’ may not be applicable.

Table 4.6 Mean step lengths are shown for each of the 7 travel routes separately (day1 – day7) and the average step length (SL), the standard deviation (SD) and average step duration (duration) were calculated over the 7 travel routes per filter distance.

Filter	day 1	day 2	day 3	day 4	day 5	day 6	day 7	SL	SD	duration
20	26.8	27.8	27.3	29.2	27.0	27.5	28.8	27.8	8.6	00:03:06
25	33.2	34.6	34.6	34.2	34.9	33.8	37.3	34.7	10.2	00:04:01
30	39.3	42.3	40.8	40.8	41.7	41.0	42.8	41.2	12.8	00:04:44
35	47.0	50.2	50.4	51.2	48.9	50.0	50.8	49.8	12.3	00:06:04
40	55.7	56.6	55.0	54.8	59.0	57.0	60.6	57.0	16.7	00:06:53
45	61.9	63.8	64.1	64.6	64.4	62.6	66.1	63.9	19.1	00:08:03
50	73.9	76.5	67.3	67.2	79.3	76.2	77.7	74.0	20.2	00:09:18
55	79.2	81.3	76.4	73.0	86.4	80.4	84.4	80.2	21.5	00:09:55
60	86.0	83.2	86.0	90.3	92.6	86.5	90.3	87.8	23.0	00:11:59
65	93.6	95.8	96.6	90.0	95.3	98.3	97.3	95.3	25.5	00:12:07
70	106.1	100.4	102.6	93.8	105.4	104.1	107.9	102.9	26.4	00:13:14
75	107.7	112.0	119.3	105.6	118.3	112.0	114.1	112.7	29.2	00:14:25
80	119.9	112.9	126.0	108.2	124.2	121.7	120.6	119.1	28.9	00:15:26
85	126.3	123.2	129.1	118.1	131.4	123.1	143.8	127.9	34.0	00:16:46
90	141.2	132.3	129.1	125.9	140.0	130.5	139.8	134.1	32.6	00:17:31
95	136.9	142.8	145.6	127.1	148.1	149.7	141.6	141.7	33.6	00:18:53
100	147.1	146.0	162.5	123.9	161.8	150.3	159.1	150.1	36.3	00:19:55

Table 4.7 Four chimpanzee (*Pan troglodytes*) travel routes (presented in Figure 7 a-d in Byrne *et al.* 2009) with the numbers of waypoints (WP), total route length and average step length (SL) in meters for each travel route separately and averaged over the 4 routes (Bates *personal communication*).

Data in Byrne *et al.* (2009)	WP	Total length (m)	Average SL (m)
Figure 7a (route 1)	68	6283	92.4
Figure 7b (route 2)	41	4407	107.5
Figure 7c (route 3)	58	6042	104.2
Figure 7d (route 4)	34	6011	176.8
Average (route 1-4)	50.3	5685.8	120.2

On the other hand, when sampling interval is relatively small compared to the scale of interest, using the *q* value at which the CPT is most sensitive to directional change, may result in identification of “too many” change-points. Figure 4.16 illustrates that when using the *q* value at which the CPT identifies the highest number of change-points (*q*=6), change-points are identified at a very fine scale. For example, the five change-points across the top detected only when using a *q* value of 6 (*blue stars*) seem to be relatively ‘trivial’ changes of direction at the spatial scale of the entire travel route and may thus not call for identification as change-points here.

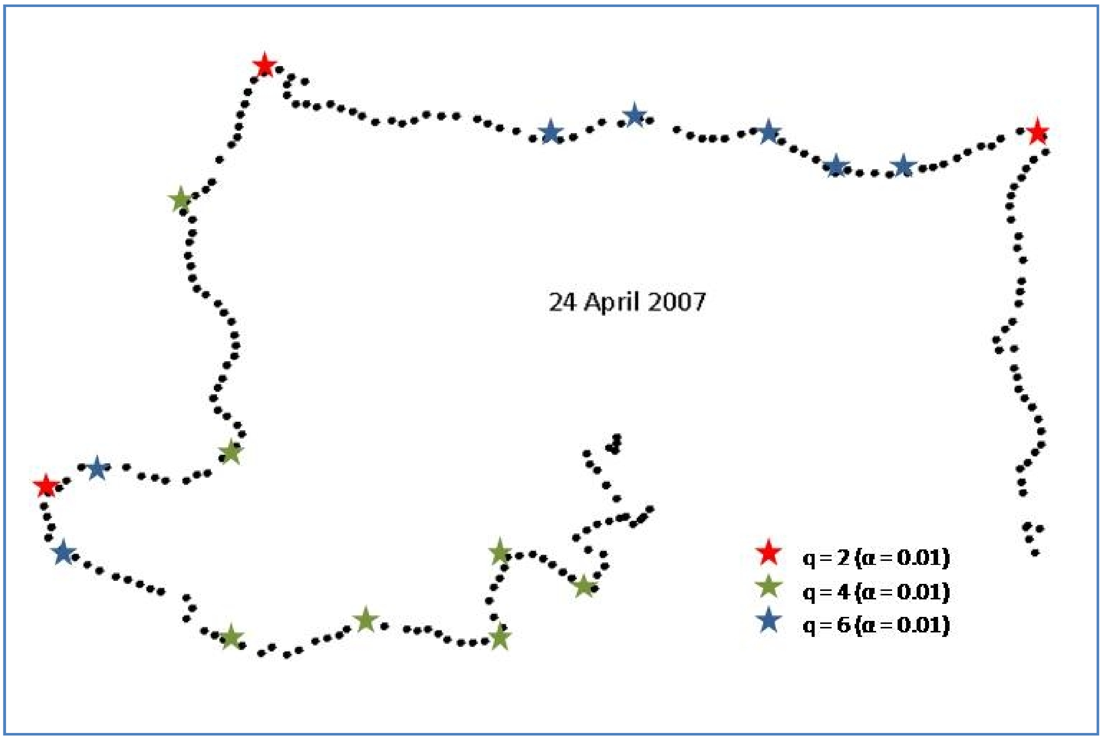

Figure 4.16 Baboon travel route (24th April 2007) to which a 20m distance filter was applied (average SL = 26.8m). Change-point identified by the CPT (α=0.01) using three different *q* values (2, 4 and 6). *Red stars* show the 3 change-points identified using *q*=2, *red* and *green stars* together show the 10 change-points identified using *q*=4 and the *red, green* and *blue stars* together show the 17 change-points identified when using *q*=6.

The '*q* rule' of maximising change-points extracted over *q* set by Byrne *et al.* (2009) therefore only seems practical when the appropriate sampling interval has been selected in advance. If not, using the rule to select the value of *q* at which the CPT is most sensitive to directional changes, may result in too few change-points being identified when the sampling interval is too large (as for the chimpanzee travel routes in Byrne *et al.* 2009), or too many change-points may be identified when the sampling interval is too small (*e.g.*, Figure 4.16). It is therefore of utmost importance to determine the correct scale of interest in advance and to select an appropriate sampling interval dependent on the study species and aim of the research. It was suggested that the effect of choice of sampling interval scale (*i.e.*, step length) on the efficiency of the '*q* rule' is inevitable and that whether a researcher has selected a sampling interval with the "right" granularity (*i.e.*, scale), can only be discerned by whether or not the results later make biological sense in terms of the animal's behaviour on the ground (Byrne *personal communication*).

In the case of the chimpanzee travel route presented by Byrne *et al.* (2009) using the '*q* rule' at a significance level of α = 0.01 resulted in too few change-points, and since sampling interval could not be increased ad-hoc, the statistical power of the CPT was subsequently decreased to a significance level of α = 0.05. Under this setting the CPT was found to be most sensitive to directional change for a *q* value of 4 (Byrne *et al.* 2009) and the results were now considered a "sufficient number of change-points for evaluation" (Byrne *et al.* 2009 pp 626). Byrne *et al.* (2009) state that: "In choosing the appropriate significance level, there is trade-off between statistical robustness of the results on the one hand and the number of locations identified as change-points on the other." The relationship between the significance level and the number of change-points identified was however not investigated further, nor discussed when the number of identified change-points is considered a "sufficient number of change-points" and when there are "too few change-points". However, this means that by adjusting the significance level, the number of change-points that is being detected by the CPT can be influenced (in the case of Byrne *et al.* 2009 the number of identified change-points was increased to what was considered to be "enough"). Varying the significance level can therefore to some degree be considered a way to compensate for data that has not been collected at the "right" granularity (*i.e.*, scale) for the study species or research question under investigation.

However, at a significance level of $\alpha=0.05$ the CPT was prone to giving false positives (identifying change-points when none were actually present), whereas at a significance level of $\alpha=0.01$ true change-points were missed (Byrne *et al.* 2009). There is thus a trade-off between the rates of correct detections and false alarms and the choice of significance level must again be made according to the goals of the researchers. Due to the large number of travel routes in the entire data set (N=234), the aim here was to limit the number of wrongly identified change-points, even if this would mean that some change-points may be missed as a consequence, since it is likely that if a missed change-point location is indeed important the CPT will identify a change-point at that location in one of the other follow days. If the avoidance of false positives were critical, a smaller value of $\alpha = 0.01$ was suggested by Byrne *et al.* (2009) to be optimal and is therefore used here.

4.4.3 Scale and sampling interval

To determine the appropriate scale and sampling interval, the CPT was applied 119 times (*i.e.*, 17 different distance filters were applied to the 7 travel routes), each time using that q value resulting in the CPT being most sensitive to directional changes and the CPT results were reviewed visually. To clarify this visual review process, first the CPT results of one of the 7 travel routes (29th April 2007) (Figure 4.17) are discussed in more detail below.

Two remarks must be made before reviewing this travel route in more detail. Firstly, the value of q which results in the highest number of identified change-points was determined per distance filter *overall* (*i.e.*, over all seven test days), and thus it is possible that for individual travel routes, this q value may not necessarily result in the highest number of change-points for that distance filter for that particular travel route. Secondly, more than one value of q may result in the same highest number of identified change-points for a particular distance filter (Table 4.8). Both these situations occur for the baboon travel route illustrated. For the 100m distance filter multiple q values resulted in the same highest number of change-points (q values 6,7, 10 and 11 all resulted in 3 change-points being identified) (Figure 4.17 s-v) and while this also happens for the 90m filter (*q* values 5 and 8 both detect 4 change-points), an additional *q* value (*q*=7) is used on the 90m filter, because *overall* (summed over all seven test days) this value of *q* gave the same highest number of identified change-points as *q* values 5 and 8 for that distance filter, but it happens to detect a lower number (3) of change-points for this particular follow day (Figure 4.17 o-q) (see also Table 4.8).

Table 4.8 Number of waypoints (WP), the average step length (SL) in meters and the average step duration (Duration) for each of the 17 filter distances (Filter) applied to the travel route on the 29th April 2007. The *q* value (*q*) at which the CPT identified the highest number of change-points (CP) for each distance filter is shown.

Filter	WP	SL	Duration	*q*	CP
20	198	27.8	00:02:58	5	13
25	158	34.6	00:03:43	6	8
30	126	42.3	00:04:38	7	7
35	106	50.2	00:05:33	10	8
40	93	56.6	00:06:20	11	6
45	81	63.8	00:07:12	12	5
50	69	76.5	00:08:34	11	6
55	63	81.3	00:09:15	8	5
60	60	83.2	00:09:43	8	5
65	53	95.8	00:11:13	8	5
70	50	100.4	00:11:40	6	4
75	45	112.0	00:13:15	6	4
80	44	112.9	00:13:34	6	4
85	42	123.2	00:14:13	7	4
90	38	132.3	00:15:45	5, 7 & 8	4, 3 & 4
95	34	142.8	00:17:40	7	3
100	34	146.0	00:17:40	6, 7, 10 & 11	3 (for all)

For the 20m distance filter (Figure 4.17a) 13 change-points were identified some of which may not represent directional changes at the appropriate scale for this study (for example change-point number 6, 10 and 13). The same goes for the 25m distance filter for which minor directional changes on the scale of this study were also identified (for example change-point number 4, 6 and 8) (Figure 4.17b). A similar argument could be made for the 30m distance filter for change-point numbers 5 and 7 (Figure 4.17c) and for the 35m distance filter for change-point number 4 and 6 (Figure 4.17d). For both the 40m and 50m distance filter 6 change-points were identified of which change-point number 5 and 6 are located close together (Figure 4.17e and Figure 4.17g). Still using a relatively small sampling interval (roughly the average step length is 55m to 75m for the 40m and 50m distance filters respectively) allowed both these locations to be identified as change-points. However, at such locations where the baboons circuitously wandered, it would be the aim to identify only one change-point. Furthermore, the locations of some of the identified change-points do not appear to be very accurate for the 40m distance filter (for example change-point number 1, 2 and 3) and the 50m distance filter (for example change-point number 1 and 4) (Figure 4.17 e and Figure 4.17g respectively). Five change-points were detected for the 45m distance (Figure 4.17f) and the 55m-65m distance filters (Figure 4.17 h-j), which seemed appropriate for this travel route at the scale of interest, despite the fact that some of the locations at which these change-points were detected are slightly imprecise (for example change-point number 4 and 5 in Figure 4.17j). For filter distances over 70m (Figure 4.17 k-v) the scale of sampling interval seems too large to detect change-points at an appropriate scale. These distance filters have average step lengths over 100m (Table 4.8) and they fail to identify a number of change-points which were consistently revealed at smaller sampling intervals (for example the change-point labelled number 2 in Figure 4.17 a-j). For the 90m distance filter using a q value of 7 (Figure 4.17p), additionally the change-point labelled number 4 in Figure 4.17 e-j was not detected. With the two largest distance filters presented here (95m and 100m) to simulate a sampling interval over 130m (Table 4.8), the location of change-points became more and more imprecise (for example change-point number 1 and 3 for the 100m distance filter in Figure 4.17 s-v).

It is expected that change-point locations become increasingly imprecise compared to the ‘actual’ travel route when using a larger sampling interval. The line representing the travel route (Figure 4.17) was created by connecting subsequent waypoints which remained after applying a 20m distance filter. Note however, that applying the different distance filters (20m – 100m) to the travel route resulted in fewer waypoints and consequently a less “accurate” travel route. The data to which the CPT was applied (*i.e.*, waypoints which remained after applying different distance filters) ranged from 34 to 198 waypoints and the sampling interval (*i.e.*, average distance between consecutive waypoints) scaled from 27.8m to 146.0m (Table 4.8). It is therefore not that the locations of detected change-points are inaccurate with larger distance filters, but instead, with increasing filter distances the travel route is represented by fewer and fewer waypoints until it becomes an unrealistic representation of the actual route travelled.

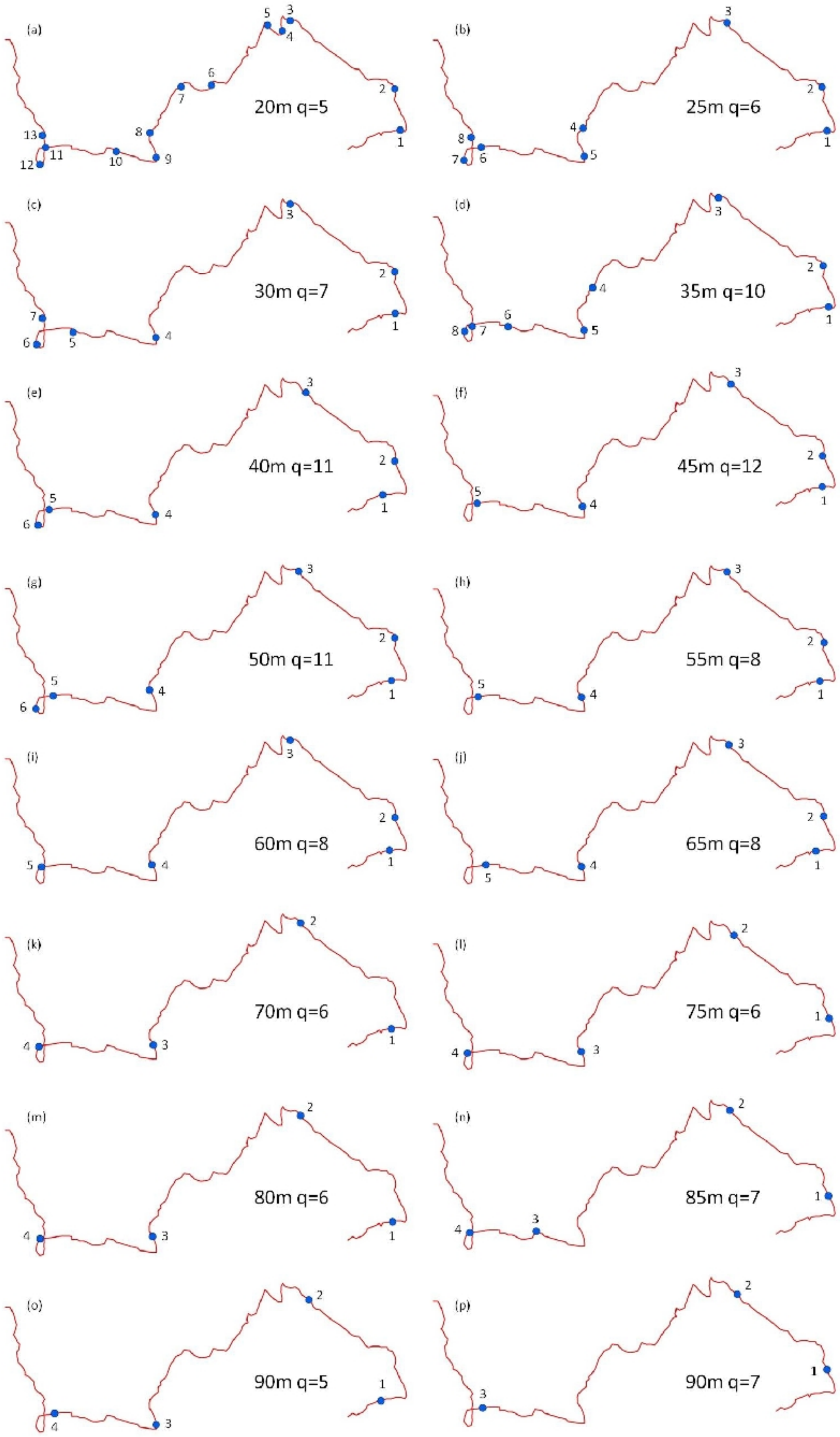

Figure 4.17 a-p See next page for figure legend.

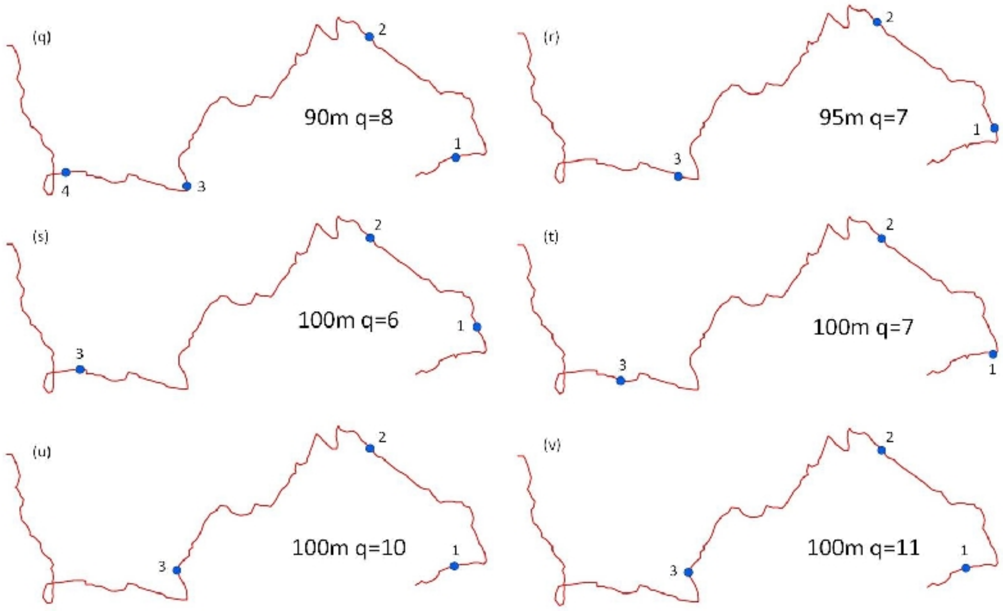

Figure 4.17 q-v Travel route (29th April 2007) (*red line*) created by connecting subsequent waypoints which remained after applying a 20m distance filter. The CPT was run using the value of *q* at which the CPT was most sensitive to directional change after applying 17 distance filters (remaining number of waypoints ranged from 34 [100m filter] to 198 [20m filter]) and identified change-points are shown as *blue dots*.

All 119 CPT results were visually reviewed as described above, to determine the appropriate scale on which to sample and analyse baboon travel routes in large scale space, keeping the research goals of this thesis in mind. The results are summarized in Table 4.9 in which sampling interval scale considered appropriate is coloured orange. Using a 60m – 70m distance filter, equivalent to average step lengths ranging from 87.8m to 102.9m (Table 4.8), attained an appropriate sampling interval scale on which to identify change-points for 5 of the follow days (Table 4.9). At these appropriate sampling intervals the numbers of detected change-points (the numbers in the orange shaded squares in Table 4.9) for each follow days were quite constant: 4 change-points for day one (24th April 2007), 5 change-points for day two (29th April 2007), 5 or 6 for day three (25th May 2007), 2 or 3 for day four (26th May 2007), 8 to 11 for both day 5 (23rd November 2007) and day 6 (12th December 2007) and finally 3 or 4 change-points for day 7 (1st March 2008).

Despite the fact that on this scale, using the '*q* rule' detects a number of change-points appropriate for analysing baboon travel routes in the context of spatial cognitive abilities, the change-point locations remain slightly imprecise when compared to the actual travel route. For example for day 2 the appropriate scale ranges from 55m – 65m (Table 4.9), but change-points identified at those scales (Figure 4.17 h-j) do not seem to be located precisely at those points where the baboons changed their travel direction. Section 4.4.1 illustrated that smaller distance filters were preferred over larger distance filters, due to their higher spatial accuracy. As a consequence it should be possible to identify the 'correct' *number* of change-points at a smaller sampling interval (thus using a different *q* value than would be used under the '*q* rule'), so that the location of the change-points can be identified more precisely in consideration of the actual route travelled.

All distance filter/*q* value combinations that resulted in the appropriate numbers of change-points were subsequently identified for each travel route and marked 'x' in Table 4.10. The 35m distance filter with a *q* value of 3 was the only combination that resulted in the appropriate number of change-points for each of the 7 test days (Table 4.10). Comparing the results of the 35m/*q*=3 combination to the original filter/*q* value combinations, showed that, as expected, change-points identified for the smaller sampling interval are located more accurately in light of the actual travel route than for the larger sampling interval, whilst detecting the same number of change-points for each travel route (as illustrated by Figure 4.18). It was therefore decided to select this relatively small sampling interval (average step length is 50m) obtained using a 35m distance filter and the CPT was run using a *q* value of 3 and a significance level of 0.01 to the other 6 follow days and the results are presented in Figure 4.19.

Table 4.9 Number of change-points detected by the CPT (α=0.01) and the *q* value under the '*q* rule'. Orange shaded squares indicate those combinations resulting in change-points at an 'appropriate' scale.

Day	20 q=5	25 q=6	30 q=7	35 q=10	40 q=11	45 q=12	50 q=11	55 q=8	60 q=8	65 q=8	70 q=6	75 q=6	80 q=6	85 q=7	90 q=5	90 q=7	90 q=8	95 q=7	100 q=5	100 q=6	100 q=10	100 q=11
1	11	11	7	8	7	8	5	7	6	4	4	3	3	3	3	3	2	4	2	3	3	3
2	13	8	7	7	6	5	6	5	5	5	4	4	4	4	3	3	4	3	3	3	3	3
3	14	12	10	10	7	7	7	6	6	5	5	4	4	5	4	4	3	4	3	4	2	2
4	6	5	3	5	4	3	1	3	2	2	2	2	2	1	1	1	1	1	2	1	1	1
5	28	22	16	12	11	9	8	6	6	6	6	5	5	5	6	6	6	5	4	5	6	5
6	27	24	15	15	15	13	13	12	11	8	10	8	7	7	7	6	7	5	3	3	4	4
7	13	7	12	11	9	7	6	4	4	5	4	4	3	3	3	4	4	3	3	3	3	4

Table 4.10 The 35m distance filter with *q*= 3 is the only combination that resulted in the "correct" number of change-points (CP) that needed to be detected in all 7 travel routes.

Filter		20m		25m		30m								35m							40m											45m											50m										
Day	CP	2	3	2	3	2	3	4	5	6	7	8	9	2	3	4	5	6	7	12	2	3	4	5	6	7	8	9	10	11	12	2	3	4	5	6	7	8	9	10	11	12	2	3	4	5	6	7	8	9	10	11	12
1	4					x	x								x	x																													x								
2	5		x		x		x								x								x			x										x		x	x	x		x							x	x	x		x
3	5			x										x								x	x		x																			x	x				x		x		
3	6					x									x	x		x						x		x		x					x		x	x	x											x		x			
4	2					x				x						x	x	x	x					x		x						x				x	x						x	x	x	x	x	x	x	x			
4	3	x		x					x		x	x	x	x	x					x	x		x		x				x				x	x	x			x	x	x	x	x											
5	8						x								x											x		x	x		x									x	x											x	
5	9																						x	x			x								x	x						x							x				
5	10	x			x			x								x									x												x																
5	11																													x																							
6	8						x								x							x																							x								x
6	9																																x																				
6	10																																			x										x							
6	11																									x								x			x	x									x	x					
7	3																																	x	x										x	x							
7	4														x							x											x			x								x			x	x	x	x			
Total		2	1	2	2	3	4	1	1	1	1	1	1	2	7	4	1	2	1	1	1	3	4	3	3	5	1	2	2	1	1	1	4	3	4	6	4	3	2	3	2	3	1	3	5	3	3	4	5	4	2	1	2

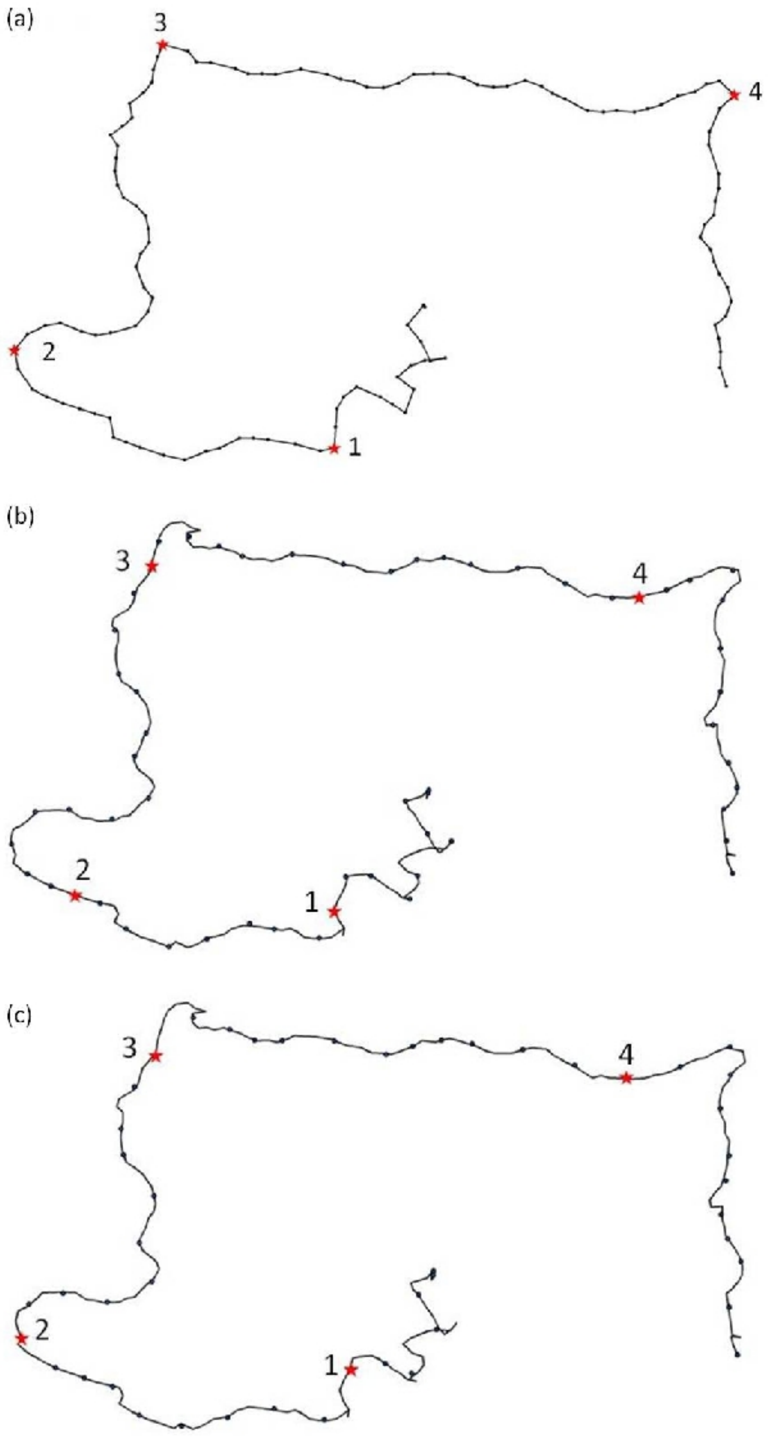

Figure 4.18 Travel route (24th April 2007) (day 1 in Table 4.9 and Table 4.10) represented by a continuous *black line* created by connecting subsequent waypoints which remained after applying a 20m distance filter, with *dots* indicating waypoints remaining after applying a distance filter of (a) 35m, (b) 65m and (c) 70m. *Red stars* represent change-points identified by the CPT using a *q* value of 3, 8 and 6 respectively and a significance level of 0.01.

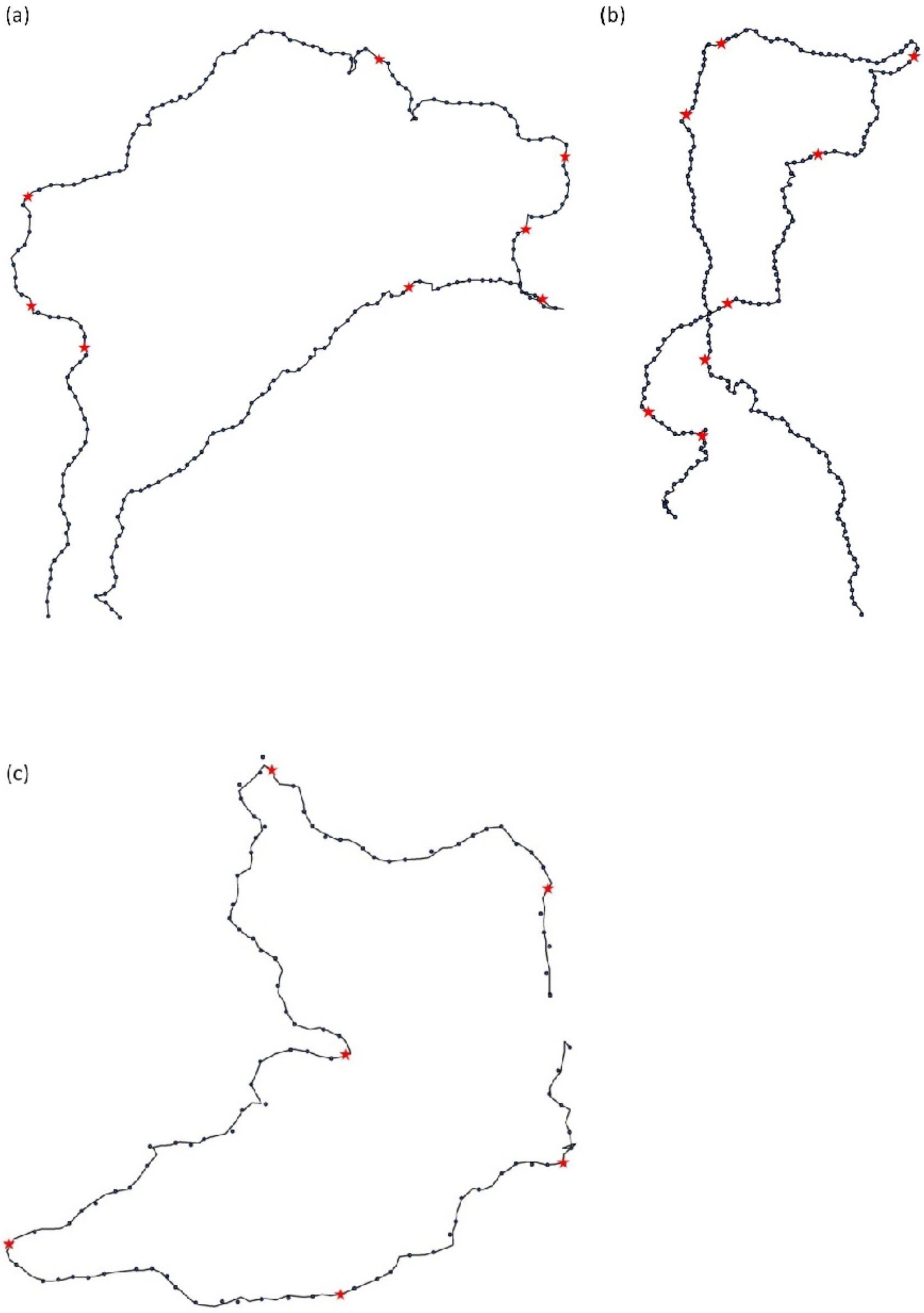

Figure 4.19 a-c Travel routes (day 2-4 in Table 4.9 and Table 4.10) represented by a continuous *black line* created by connecting subsequent waypoints which remained after applying a 20m distance filter, with *dots* indicating waypoints remaining after applying a distance filter of 35m. *Red stars* represent change-points identified by the CPT using a *q* value of 3 and a significance level of 0.01.

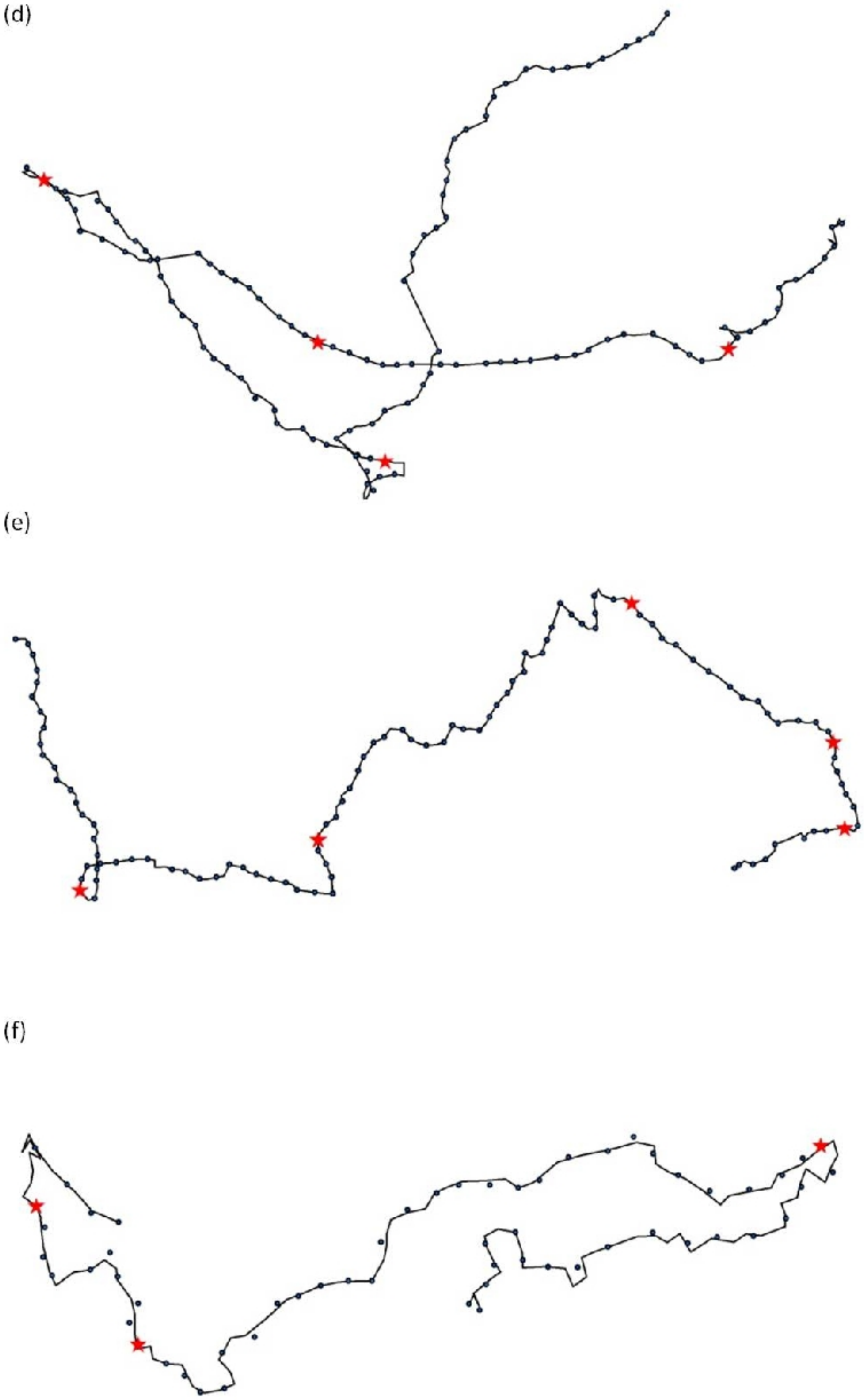

Figure 4.19 d-f Travel routes (day 5-7 in Table 4.9 and Table 4.10) represented by a continuous *black line* created by connecting subsequent waypoints which remained after applying a 20m distance filter, with *dots* indicating waypoints remaining after applying a distance filter of 35m. *Red stars* represent change-points identified by the CPT using a *q* value of 3 and a significance level of 0.01.

4.5 Discussion

Ultimately the aim of this thesis is to give insight into the spatial cognitive abilities of baboons and as a first step, the objective of this chapter was to use a novel statistical method devised by Byrne *et al.* (2009) called the CPT to identify those locations at which baboons start orienting towards new goals. Due to the nature of CPT, vector length (*i.e.*, step length) and its variability was expected to affect the output and therefore the effect of sampling protocol type on the success of the CPT was evaluated. Results showed that both a time and time/distance sampling protocol had significantly larger variability in step length than a distance sampling protocol, even when the daily average step length was kept constant. When the locations at which change-points were detected were further investigated for each protocol, it was revealed that when a travel route is relatively straight, variation in step length does not necessarily influence the results of the CPT, but when seemingly important changes of direction occurred, the time and time/distance filter frequently failed to identify these locations as change-points due to highly uneven spacing of the waypoints. Furthermore, when a distance sampling protocol was used, smaller sampling intervals allowed the CPT to detect changes of direction at a smaller scale than at larger sampling intervals. Accordingly, future studies aiming to incorporate the CPT are strongly recommended to collect data using a distance based sampling protocol or to manipulate the data post-hoc to obtain data points at a regularly spaced distance interval with the selection of sampling interval depending on the on the scale of interest. The distance filter function available in Trip and Waypoint Manager V3 software (Garmin Ltd. 1995) allows setting of a minimum distance interval and results in only minor variation in distance between consecutive waypoints, which has been shown to outperform time interval and combinations of time and distance interval based sampling protocols. However, to obtain waypoints at an *exact* distance interval it is recommended to create continuous travel paths from the data and then to convert those travel paths back to waypoints. This can for instance be done using the "Convert Locations to Paths" and "Convert Paths to Locations" functions of Hawth's Analysis Tool 3.26 (Beyer 2004) as used in Chapter 7.

The sampling interval, represented by different filter distances, was shown to affect the maximum number of change-points that can be identified in the first place (irrespective of the value of q), and to also affect the value of q at which the CPT identifies the highest number of change-points. Byrne *et al*. (2009) have suggested selecting the value of q at which the CPT is most sensitive to directional change and as such, identifies the highest number of change-points. However, the sensitivity test conducted here showed that this 'q rule' only seems practical when the researcher has selected a sampling interval with the "right" granularity (*i.e.*, scale) in advance. If not, using the value of q under the 'q rule', may result in too few change-points being identified when the sampling interval is too large, or too many change-points may be identified when the sampling interval is too small for the research question of interest. It is therefore of utmost importance to determine the correct scale of interest in advance and to select an appropriate sampling interval dependent on the study species and aim of the research.

These findings were validated in the study of Byrne *et al.* (2009) in which the CPT was applied to four chimpanzee (*Pan troglodytes*) travel routes with a relative large sampling interval. Using the '*q* rule' at a stringent significance level (α=0.01) resulted in detection of "too few" change-points and since sampling interval could not be increased ad-hoc, the statistical power of the CPT was subsequently decreased (α=0.05) to increase the number of change-points detected. Byrne *et al.* (2009) state that: "In choosing the appropriate significance level, there is trade-off between statistical robustness of the results on the one hand and the number of locations identified as change-points on the other." By adjusting the significance level, the number of change-points that is being detected by the CPT can thus be influenced. Varying the significance level can therefore to some degree compensate for data that have not been collected at the "right" granularity (*i.e.*, scale) for the study species or research question under investigation. Furthermore, the CPT is prone to giving false positives (identifying change-points when none were actually present) at more relaxed significance levels (e.g., α=0.05 or α=0.10), whereas at more stringent significance levels (α=0.01) true change-points could be missed (Byrne *et al.* 2009). There is thus a trade-off between the rates of correct detections and 'false alarms'. Due to the large number of travel routes in the entire data set (N=234), the aim in this study was to limit the number of wrongly identified change-points, even if this would mean that some change-points may be missed as a consequence, since it is likely that a missed 'true' change-point location will still be identified in one of the other travel routes. Thus avoidance of false positives was considered critical and as such a more stringent significant level (α=0.01) was used.

With the level of significance set and the aim of this thesis in mind, an extensive sensitivity test was conducted to determine the appropriate sampling interval when investigating baboon travel routes. In Section 4.4.3 the appropriate sampling interval at which the '*q* rule' could be successfully applied, was determined to range from 87.8m to 102.9m, obtained by applying a 60m – 70m distance filter to the data. This finding is consistent with the study of Byrne *et al.* (2009) in which the CPT was applied to four baboon (*Papio ursinus*) travel routes using the '*q* rule' (with α=0.01). These travel routes had an average sampling interval of 90.2m (average daily sampling intervals ranged from 72m – 123m) (Noser *personal communication*), which supports the proposal in this chapter that this is an appropriate sampling interval for which the '*q* rule' identifies change-points at the right scale when studying spatial cognition.

Nevertheless, by using these appropriate sampling intervals, which were relatively large, the locations of the identified change-points were somewhat imprecise. That smaller distance intervals were preferred over larger distance intervals due to their higher spatial accuracy was illustrated already in Section 4.4.1. This is not because the wrong waypoints are identified as change-points when using larger sampling intervals, but instead, with increasing sampling interval the travel route is represented by fewer and fewer waypoints, until it becomes an unrealistic representation of the actual route travelled.

Therefore, the ‘correct’ number of change-points (*i.e.*, the number of change-points identified using the ‘*q* rule’ at the appropriate sampling interval determined in Section 4.4.3) were identified by a smaller sampling interval (thus using a different *q* value than would be used under the ‘*q* rule’), so that the location of the change-points was identified more precisely in consideration of the actual route travelled.

At the appropriate sampling interval (87.8m to 102.9m) the numbers of change-points that were identified under the ‘*q* rule’ for each follow day were highly consistent and thus seem to represent those important locations at which baboons start orienting towards new goals. To identify the location of the change-points more precisely in consideration of the actual route travelled, all combinations of (smaller) sampling interval and *q* value that resulted in the same ‘appropriate’ number of change-points were identified for each travel route. The combination of a sampling interval of 50m (obtained here by a 35m distance filter) with a *q* value of 3 resulted in the appropriate number of change-points as identified under the ‘*q* rule’ for all 7 travel routes, and the location of these change-points were indeed more accurate in light of the actual route travelled than they were at the larger appropriate sampling intervals.

Taking the results of this extensive sensitivity test into consideration, a *q* value of 3 in combination with a distance filter of 35m was used for the analysis of the entire data set to identify those locations in the travel routes of wild chacma baboons at which they start orienting towards new goals (Chapter 5) to provide further insight into their spatial abilities (Chapter 6 to Chapter 8).

CHAPTER 5

CHANGE POINTS

5.1 Introduction

Although there is abundant evidence that animals navigate adaptively through their natural environments (Janson & Byrne 2007), there is still much to learn about the cognitive mechanisms that underpin this ability. To date, our understanding of the content and complexity of cognitive maps is limited (Janson & Byrne 2007; Di Fiore & Suarez 2007), although an increasing body of evidence suggests that some primates may navigate via network maps (Noser & Byrne 2007a; Di Fiore & Suarez 2007). For group-living animals, there is the additional complexity of needing to understand how the collective movements required for groups to navigate cohesively within their environment emerges from individual decisions (Petit & Bon 2010), and group decision-making remains a topic of great theoretical and empirical interest. Central to addressing both of these issues, however, is determining when and where travel decisions are made (Byrne *et al.* 2009).

Byrne and colleagues (2009) introduced the change-point test (CPT) to identify locations where animals start orienting towards the next goal. However, given the challenges in selecting the appropriate parameter values and sampling interval associated with the CPT (see Chapter 4 for more details) the utility of a second more straight-forward method to identify significant changes in travel direction was investigated. This second method is based on the average and standard deviation of turn angles and is referred to as the turn angle (TA) method. The aim of this chapter is to examine the utility of the change-point test and turn angle method in identifying locations at which animals start orienting towards a new goal and therewith their ability to identify locations where travel decisions are being made.

5.2 Methodology

5.2.1 Data collection

Location data analysed in this chapter were of full-day follows only (sunrise to sunset) (N=234) collected between April 2007 and November 2008 (see Chapter 2 for more details). Data were filtered using a 35m distance filter in Trip and Waypoint Manager (Chapter 4 Section 4.3.1) to avoid potential errors arising from time sampling (Chapter 4 Section 4.4.1). After applying the 35m distance filter, travel routes were represented on average by 119 (± 38) waypoints with a mean interval of 354 (± 550) seconds and an average step length of 50.2 (± 21) meters for each follow day (N=234).

The baboons travelled an average of 5.9 (± 1.9) kilometres per day, with a significant difference in mean daily travel distances between summer (7.1 ± 1.8 km/day) and winter (5.4 ± 1.6 km/day) (T-test: t= -7.291, df=233, p<0.001).

5.2.2 Change-point test

The first method used to identify significant changes of direction is the change-point test (CPT) (Byrne *et al.* 2009) in which choosing an optimal *q* value is critical to its successful application. In Chapter 4, an extensive sensitivity analysis to determine the optimal value of *q* was conducted and the results indicated that the optimal *q* value is influenced by the original sampling protocol and subsequent distance between waypoints. The data were analysed using $\alpha = 0.01$ and a $q = 3$ to optimise the spatial resolution of change-points (Chapter 4). The original code for performing the CPT was downloaded from http://www.mcs.st-andrews.ac.uk/wpej/CPT.html (accessed 10 April 2010) and modified to automate the process of identifying all change-points within a single daily travel path (Appendix II) based on the ‘peak rule’ (Chapter 4 Section 4.2.4.3). The automated CPT code was run in R and the resulting data set is referred to as the CPT data set.

5.2.3 Turn angle method and circular statistics

The second method used to identify significant changes of travel direction is the turn angle (TA) method. This method was based on an approach of Normand & Boesch (*submitted*), where ‘decision points’ were defined as resources at which the study animal deviated significantly between the direction to reach the resource and the direction to leave (*i.e.*, resource locations with significantly larger turn angles). In their study, the deviation was considered significant when a turn angle (identified between 0° and 180°) at a resource was superior to the daily mean turn angle plus the standard deviation (Normand & Boesch *submitted*). They did not consider that measurements of turn angles require special analysing techniques and statistics.

In many diverse scientific fields measurements are in directions. Examples of directional data are direction of flight of birds, wind direction and the direction of the earth’s magnetic pole. Since directional data are substantially different from linear data, many of the usual linear statistical techniques and measures often misleading, if not entirely meaningless and directional data thus calls for the use of specialised statistical tools and techniques (Jammalamadaka & Sengupta 2001). The sample mean as well as standard deviation of directional data can suffer from their strong dependence on the choice of zero direction (*i.e.*, the starting point) and the sense of rotation (*i.e.*, clockwise or anti-clockwise) (Mardia & Jupp 2000; Jammalamadaka & Sengupta 2001). Even when directional angles fall between 0° and 180°, the type of statistics used determines the results of summary statistics such as sample mean and standard deviation. Consider for instance the following 5 deviations: 10°, 25°, 40°, 3° and 160°. Using linear statistics, the average (μ) of these 5 angles is 47.6° and the standard deviation (SD) is 57.6° (Equation 1 and Equation 2 respectively). However, when using circular statistics the average (μ) of these 5 angles is 31.0° and the standard deviation (SD) is 54.7° (Equation 3 and Equation 4 respectively). Therefore circular statistics are used in this chapter to calculate turn angles between 0° and 360° degrees, with 0° representing the current direction of travel (Figure 5.1). Also the daily mean and daily standard deviation were calculated using circular statistics (Gaile & Burt 1980).

Equation 1

$$\mu = \frac{(10 + 25 + 40 + 3 + 160)}{5} = 47.6$$

Equation 2

$$SD = \sqrt{\frac{(10 - 47.6)^2 + (25 - 47.6)^2 + (40 - 47.6)^2 + (3 - 47.6)^2 + (160 - 47.6)^2}{5}} = 57.6$$

Equation 3

$$\mu = \operatorname{atan}\left(\frac{x}{y}\right)$$

with

$$x = \frac{1}{5}\,[\sin(10) + \sin(25) + \sin(40) + \sin(3) + \sin(160)]$$

$$y = \frac{1}{5}\,[\cos(10) + \cos(25) + \cos(40) + \cos(3) + \cos(160)]$$

Equation 4

$$SD = \sqrt{-2\ln(R)}$$

with

$$R = \sqrt{x^2 + y^2}$$

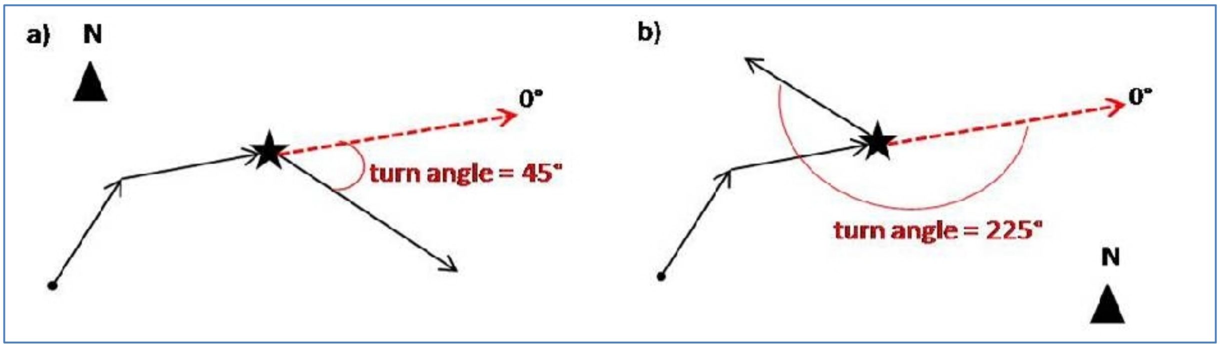

Figure 5.1 Calculation of turn angles in travel routes between 0° and 360°, where 0° represents the current travel direction.

The TA method thus differed from the approach used by Normand & Boesch (*submitted*) in that it measures deviations between 0° and 360° and applies circular statistics to calculate sample mean and standard deviation, whereas Normand & Boesch (2009, *submitted*) determined deviations between 0° and 180° (*i.e.*, whether animals turned clockwise or anti-clockwise was irrelevant) and applied linear statistics to calculate the mean and standard deviation. This means for example that if animals made a left turn of 45° at a resource location, Normand & Boesch (*submitted*) measured a deviation of 45° from the previous travel direction, whereas in this study a turn angle of 315° was measured (Figure 5.2).

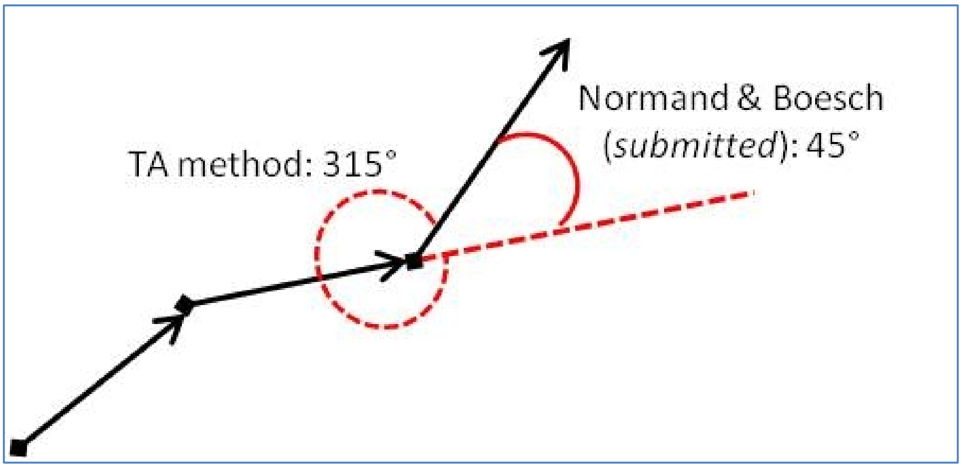

Figure 5.2 The deviation between the direction followed to reach a resource and the direction taken when leaving a resource (Normand & Boesch *submitted*) results in a turn angle of 125°, whereas the TA method used in this chapter measures a turn angle as the deviation from the current direction resulting in a turn angle of 315°.

Another difference between the TA and the approach used by Normand & Boesch (*submitted*) in that locations were identified as change-points if the turn angle at a location was superior to the daily mean ± 2 times the standard deviation (in contrast to a 1 standard deviation criterion). Thus if the mean turn angle for a day is 3° and the standard deviation is 35°, change-points for that day were considered all points for which the deviation fell outside 360° - (2x35°-3°) = 293° and 73° (*i.e.*, locations with turn angles between 73° and 293° were identified as change-points). The more stringent criterion of two standard deviation was used, since potential change-points were not limited to pre-identified resource locations (Normand & Boesch *submitted*), which would have automatically set an upper limit to the number of change-points that can be identified. Instead, change-points can occur at any location and setting a one standard deviation criterion would have resulted in too many change-points being identified to be informative. Only highly significant changes of direction are of interest here and due to the large size of the data set, it is likely that if at a certain location baboons change direction frequently, this location will identified as a change-point in at least one of the follow days.

Although it is often tempting to cut the circle at a suitable point and to use conventional summary statistics on the resulting observations on the line, the appropriate way of constructing summary statistics from directional data is to regard points on the circle as unit vectors in the plane and then to take polar coordinates of the sample of these vectors (Mardia & Jupp 2000) as shown by Equation 3 and Equation 4. In this case applying circular statistics instead of linear statistics produced different thresholds to identify locations (turn angles) as change-points (Table 5.1). These two thresholds may not differ to a very great extent, it is nevertheless recommended that for any type of directional data, such as the one analysed in this chapter, circular statistics are used for constructing summery statistics (*e.g.*, Fischer 1996; Mardia & Jupp 2000; Jammalamadaka & Sengupta 2001). The change-point data set resulting from the turn angle method is referred to as the TA data set.

Table 5.1 Mean daily turn angle, 1 standard deviation (1SD) and 2 standard deviation (2SD) of the mean daily turn angle, and the threshold when turn angels were identified as change-points (CP) for the turn angle (TA) method using circular statistics and the approach used by Normand & Boesch (*submitted*) (N&B). Note that the TA method measured turn angles between 0° and 360° and N&B measured turn angles between 0° and 180°.

	mean daily turn angle	1SD	2SD	CP identified between
TA	359.9°	45.3°	90.6°	88.9° - 268.9°
N&B	35.2°	36.6°	73.2°	108.4° - 180°

Since the identified numbers of change-points per day were not normally distributed (one sample Kolmogorov-Smirnov test: p<0.05) for neither the CPT data set nor the TA data set, non-parametric tests were used to investigate differences in the number of change-points per day between data sets. Data sets were analysed as a whole, as well as for the summer and winter season separately.

5.3 Results

5.3.1 *Identifying change-points*

The results of the CPT and TA method are shown in Table 5.2 and an example of the results of the two change-point identification methods is shown in Figure 5.3. The CPT resulted in identification of a total of 1058 change-points (441 in summer and 617 in winter) over 234 follow days (Figure 5.4a and Figure 5.4b). The CPT identified an average of 4.6 (±2.2) change-points per day, with significantly more change-points per day in summer (5.5 ±2.4) than in winter (4.1 ±1.9) (Mann-Whitney U test Z= -4.314, p<0.001). On average 0.76 (±0.31) change-points were identified per kilometre (no significant difference in the number of change-points per kilometre between the whole year and summer or winter separately) and the average distance between change-points was 1011 ±738m (for winter 991 ±731m and for summer 1038 ±747m NS). There was a positive linear correlation between the number of change-points and the distance travelled in a day (Pearson’s correlation: p<0.001, r = 0.607, N=234) (Figure 5.5).

Table 5.2 Change-points (CP) identified using the change-point test (CPT) and the turn angle method (TA).

	CPT	TA
Total number of CP		
Year	1058	2106
Summer	441	868
Winter	617	1238
Average number of CP per day		
Year	4.6 (± 2.2)	9.0 (± 3.8)
Summer	5.5 (± 2.4)	10.9 (± 4.2)
Winter	4.1 (± 1.9)	8.0 (± 3.1)
Average number of CP per km		
Year	0.76 (± 0.31)	0.51 (± 0.40)
Summer	0.76 (± 0.31)	1.50 (± 0.38)
Winter	0.76 (± 0.31)	1.54 (± 0.44)
Average distance between CP		
Year	1011 (± 738)	622 (± 730)
Summer	991 (± 731)	618 (± 718)
Winter	1038 (± 747)	628 (± 746)

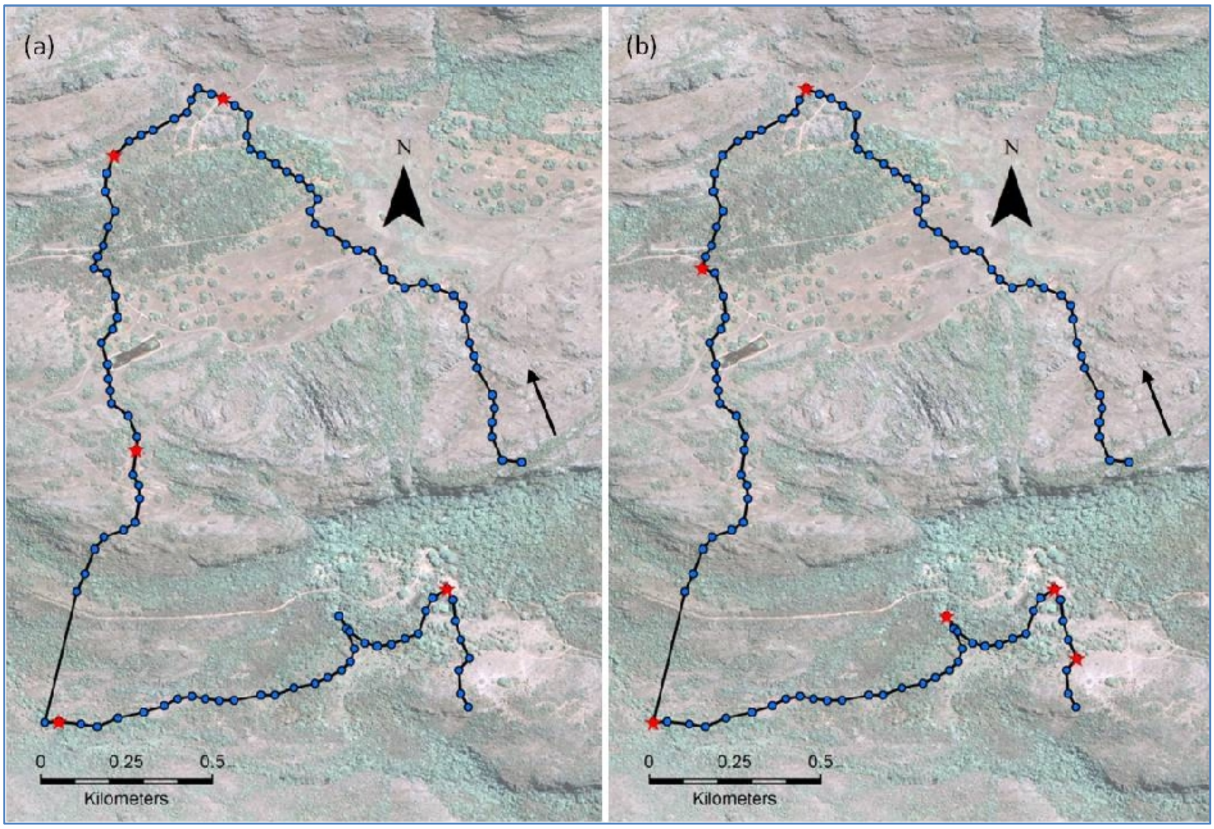

Figure 5.3 Travel route on the 24th of February 2008 (5.73 km) with change-points (*stars*) identified using (a) the CPT and (b) the TA method. The black arrow indicates the travel direction of the baboons.

The TA method resulted in identification of 2106 change-points (868 in summer and 1238 in winter) (Figure 5.4b and Figure 5.4c). On average the TA method identified 9.0 (± 3.8) change-points per day, with significantly more change-points per day in summer 10.9 (± 4.2) than in winter 8.0 (± 3.1) (Mann-Whitney U test Z= -5.340, p<0.001). On average 1.51 (±0.40) change-points were identified per kilometre and the average distance between change-points was 622 ±730m (for winter 618 ±718m and for summer 628 ±746m). The number of change-points identified was positively correlated to the distance travelled in a day (Pearson's correlation: p<0.001, r = 0.756, N=234) (Figure 5.5).

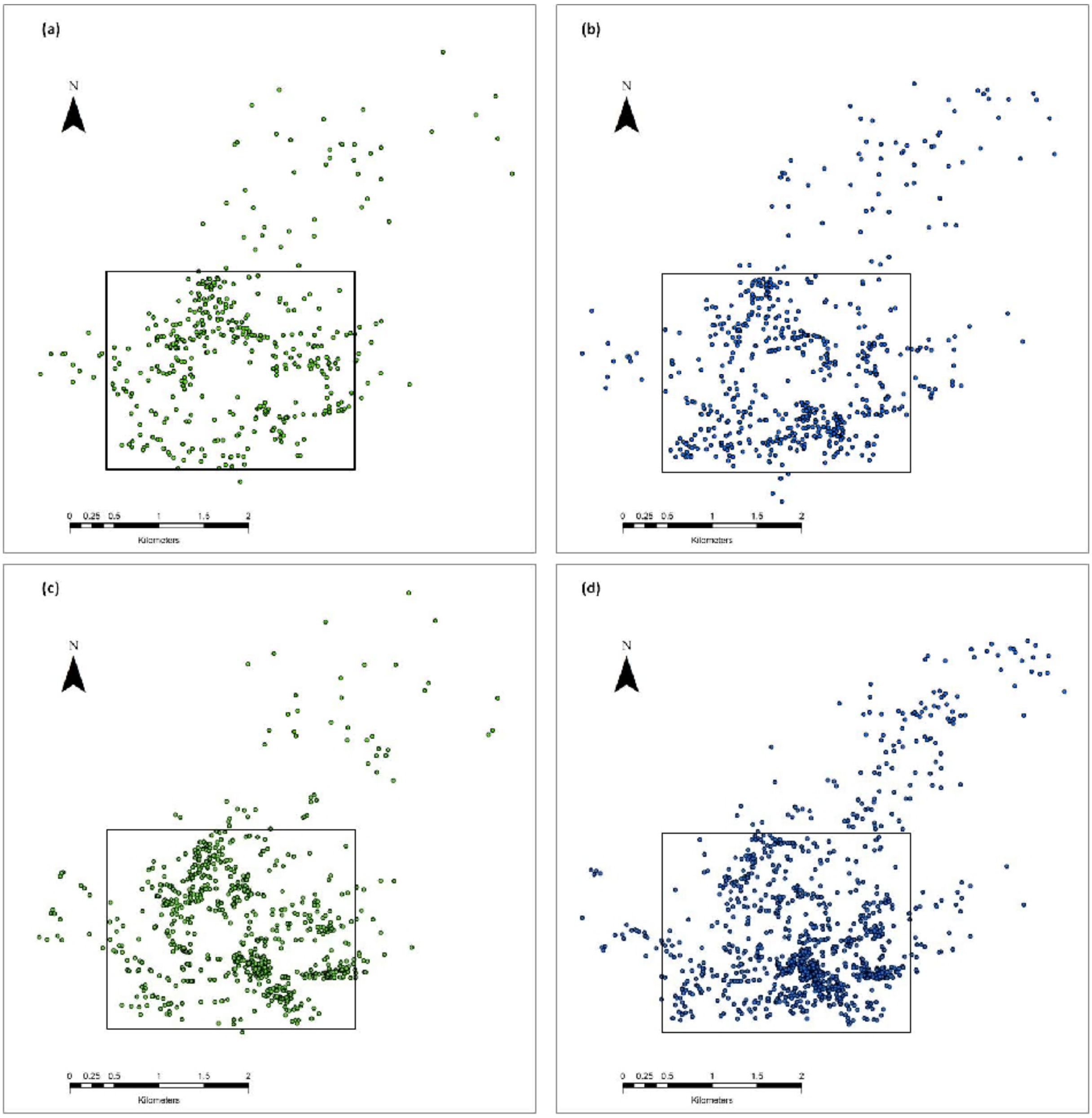

Figure 5.4 Change-points identified using the CPT in (a) summer (N=441) and (b) winter (N=617) and using the TA method in (c) summer (N=820) and (d) winter (N=1286). The square black rectangle represents the area in which clusters of change-points are identified in Chapter 6 (also the extent of Figure 6.2-6.3, Figure 6.5-6.6 and Figure 6.8).

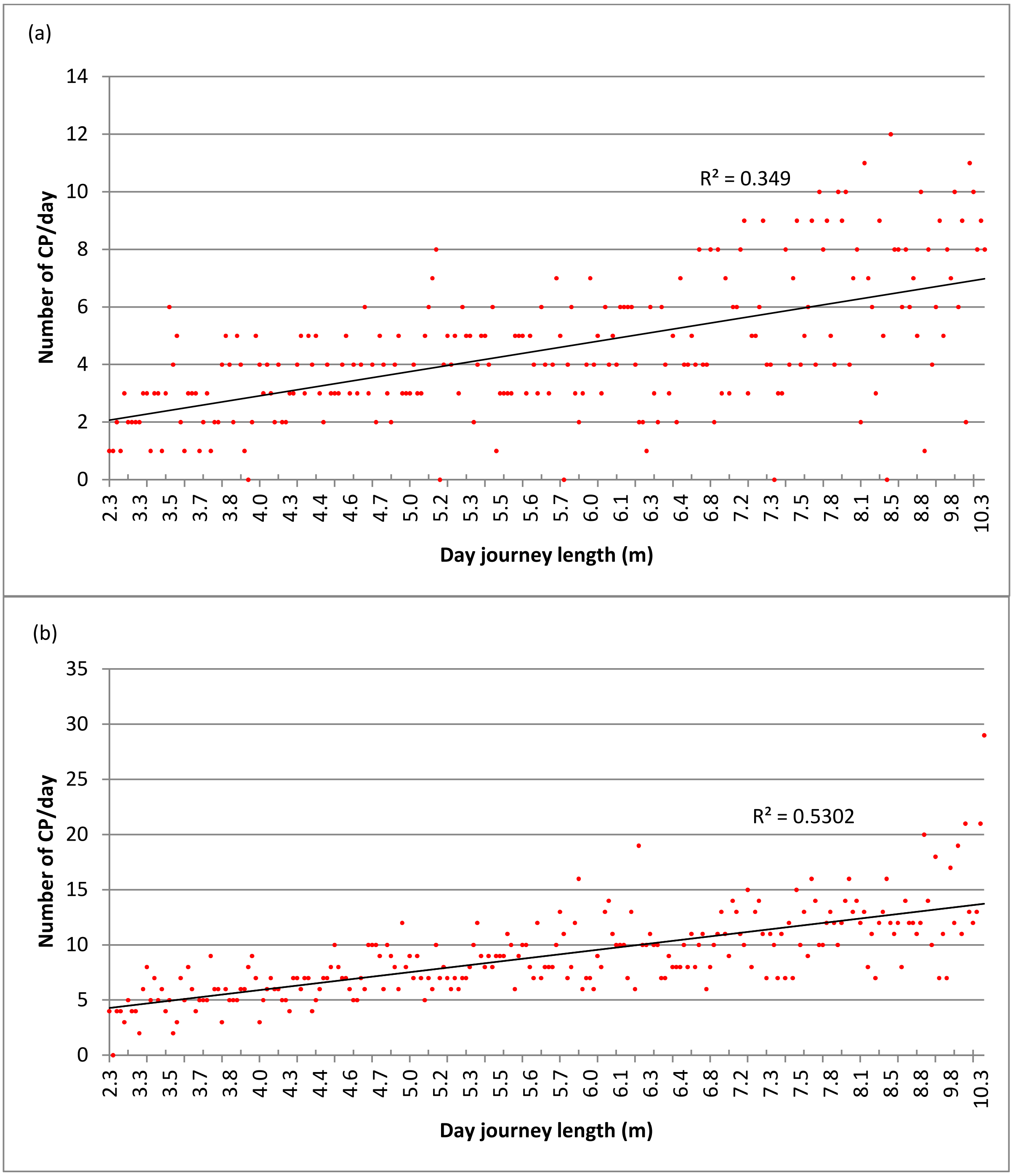

Figure 5.5 Positive linear correlation between numbers of change-points identified per day and day journey length for (a) the CPT and (b) the TA method.

Both the CPT and the TA method identified significantly more change-points in winter than in summer. This is unsurprising, given that entire sample of 234 full-day follows was drawn from an uneven sample of winter and summer months (12 winter months and 7 summer months), resulting in 153 days in winter and 81 days in summer (Chapter 2 Section 2.3.1). This difference in sample size did not however, affect the differences found between winter and summer in the distance baboons travelled per day or in the number of change-points per day identified. This was confirmed when both the distance that baboons travelled per day (km/day) and the number of change-points identified per day (CP/day) were calculated for winter and summer using 1) only data from the first 12-months of the study period and 2) only 81 randomly selected winter days and all 81 summer days. Differences between winter and summer remained significant in both cases.

5.3.2 Change-Point Test versus Turn Angle method

The TA method identified almost twice as many change-points (N=2106) compared to the CPT (N=1058). However, this did not mean that the TA identified the 1058 change-points the CPT identified plus an additional 1048 change-points. When the locations of the identified change-points were investigated further, it showed that only a very small percentage (2.2%) of the total number of change-points identified by the two different methods was found at the same location (Figure 5.6). The CPT has been suggested to indicate significant directional changes a locations or two ahead of the 'true' change-point when using high values of *q* (Byrne *et al.* 2009). Although *q* was set here to a relatively low value of 3 and such events should be thus be minimized, the "overlap" in change-point location between the two methods was also investigated when change-points were identified one or two locations apart. Nonetheless, this still showed an "overlap" in change-point locations of only 11.3% (one location apart) and 12.8% (two locations apart). The small percentages of change-point location overlap indicate that the two methods appear to be measuring different things.

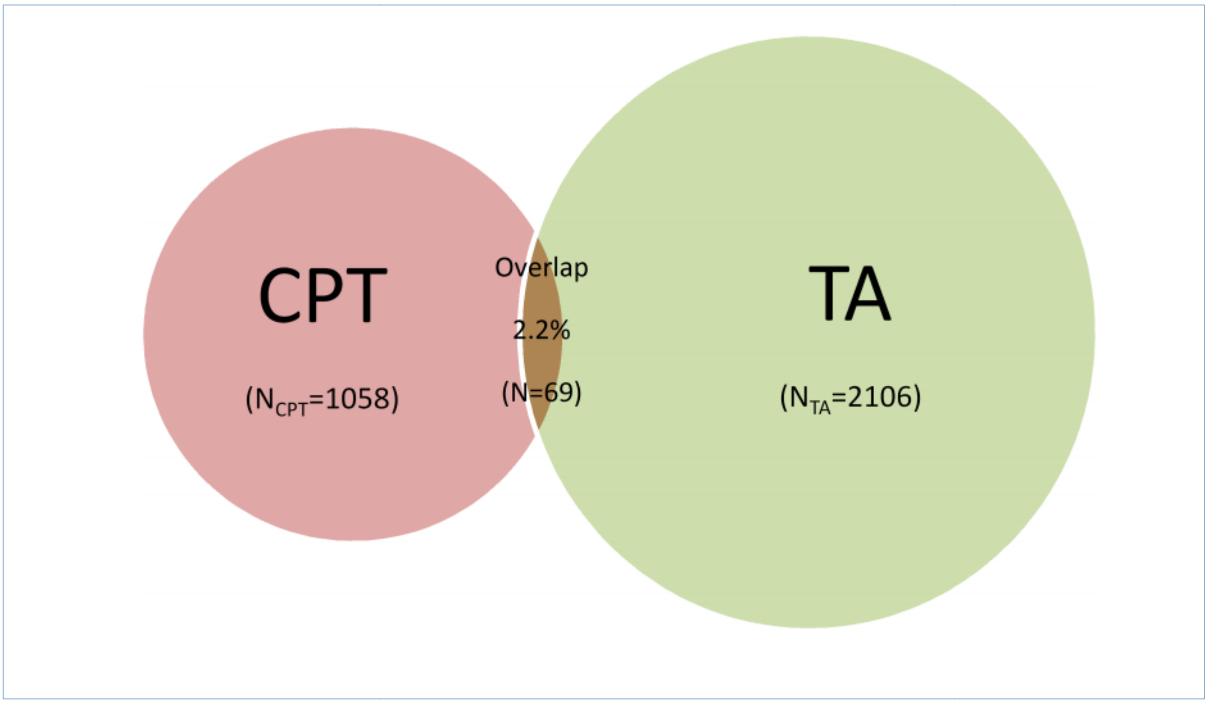

Figure 5.6 Venn diagram illustrates that the overlap in identified change-points for the change-point test (CPT) and the turn angle method (TA) is 2.2%.

To give an explanation as to what the two different methods are then in fact measuring, the way the two methods operate needs to be reconsidered. As described in more detail in the previous chapter, the CPT operates by comparing a set of *k* vectors, describing travel *after* a potential change-point to a set of *q* vectors describing travel *before* the potential change-point, with *q* set to 3 here. The TA method operates by comparing the turn angle at a given location to the daily average turn angle ± 2 standard deviation. The CPT thus evaluates changes of direction on a larger scale than the TA method does and therefore is not just identifying locations at which directional changes occur at one given point in time. In other words, the CPT seems to be identifying locations where an animal starts orienting towards a new goal, whereas the TA method identifies turn angles greater than threshold angle.

In practise this means that the TA method is predisposed to (1) not identify change-points at locations where baboons started orienting in a new direction when this is done with a relative wide turn and (2) identify change-points at locations where the baboons made sharp, back-and-forth changes of direction at small scale, even though they maintain the same overall orientation when looking at a larger scale. These two tendencies, which are inherent to the TA method, are illustrated in Figure 5.7 where location 1.1 and location 1.2 are points at which change-points have been identified by the CPT because the baboons have started orienting towards a new goal, but the locations are not identified as change-points by the TA method, since the baboons’ have turned gradually and no one single turn angle exceeds the threshold. In contrast, locations 2.1 and 2.2 (Figure 5.7) show examples where the TA method identifies change-points where the travel route has single sharp turn angles exceeding the threshold, but the general route orientation does not change. This is also illustrated by the change-points identified by the TA method situated between CP-overlap-1 and CP-overlap-2 and between CP-overlap-2 and location 1.2 (Figure 5.7).

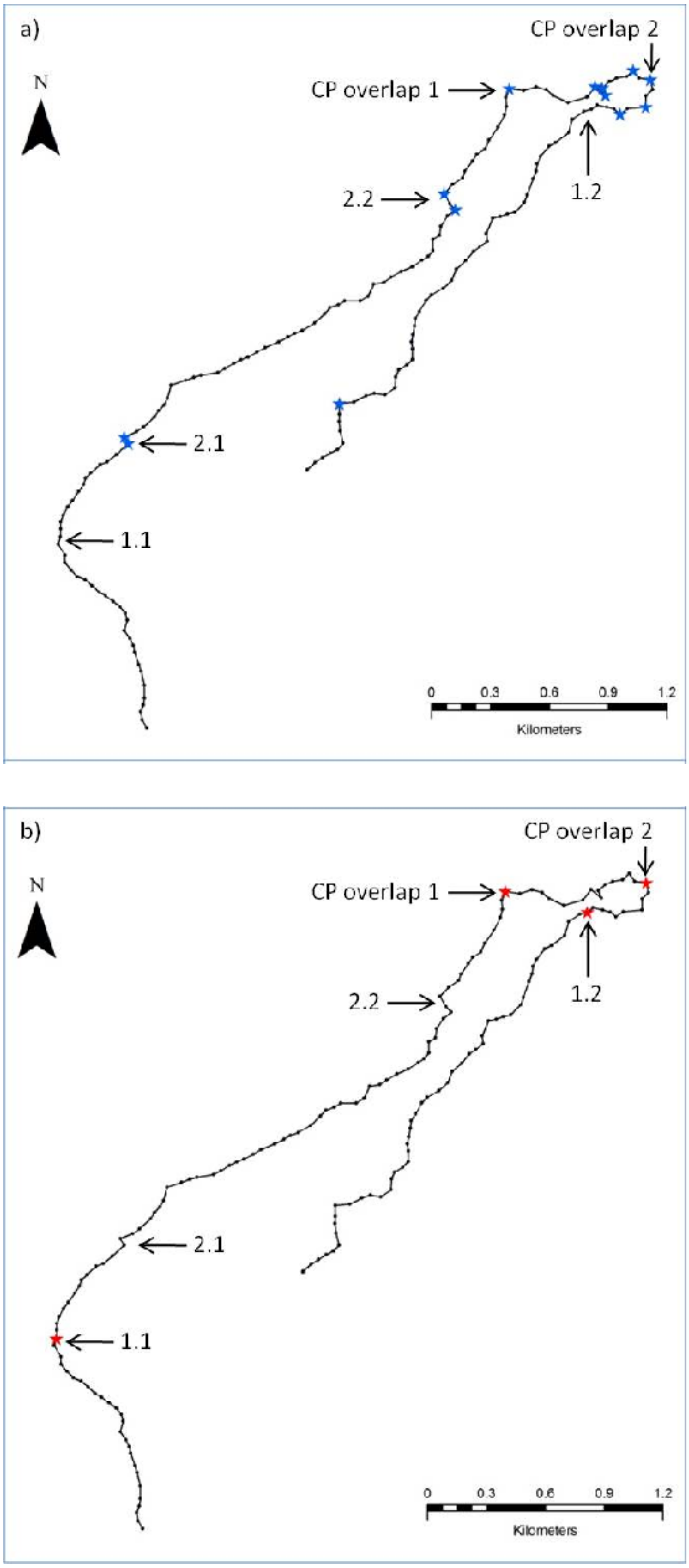

Figure 5.7 The baboons' travel route on the 19th of June 2008 with (a) 13 change-points identified by the TA method represented by blue stars and (b) 4 change-points identified by the CPT represented by red stars (with 2 overlapping change-point [CP] locations). The TA method fails to identify change-points when baboons start orienting in a new direction when this is done gradually and no single turn angle exceeds the threshold (location 1.1 and 1.2), whilst the TA method does identify change-points at locations where general route orientation does not change, but the travel route has single sharp turn angles (for example location 2.1 and 2.2, but also the change-points between CP overlap 1 and CP overlap2 and between CP overlap 2 and location 1.2).

5.4 Discussion

The aim of this chapter was to examine the utility of the TA method and the CPT in identifying locations at which animals start orienting towards a new goal, which was promoted as a routine first step in interpreting the decision making behind animal travel (Byrne *et al.* 2009). Despite the challenges in selecting the appropriate parameter values and sampling interval associated with the CPT (see Chapter 4 for more details) and the tendency of the CPT to indicate significant directional changes one or two locations or two ahead of the ‘true’ change-points when using high values of *q*, the CPT is considered a more suitable method for studying spatial cognition and spatial representation (the goal of this thesis), than the TA method. The CPT examines changes of direction on a larger scale than the TA method and therewith successfully identified locations at which the baboons started orienting towards a new goal in the vast majority of the data, whereas the TA method identified locations at one given point in time at which turn angles were greater than the daily threshold turn angle. As such, the TA method did not identify change-points at locations where baboons started orienting in a new direction when this was done with a relative wide turn and it wrongly identified change-points at locations where sharp, back-and-forth changes of direction at small scale were made, even though the same overall orientation was maintained at a larger scale. For this reason the TA method was considered inappropriate to identify locations at which animals start orienting towards a next goal and therewith to determine locations where travel decisions are being made, whereas the utility of the CPT to do so was confirmed.

The approach used by Normand & Boesch (*submitted*), may thus have identified some locations as decision-points where their study animals made sharp, back-and-forth changes of direction at small scale, even though they maintained the same overall orientation at a larger scale. However, since they excluded travel where two decision points were visited in succession from their analysis (Normand & Boesch *submitted*), it is likely that this will have excluded such small scale directional changes. Although the TA method in this chapter did not identify change-points at locations when baboons started orienting towards a new goal in a relative wide turn, this may have been less of a concern in the study of Normand & Boesch (*submitted*), since they identified decision-points when the deviation angle was superior to the daily mean plus one standard deviation, instead of two, thus using a lower the threshold compared to the TA method. Moreover, since linear statistics were used to analyse deviation angles between 0° and 180°, the threshold for when resource locations were identified as decision-points was lower still (see discussion above on circular versus linear statistics). Finally, the approach used by Normand & Boesch (*submitted*) differed mostly from the TA method in that their identification of potential ‘decision-points’ was limited to food resource locations. Their results showed that the deviation angle was mainly influenced by the time spent eating a resource, indicating that the decision points represent major resources and furthermore, that their study animals showed goal-directed travel towards decision-points (Normand & Boesch *submitted*). It thus seems that under certain conditions (*i.e*., limiting analysis to travel between food resources, excluding consecutive decision-points and handling a one standard deviation criterion) a method that analyses travel 'one step at a time', is able to identify locations at which animals start orienting towards a new goal and as such, where travel decisions are being made.

In the following chapters the spatial representation of baboons is further investigated using the results of the CPT method. In Chapter 6, the utility of the CPT is extended with a novel application of *CrimeStat* software, to provide the first quantitative analysis of the spatial distribution of change-points by identifying clusters of change-points where animals repeatedly change direction on multiple travel days through hotspot analysis. Delimiting such 'decision hotspots' has the potential to greatly enhance the understanding of cognitive maps in animals, whilst simultaneously identifying precise locations to focus behavioural research on the processes of collective decision-making in groups. In Chapter 7 movement patterns to and from travel goals, as identified by the CPT, are investigated.

CHAPTER 6

DECISION HOTSPOTS

6.1 Introduction

Determining when and where travel decisions are made is essential for studying decision making and spatial cognition (Normand & Boesch 2009; Noser & Byrne 2007a, 2007b; Byrne *et al.* 2009). Recently, locations where travel decisions are made have been suggested to be those at which a travelling animal or group of animals significantly changes travel direction and as such, starts orienting towards the next goal (Byrne *et al.* 2009). The change-point test (CPT) was proposed as a robust statistical method for determining such locations, referred to as change-points, independent of the possible reasons for the change of direction, such as the animal's behaviour, or any resources to which the travel led (Byrne *et al.* 2009).

In Chapter 4 the background of the CPT was discussed and an extensive sensitivity test was conducted to determine the optimal parameter values to be used in the CPT. Subsequently, the CPT was successfully applied to 234 baboon travel routes to identify change-points in Chapter 5. To further extend the utility of the change-point test (CPT) a quantitative analysis of the spatial distribution of change-points is conducted in this chapter. The aim of this chapter is to identify clusters of change-points where animals repeatedly change direction on multiple travel days using an objective and repeatable method. Delimiting such 'decision hotspots' has the potential to greatly enhance the understanding of cognitive maps in animals, whilst simultaneously identifying precise locations to focus behavioural research on the processes of collective decision-making in groups (King & Sueur 2011).

6.2 Methodology

6.2.1 Change-Points

Locational data were recorded as described in Chapter 2 (Section 2.3.1). The CPT was applied to 234 full-day travel routes as described in Chapter 5 (Section 5.2.2). This resulted in the identification of 1058 change-points (441 in summer and 617 in winter) with significantly more change-points per day in summer (5.5 ±2.4) than in winter (4.1 ±1.9) (Mann-Whitney U test Z= -4.314, p<0.001) (Chapter 5 Section 5.3.1). Due to these seasonal differences the change-point data set was analysed as a whole (CPT year), as well as for the summer (CPT summer) and winter (CPT winter) season separately.

6.2.2 Nearest Neighbour Index

To investigate whether change-points were located closer together than expected due to chance, the change-point data set was imported into *CrimeStat* III (update version 3.2a) (Levine 2009) and analysed for spatial clustering using a nearest neighbour analysis. The nearest neighbour index (NNI) (Clark & Evans 1954) compares the average distance from the closest neighbour to each point with a distance that would be expected on the basis of chance, as shown by Equation 1 below where Min (d_{ij}) is the distance between each point and its nearest neighbour, N is the number of points in the distribution and A is the area of the region in which the points are distributed. If the observed average distance is smaller than the mean random distance, that is, points are actually closer together than would be expected on the basis of chance, then the nearest neighbour index will be less than 1.0 and is evidence for clustering. Conversely, if the observed average distance is greater than the mean random distance then the index will be greater than 1.0 and is evidence for dispersion. The significance of the NNI is tested using a Z-test (Equation 2) derived from Levine (2009).

Equation 1

$$\boldsymbol{NNI = \frac{d\,(NN)}{d\,(ran)} = \frac{\sum_{i=1}^{N}\left|\frac{Min(d_{ij})}{N}\right|}{0.5\sqrt{\left[\frac{A}{N}\right]}}}$$

Equation 2

$$Z = \frac{d\,(NN) - d(ran)}{SE_{d(ran)}} = \frac{d\,(NN) - d(ran)}{\sqrt{\left[\frac{(4-\pi)A}{4\pi N^2}\right]}}$$

It should be noted that the Z-test for the NNI only tests whether the average nearest neighbour distance is significantly different than what would be expected on the basis of chance and it is therefore a test of first-order (first nearest neighbour) spatial randomness, not a test for complete spatial randomness. There are also second-order (second nearest neighbour), third-order (third nearest neighbour), up to the K_{th}-order (K_{th} nearest neighbour) that may or may not be significantly different from their corresponding orders under complete spatial randomness. Therefore the K-order nearest neighbour routine was performed, including up to the 100th nearest neighbour to investigate overall spatial distribution. There is not a good significance test for the K_{th} nearest neighbour index due to the non-independence of the different orders and consequently *CrimeStat* does not provide a test of significance (Levine 2009). When graphed the K-order nearest neighbour index is nevertheless very useful for understanding the overall spatial distribution and gives a picture whether the distribution is clustered or not (Levine 2009).

6.2.3 Selection of decision hotspot identification technique

Any variable that is measured, here the density of change-points, will be continuous over an area, being higher in some parts and lower in others. Where a line is drawn to define a hotspot remains somewhat arbitrary (Levine 2009). Potential techniques to identify decision hotspots are typically known as *cluster analysis*. These are statistical techniques aimed at grouping "events" (here, locations where baboons orientate towards goals) together into relatively coherent clusters. All of the techniques depend on optimising various statistical criteria, but the techniques differ among themselves in their methodology as well as in the criteria used for identification. Levine (2009) defines seven different clustering techniques, although hybrids between these techniques also exist:

1. *Point locations*. This is the most straight forward type of clustering which involves the number of events at different locations; locations with the most number of events are defined as hotspots.
2. Techniques applied to *zones*, not events, such as *Anselin's Local Moran* technique for identifying neighbourhood discrepancies (Anselin 1995).
3. *Partitioning* techniques, frequently called the K-means technique, partition the incidents into a specified number of groupings, usually defined by the user, so that all points are assigned to one, and only one, group.
4. *Risk-based* techniques identify clusters in relation to an underlying base 'at risk' variable, such as population, employment, or active targets.
5. *Clumping* techniques involve the partitioning of incidents into clusters, but allow overlapping membership.
6. *Hierarchica*l techniques are like an inverted tree diagram in which two or more incidents are first grouped on the basis of some criteria (*e.g.*, nearest neighbour) which can be displayed with a dendogram. Then, the pairs are grouped into second-order clusters, which in turn are grouped into third-order clusters, and this process is repeated until either all events fall into a single cluster or else the grouping criteria fails. Many hierarchical techniques do not group all events or all clusters into the next highest level.
7. *Density* techniques, such as the kernel density, provide density measures for any part of the area by interpolation and subsequently can identify clusters by delimiting a certain percentage volume isopleths.

The aim was to identify hotspot *areas* of high densities of change-points, not to identify single locations in space, and for this reason point locations techniques were not useful here. Also, the baboon change-point data set was not divided into zones (*e.g.*, data sets can for instance be divided into postal codes or provinces) and so techniques using *zones* instead of *events* were not appropriate either. In addition, not *every* change-point had to fall within an identified cluster, and so partitioning techniques, which divide an entire data-set into a pre-defined number of clusters, were not considered relevant for identifying hotspots. Risk-based techniques control for the density of data points by dynamically adjusting the threshold distance according to the distribution of a second, baseline variable, which can be very useful for other types data (*e.g.*, when analyzing crime events, more crimes can be expected in densely populated areas and a risk-based technique can then be used to investigate the number of crimes relative to the population density), but for the data set analysed in this chapter there was no second variable to control for, which ruled out the use of risk-based techniques. One of the conditions for identifying decision hotspots was that each change-point could only fall into *one* hotspot. This further ruled out the use of any clumping techniques, which allow the same event to fall within several clusters.

This has left the potential use of hierarchical techniques and density techniques to identify decision hotspots for the change-point data set. To test the suitability of these techniques, a kernel density, a simple density surface and the nearest neighbour hierarchical clustering technique (Nnh) (see section 6.2.4 below for further explanation on the Nnh) were applied to the CPT winter change-point data set (N=617) and resulting decision hotspots identified by the different techniques were compared. The kernel function was based on the quadratic kernel function described in Silverman (1986, p. 76, equation 4.5) and both the kernel function as the density surface were created using default settings in ESRI® ArcMap™ 9.3 and decision hotspots were delineated by 5%, 10%, 25% and 50% volume contours to allow comparison with the Nnh technique. The Nnh technique was applied with a default, pre-defined minimum number of change-points per hotspot of 10 and a confidence interval p=0.001 using *CrimeStat* (Levine 2009).

6.2.4 Neighbour Hierarchical Clustering (Nnh)

In the Nnh routine, the user has to define three parameters – 1) the threshold distance, which can be set to a pre-determined fixed distance or to the expected random nearest neighbour distance for first order nearest neighbours, 2) the minimum number of points to be included in a cluster (default of 10) and 3) the one-tailed confidence interval around the random expected nearest neighbour distance needs to be specified when this option is selected over the pre-determined fixed distance. The t-value corresponding to this probability level (*t*) is selected from the Student's t-distribution under the assumption that the degrees of freedom are at least 120.

When the expected random nearest neighbour distance is used as the threshold distance criterion, the size of the decision hotspot is dependent on the sample size. This means that for a data set with many change-points, the threshold distance will be a lot smaller than a data set that has a lower number of change-points. In theory, hotspot size is dependent on an environment, not the number of 'incidents' and so this approach does not quite produce a consistent definition of a hotspot area. Using a fixed distance for the threshold distance could overcome this, but one of the main aims was to reduce the number of user defined parameters to keep the method as objective as possible, and so the threshold distance was kept to the default choice of using the expected random nearest neighbour distance.

Which exact parameter values (*i.e.*, level of confidence interval and minimum number of points to be included in a cluster) are appropriate will depend on the goal of the analysis. One of the goals of this chapter was to identify a number of decision hotspots of a size that would prove useful for focusing behavioural research to specific locations to further study of the processes of decision-making and give insight to animal spatial cognition. With this goal in mind several different values of one-tailed confidence intervals and minimum numbers of change-points to be included into a cluster were reviewed.

Testing the significance of the identified decision hotspots from the Nnh is difficult, since the specified confidence interval defines a probability for the distance between any *two points* on the basis of a chance distribution, not the probability of finding a *decision hotspot*. If the probability level is p%, then approximately p% of all pairs of points would be found under a random distribution and it would indicate whether the number of pairs that were found is significantly greater than would be expected by chance. However, the Nnh routine is not to cluster pairs of points, but to cluster as many points as possible that fall within the threshold distance with the pre-defined minimum number of points within a hotspot. To obtain the probability distribution for the settings specified above, confidence intervals were simulated by conducting 1000 Monte Carlo runs of simulation data for each data set under the selected settings of the Nnh test.

The identified decision hotspots can be visualized as a convex hull, a polygon that corresponds exactly to the cluster, or as a 1 SD, 1½ SD or 2 SD ellipse, which is an abstraction that will typically cover more than 50%, 90% and 99% of the cases respectively, although the exact percentage will depend on the distribution. Unless stated otherwise, 1SD ellipses are used to visualize hotspots, although the exact change-points that make up a decision hotspot (*i.e.*, the convex hull) were identified and used for analyses in further chapters.

6.2.5 Hotspot categorisation

To investigate the biological meaning of the decision hotspots, decision hotspots were categorised into resource decision hotspots (RH) or non-resource decision hotspots (N-RH) and for the year data set a third category ‘both’ (B) was used, based on the availability of important resources (Chapter 2 Section 2.3.2) ‘within’ the decision hotspots and the number of change-points that were included in a decision hotspot. Since important resources (IR) were recorded as one single location, important resource waypoints in close proximity of hotspots were investigated to whether they represented discreet resource locations or areas (Chapter 2 Section 2.3.2), and they were considered to fall ‘within’ a decision hotspot if the important resource represented a location and fell ‘within’ the decision hotspot area or if the important resource represented an area and was located within 25 meter of the decision hotspot. Furthermore, the season in which the important resource was available was recorded and each IR was therewith identified as IR sum (summer) or IR win (winter). It was assumed that the important resource was available throughout that season.

For all three data sets (year, summer and winter), if no important resources were present within the decision hotspot in either season (*i.e.*, IR sum and IR win are both 0), the decision hotspot was categorised as a non-resource hotspots (N-RH). Decision hotspots identified for summer and winter separately (based on change-points identified in summer and winter respectively) were categorised either as resource hotspots (RH) or non-resource hotspots (N-RH) based on the availability of important resources within each decision hotspot (for that season). Summer decision hotspots were thus categorised as RH when important resources were available within the decision hotspot in the summer season (*i.e.*, IR sum > 1) and similarly, winter decision hotspots were categorised as RH when important resources were recorded within the decision hotspot in the winter season (*i.e.*, IR win > 1). Furthermore, decision hotspots were identified for the year data set, analysing all 1058 change-points together. For these 'year decision hotspots', a hotspot was categorised as a RH when important resources were available throughout the year (*i.e.*, both summer and winter important resources fell within the decision hotspot: both IR sum and IR win > 0) and hotspots were categorised as N-RH when there were no important resources available in either season. In addition, a third category was used for when important resources were available only in one season, but change-points were identified throughout the year. This category only applied to 'year decision hotspots' and was referred to as 'both' (B).

6.3 Results

6.3.1 *Nearest Neighbour Index*

The nearest neighbour statistics, which are indicators of first-order spatial randomness, are summarized in Table 6.1. The nearest neighbour indices (NNI) for all data sets are well under 1.0 and all the Z values are highly significant (Table 6.1). These results show that change-points in all data sets are more closely located to one another than would be expected on the basis of chance.

Table 6.1 Nearest Neighbour (NN) test statistics (year and for summer and winter separately) including the mean nearest neighbour distance (mean NN), mean random nearest neighbour distance (random NN), first order nearest neighbour index (NNI), test statistic (Z) and the 2-tailed *p* value (p). Data sets were significantly more clustered than would be expected by chance.

Data Set	N	mean NN	random NN	NNI	Z	p
CPT-year	1058	41.36	76.72	0.5392	-28.6765	<0.001
CPT-sum	441	64.66	114.81	0.5632	-17.5496	<0.001
CPT-win	617	53.70	95.78	0.5606	-20.8804	<0.001

Since the nearest neighbour index is only an indicator of first-order spatial randomness, a K-order of spatial randomness was conducted. Figure 6.1 shows the NNI for all change-point data sets up to the 100th order (*i.e.*, the 100th nearest neighbour). The nearest neighbour index scales from 0 (extreme clustering) up to 1 (expected under randomness) and the red straight line at 1.0 thus indicates the expected K-order index. The change-point data sets for the whole year, and for both seasons separately, are much more concentrated than K-order spatial randomness for each change-point identification method and the change-points in winter are more concentrated than summer (Figure 6.1). Although this finding is not independent of sample size, higher sample sizes do not inevitably result in a higher concentration, as illustrated by the NNI year data set which has the largest sample size but the lowest concentration of change-points (Figure 6.1). It is therefore also unlikely that the larger sample of winter months compared to summer months (12 and 7 months respectively) is responsible for the higher concentration of change-points in winter than in summer. The graphs thus reinforce the analyses conducted above and indicate that change-points are indeed more clustered than would be expected under a random distribution.

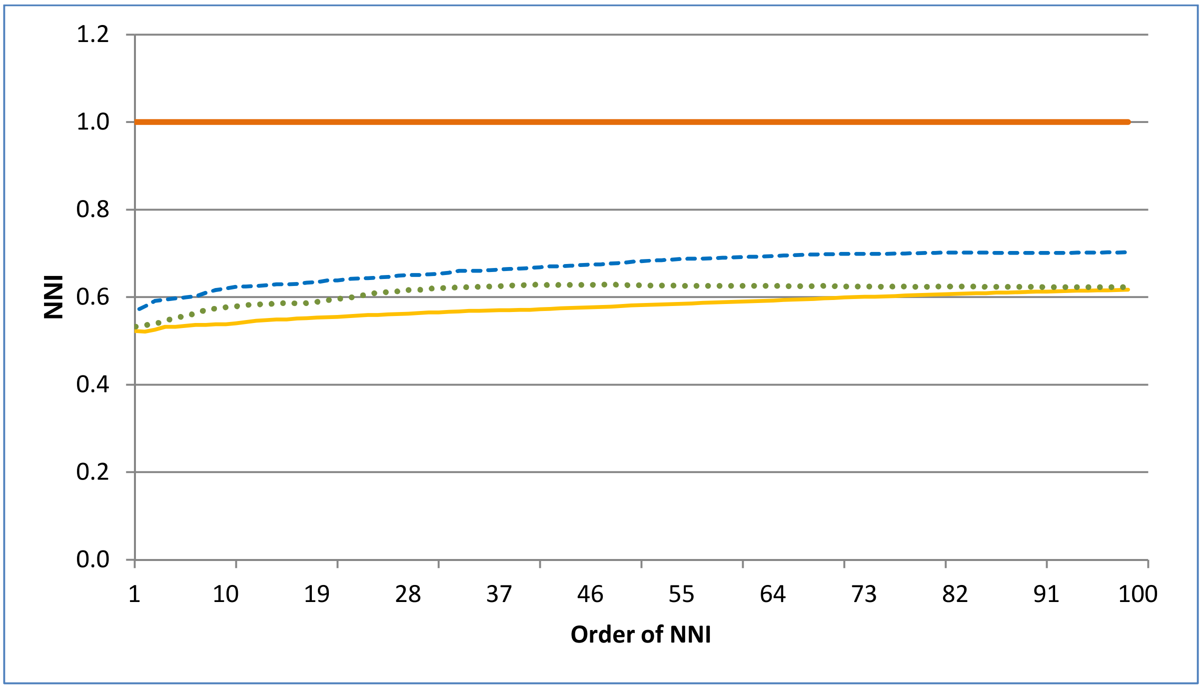

Figure 6.1 The K-Order nearest neighbour indices (NNI) for the year (*continuous orange line*), summer (*dotted green line*) and winter (*blue dashed line*). Under randomness (*i.e.*, no clustering or dispersion) the expected K-order NNI of 1 is expected (*thick red line*). Change-points are more concentrated than K-order randomness for the year, summer and winter.

6.3.2 Selection of decision hotspot identification technique

Decision hotspots identified using the Nearest Neighbour Hierarchical Clustering (Nnh) are visualized by 1 standard deviation ellipses and are superposed on the kernel density output (Figure 6.2a) and the simple density surface (Figure 6.2b). The output of the kernel density (Figure 6.2a) was, as expected, much smoother than of the density surface (Figure 6.2b), and the decision hotspots, delineated by 5%, 10%, 25% and 50% volume contours, were rather more jagged for the density surface than for the kernel density. Despite this clear difference between the output of the kernel density and the density surface, they have in common that decision hotspots are identified at a larger spatial scale, representing large areas, than decision hotspots identified by the Nnh. To compare the techniques at a similar scale, only the 5% or 10% volume contour of the kernel density and simple density surface may be compared to the Nnh output. However when investigating these volume contours, the kernel density and density surface identify 2 and 3 hotspots respectively, missing seemingly highly clustered change-point areas, which are indeed identified as decision hotspots by the Nnh technique, which identified 7 and 5 decision hotspots more than the kernel density and the simple density surface respectively.

The Nnh thus allows for identification of relatively precise decision hotspots and moreover, it seems more accurate in doing so. Furthermore, using the Nnh allow decision hotspots to be strictly delineated, thereby providing a geographical focus for subsequent analyses, which would not be possible using a simple density calculation. Although density estimates may offer alternative insights when studying route-based travel and network maps, which are explored further in Chapter 8, it was decided to use the Nnh technique to identify decision hotspots in this chapter.

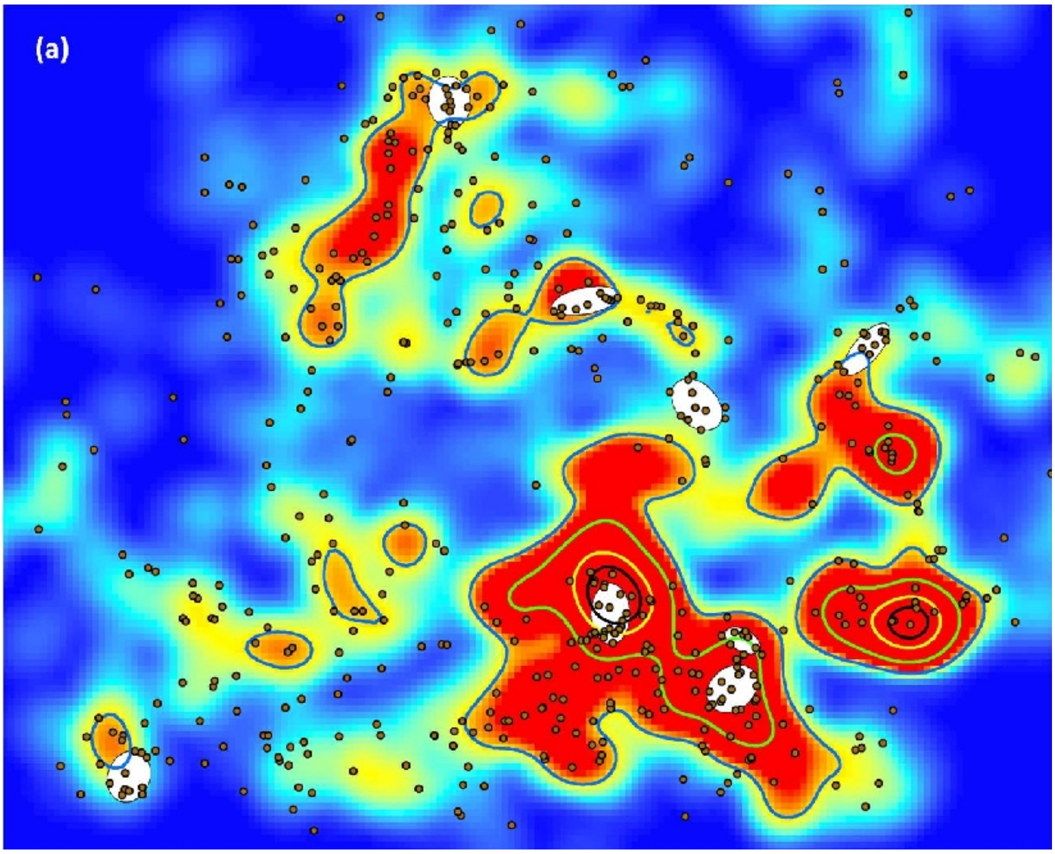

Figure 6.2a See next page for figure legend.

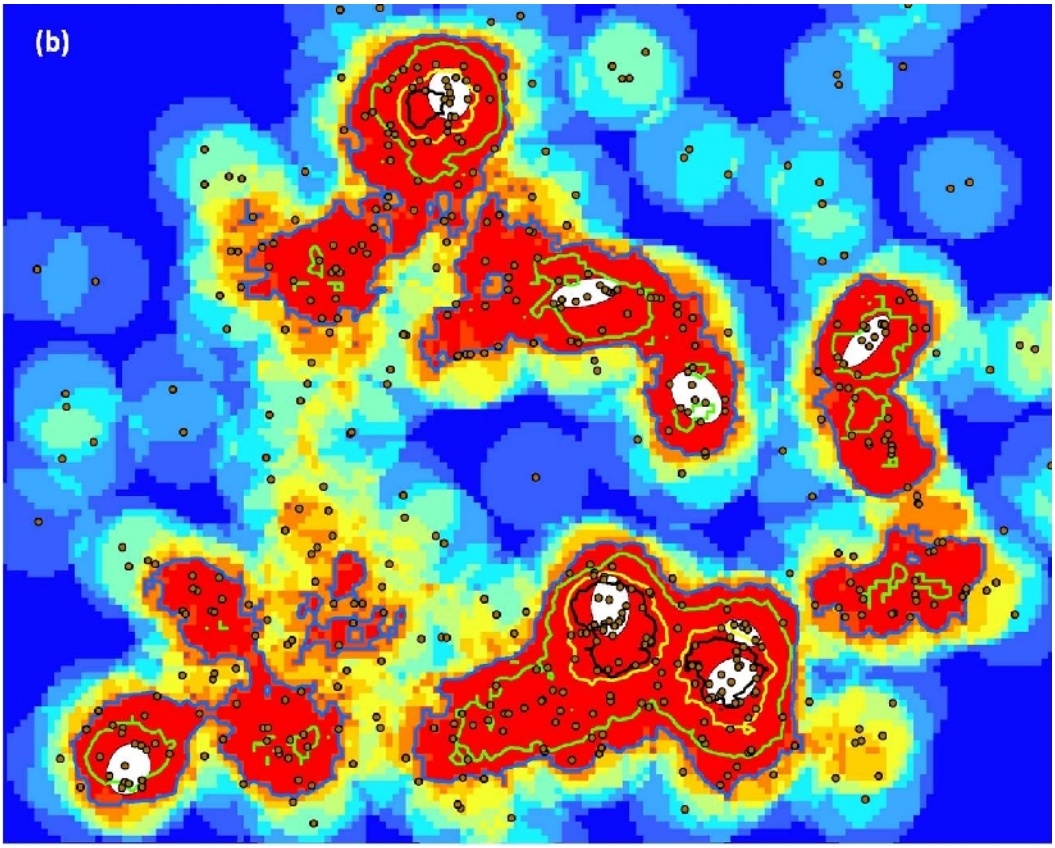

Figure 6.2 (a) Kernel density and (b) density plot derived from the CPT-winter data set (N=617) (*brown dots*). Percent volume contours are shown for 5% (*black contour line*), 10% (yellow contour line), 25% (*green contour line*) and 50% (*blue contour line*). Hotspots identified through hotspot analysis are displayed as 1 standard deviation white ellipses.

6.3.3 Neighbour Hierarchical Clustering setting selection

Several combinations of one-tailed confidence intervals and minimum numbers of change-points to be included into a cluster were reviewed. Since the expected random nearest neighbour distance was used as the threshold distance, hotspot size decreased with increasing sample size even if the other parameters were kept constant. This is illustrated by conducting the Nnh routine under the same settings on the year and summer dataset, selected here only for their difference in sample size (N=1058 and N=441 respectively). The number of change-points per decision hotspot did not differ between the year and summer (Mann-Whitney test: N=9, U=0.800, Z= -0.130, p=0.905), but as expected hotspot size (area) was significantly larger for the summer (N=441) than for the year (N=1058) (Mann-Whitney test: N=9, U<0.001, Z= -2.324, p<0.05) (Table 6.2).

Table 6.2 Decision hotspots were identified for summer and for year using a pre-defined minimum number of change-points to be included into a hotspots of 15 and a confidence interval p=0.01

	summer	year
Sample size	441	1058
Number of hotspots identified	3	6
Mean number of CP within decision hotspots	18.7	20.0
Mean decision hotspot area (ha) (±SD)	1.51 (±0.27)	0.77 (±0.13)

Furthermore, the ‘minimum points’ parameter was found to have a much greater effect on the resulting decision hotspots, much more so on the number of decision hotspots identified than on the size of decision hotspots, than did the confidence level (Table 6.3). To illustrate this, the results of the Nnh, run 15 times on the same CPT-summer change-point data set (N=441) using a minimum number of change-points to be included into decision hotspots of 5, 10 and 15 and five different confidence interval settings (p=0.0001, p=0.001, p=0.01, p=0.05 and p=0.10) are shown in Table 6.3. The number of decision hotspots that is identified decreases when the minimum number of points to be included into each decision hotspot is increased, but the setting of the confidence level seems to have no effect on the number of decision hotspots that is identified. Neither the minimum number of change-points to be included into a decision hotspot or the confidence interval setting had significant effects on the size of the identified decision hotspots (Table 6.3). The ‘minimum points’ parameter thus gives the user an adaptive way to respond to sample size, since by increasing the minimum number of points to be included in a decision hotspot, fewer decision hotspots will be identified.

Table 6.3 The minimum number of change-points defined by the user to be included in hotspots has a much larger effect on the number of hotspots identified than does the selected confidence interval: results of the CPT summer data set (N=441).

Minimum number of CP in decision hotspot	Confidence interval	Number of identified decision hotspots	Average hotspot area (ha)
5	0.0001	22	1.48
5	0.001	22	1.44
5	0.01	23	1.42
5	0.05	23	1.49
5	0.1	23	1.49
10	0.0001	5	1.52
10	0.001	5	1.69
10	0.01	5	1.72
10	0.05	7	1.66
10	0.1	8	1.73
15	0.0001	3	1.49
15	0.001	3	1.51
15	0.01	3	1.51
15	0.05	3	1.54
15	0.1	3	1.58

To control for the effect of different sample sizes (*i.e.*, the different number of change-points in the year, summer and winter data sets) on the number of decision hotspots identified, 3 different minimum points rules (ranging from a minimum of 5 – 20 points to be included in hotspots) were applied to all three data sets using 3 different significance levels (Table 6.4). The number of decision hotspots identified when the minimum number of change-points to be included in a hotspot was set to

5, was considered too high even for the summer dataset that has the lowest sample size (23 hotspots were identified for summer), whereas when the minimum number of change-points to be included in a hotspot was set to 20 the number of decision hotspots identified was considered too low even for the year dataset that has the highest sample size (only 1 to 3 decision hotspots were identified for year, depending on the significance level) (Table 6.4).

For comparison sake the aim was to identify a similar number of decision hotspots for each data set despite their different sample sizes. Therefore, the minimum number of points to be included in a decision hotspot was kept at the default number of 10 for the CPT summer and winter data set and set to 15 for the CPT year data set. Since the one-tailed confidence interval around the random expected nearest neighbour distance was shown to have little effect on the number or size of the decision hotspots identified (Table 6.3), the p value was set to a stringent $p \leq 0.01$ for all data sets. The resulting numbers of decision hotspots that were identified under these selected settings are highlighted in Table 6.4.

Table 6.4 The minimum number of points to be included in hotspots was varied from 5 to 20 using three different significance levels (α). Resulting number of decision hotspots identified for each data set under the final selected settings are highlighted.

	year (N=1058)	summer (N=441)	winter (N=617)
Minimum points in hotspot 20			
α = 0.0001	1	1	1
α = 0.01	1	1	1
α = 0.10	3	1	1
Minimum points in hotspot 15			
α = 0.0001	5	3	3
α = 0.01	6	3	3
α = 0.10	7	3	3
Minimum points in hotspot 10			
α = 0.0001	14	5	7
α = 0.01	13	5	8
α = 0.10	17	8	9
Minimum points in hotspot 5			
α = 0.0001	57	23	30
α = 0.01	57	23	30
α = 0.10	56	23	29

To obtain the probability distribution for these settings, confidence intervals were simulated by conducting 1000 Monte Carlo runs of simulation data for each data set under the selected settings of the Nnh. No clusters were found in any of the 1000 Monte Carlo simulations runs. Had the simulation runs resulted in a certain number of decision hotspots identified, the 95th percentile would have been used to examine them, that is, a one-tailed Type I error of 5% would have been accepted. However, since no decision hotspots were found in the simulation in any of the 1000 runs, the 95th percentile was 0 (*i.e.*, at most zero of the decision hotspots would have been expected due to chance). It is therefore highly unlikely that the decision hotspots that were identified for the three data sets were due to chance and therefore the change-point data are considered to be significantly clustered and the identified decision hotspots is considered significant and were not identified due to chance.

6.3.4 Identifying Decision Hotspots

Using the selected Nnh settings (Section 6.3.3) the routine identified 5 to 8 decision hotspots for the different data sets (Table 6.4). More decision hotspots were identified in winter than in summer (Table 6.5), which was expected due to higher clustering of change-points and larger sample size in winter than in summer (Figure 6.1 and Section 6.3.3 respectively).

Table 6.5 Number of decision hotspots identified using the Nnh and the range, average and standard deviation of the number of change-points included in each hotspot for each data set.

Data set	Number of hotspots	Range: CP/hotspot	Average (±SD): CP/hotspot
CPT-year	6	16-29	20.0 (± 5.0)
CPT-sum	5	12-21	16.0 (± 4.1)
CPT-win	8	13-21	14.5 (± 5.0)

All decision hotspots identified in the three different data sets were coded based on their location, resulting in 12 different decision hotspot locations (Table 6.6 and Figure 6.3). Each decision hotspot location could thus hold up to 3 decision hotspots (one for each data set). The number of decision hotspots per decision hotspot location ranged from 1 to 3, with decision hotspot locations FS-P and P1 having 3 decision hotspots identified (*i.e.*, a decision hotspot was identified at location FS-P and P1 (Figure 6.3) for the year, summer and winter season). These highly important decision hotspot locations are highlighted in Figure 6.3 by their red colour. The "intensity of use" for all 25 decision hotspot locations is shown in Table 6.6 and gives some notion of the importance of a decision hotspot location.

Table 6.6 Decision hotspot locations (N=12) were coded and the number of datasets (maximum 3) in which the location was identified as decision hotspot is shown.

Decision hotspot location code	Datasets
A	1
B	2
C	1
FS-P	3
H1	1
H-J	2
K1	1
P1	3
P2	1
P3	1
P4	1
P5	2

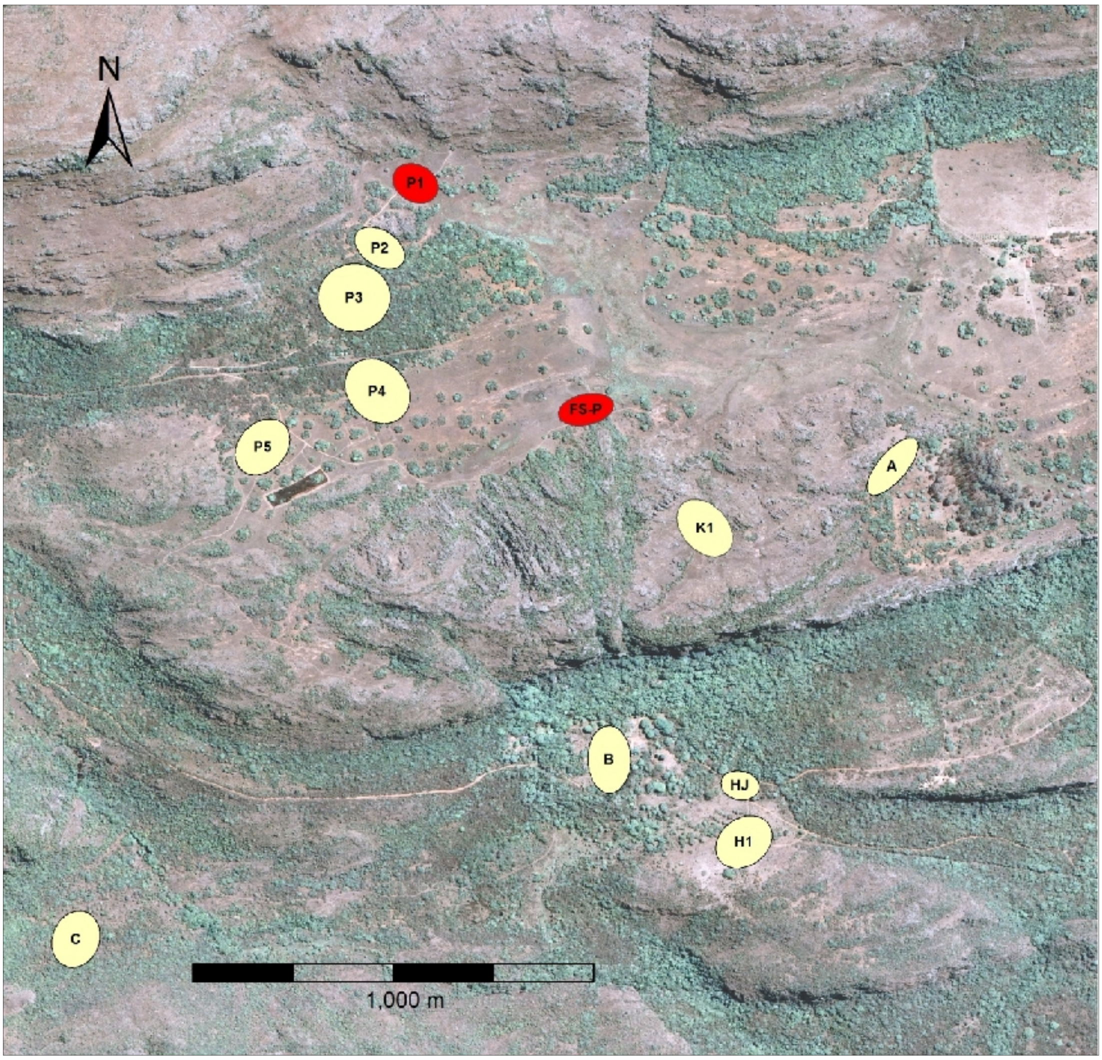

Figure 6.3 In total 12 decision hotspot locations (*ellipses*) were identified across the 6 different data sets. The two decision hotspot locations that were identified in all 3 datasets (year, summer and winter) are highlighted (*red ellipses*).

6.3.5 Categorising Decision Hotspots

Table 6.7 shows the number of food and water resources that were recorded during the study period. Clusters of important resources were identified using the same technique as for identifying decision hotspots. The Nearest Neighbour Hierarchical cluster method was applied using a minimum of 5 IR per cluster and a confidence interval of 0.01. The distribution of important resources and the identified clusters of important resources throughout the study area are shown in Figure 6.4.

Table 6.7 Resources analysed to categorise hotspots.

	Summer	Winter	Year
Food	134	86	220
Water	5	39	44
Total	139	125	264

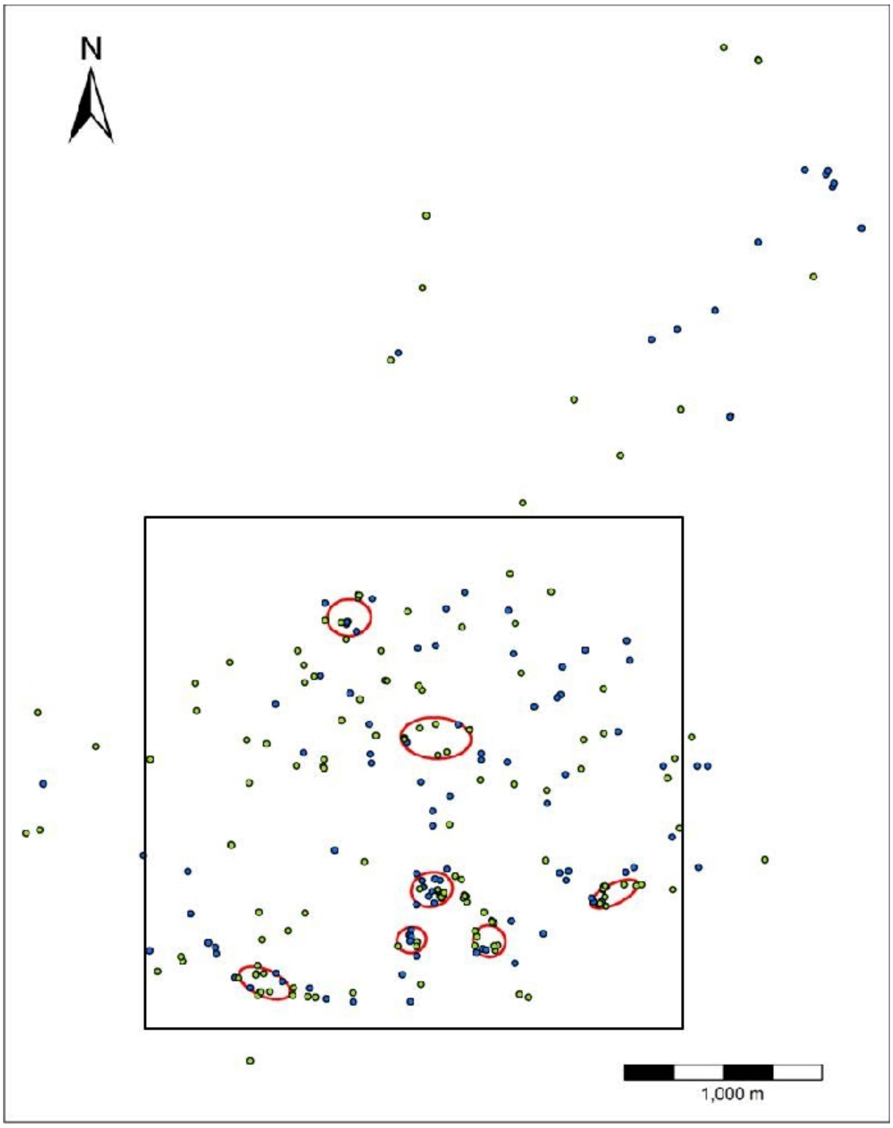

Figure 6.4 Food and water resources (N=264) available in summer (*green dots*) and winter (*blue dots*) recorded throughout the study area. Clusters of resources were identified (*red ellipses*). The square box represents the area in which decision hotspots were identified (*i.e.*, the extent of Figure 6.3).

The data used to categorise decision hotspots are presented below in Table 6.8 including the number of important resources overlapping with the hotspot and the number of change-points incorporated in decision hotspots. The category assigned to each decision hotspot can be found in the last column of Table 6.8 and these results are further illustrated for each season separately by Figure 6.5a-c.

Table 6.8 Decision hotspot categories assigned to each decision. The location of the decision hotspot (see also Figure 6.3) is presented in the second column (Location), in the third and fourth column the number of important resources overlapping with the hotspot can be found for winter (IR win) and summer (IR sum) respectively, and in the fifth and sixth column the number of change-points included in each decision hotspot are shown for winter (CP win) and summer (CP sum) respectively. Finally, the decision hotspot category (Category) assigned to the decision hotspot based on this information is presented in the last column (resource hotspot: RH, non-resource hotspot: N-RH or both: B).

Data set	Location	IR win	IR sum	CP win	CP sum	Category
year	P1	3	0	13	16	B
year	P2	0	0	7	9	N-RH
year	P5	0	1	3	16	B
year	FS-P	0	2	9	8	B
year	H-J	0	0	15	5	N-RH
year	B	4	3	18	2	RH
summer	P1	3	0	0	21	N-RH
summer	P3	0	1	0	12	RH
summer	P4	0	1	0	12	RH
summer	P5	0	1	0	19	RH
summer	FS-P	0	1	0	16	RH
winter	P1	4	0	19	0	RH
winter	FS-P	0	2	12	0	N-RH
winter	K1	0	1	11	0	N-RH
winter	A	0	0	11	0	N-RH
winter	B	6	8	23	0	RH
winter	H1	0	1	19	0	N-RH
winter	H-J	0	0	10	0	N-RH
winter	C	0	0	11	0	N-RH

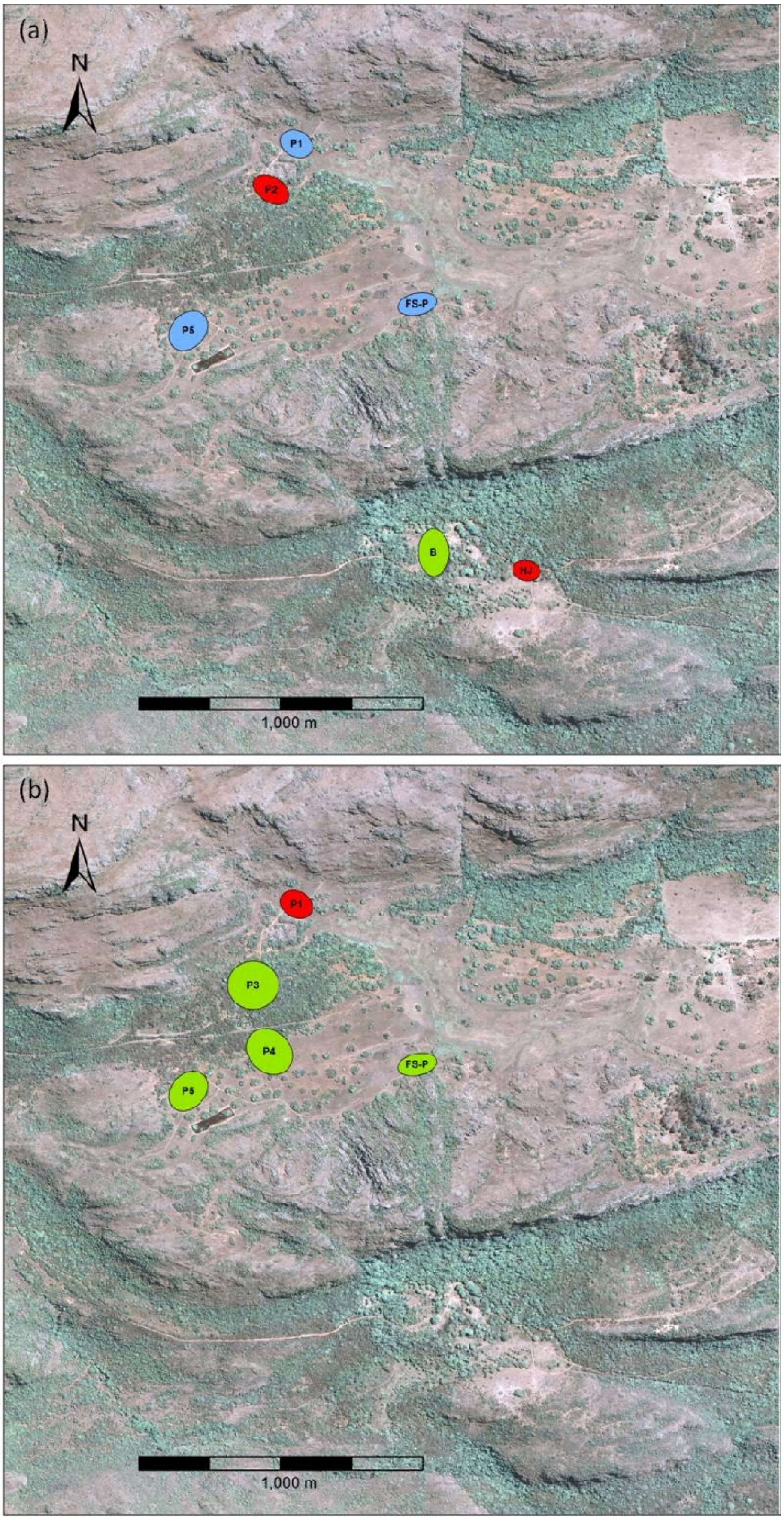

Figure 6.5 a-b See next page for figure legend.

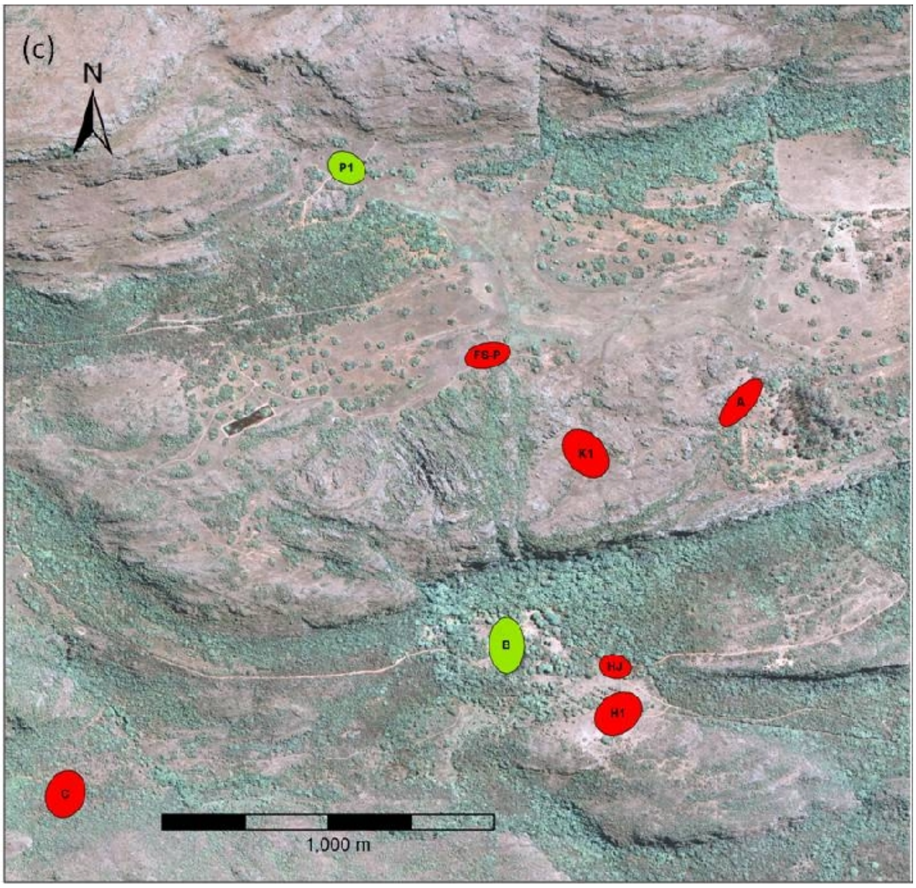

Figure 6.5 Decision hotspots identified for (a) the year data set, (b) summer data set and (c) winter data set, were categorised into resource hotspots [RH] (*green ellipses*), non-resource hotspots [N-RH] (*red ellipses*) or both [B] (*blue ellipses*). Location codes are presented for each decision hotspot.

6.3.6 Interpretation

In summer more resource hotspots were identified than non-resource hotspots, whereas the opposite is true in winter when more non-resource hotspots than resource hotspots were identified (Table 6.9). This is consistent with the fact that more important food resources were recorded in summer (N=134) than in winter (N=86) and that more tree species produce flowers and fruits in summer (N=117) than in winter (N=84) providing a potential food source for baboons (Appendix III). However, since important resources included food and water resources but additional resources such as resting locations and sleeping sites were not considered in this thesis (Chapter 2 Section 2.3.2), non-resource hotspots may in fact contain resources which remain to be identified.

Table 6.9 Number of different categories of decision hotspots identified for each data set: resource decision hotspots (RH), non-resource decision hotspots (N-RH) and both decision hotspots (B), and the total number of decision hotspots (Total) identified in each data set and in each category.

Data set	RH	N-RH	B	Total
year	1	2	3	6
summer	4	1	0	5
winter	2	6	0	8
total	7	9	3	19

Half of the identified resource decision hotspots (P1, FS-P and B) coincide with locations at which important resources were significantly clustered (Figure 6.6). However, decision hotspots were also identified at locations where important resources were, although present, not significantly clustered (P3, P4 and P5). The important resources that were present at these locations represented an *area* rather than one single location (see Section 6.2.3) with for example the highly preferred wild apricot (*Dovyalis zeyheri*) at location P5 and several acacia trees (*Acacia ataxacantha*, *Acacia karroo* and *Acacia sieberiana*) at locations P3 and P4. For example, many acacia trees (*Acacia karroo*) grow in the area surrounding location P3, which all produce pods around the same time of the year (Dec-Jan). However, there would usually only be a few baboons feeding per tree and as such, not one single acacia tree would be recorded as an important resource (in contrast to, for instance, a large fig tree on which half the troop may feed at the same time). Instead, the area as a whole would be recorded as an important resource. It was more difficult to determine whether such an area should be recorded as an important resource, since it was difficult to determine the total number of individuals feeding and the duration of feeding bouts due to large troop spread and generally low visibility. More importantly, when such areas were recorded as an important resource, it was difficult to accurately determine the 'centre' at which to record the important resource and as such, recordings are more dispersed. As a result, important resources that were distributed over larger areas were recorded less systematically as would have been the case for discrete resources (*e.g.*, a water point or a large fig tree: *Ficus burkei*), which may account for the lack of identification of important resource clusters at these locations. In conclusion it seems that resource decision hotspots indicate locations where important resources are significantly clustered, but also locations where important resources are more widely dispersed.

Furthermore, baboons spent significantly more time at change-points that fell within resource hotspots than they did at change-points that fell outside resource hotspots (T-test: df=90277, t= -2.250, p<0.05). The principle of 'time = value' is an objective one, despite the fact that there may be some resources which are nutritionally important but do not take much time to process or cause delays to travel (Valero & Byrne 2007). As such, the hotspot analysis thus seems to provide an assessment of resource value, independent of the animals' behaviour, where resulting resource hotspots represent highly valuable resources.

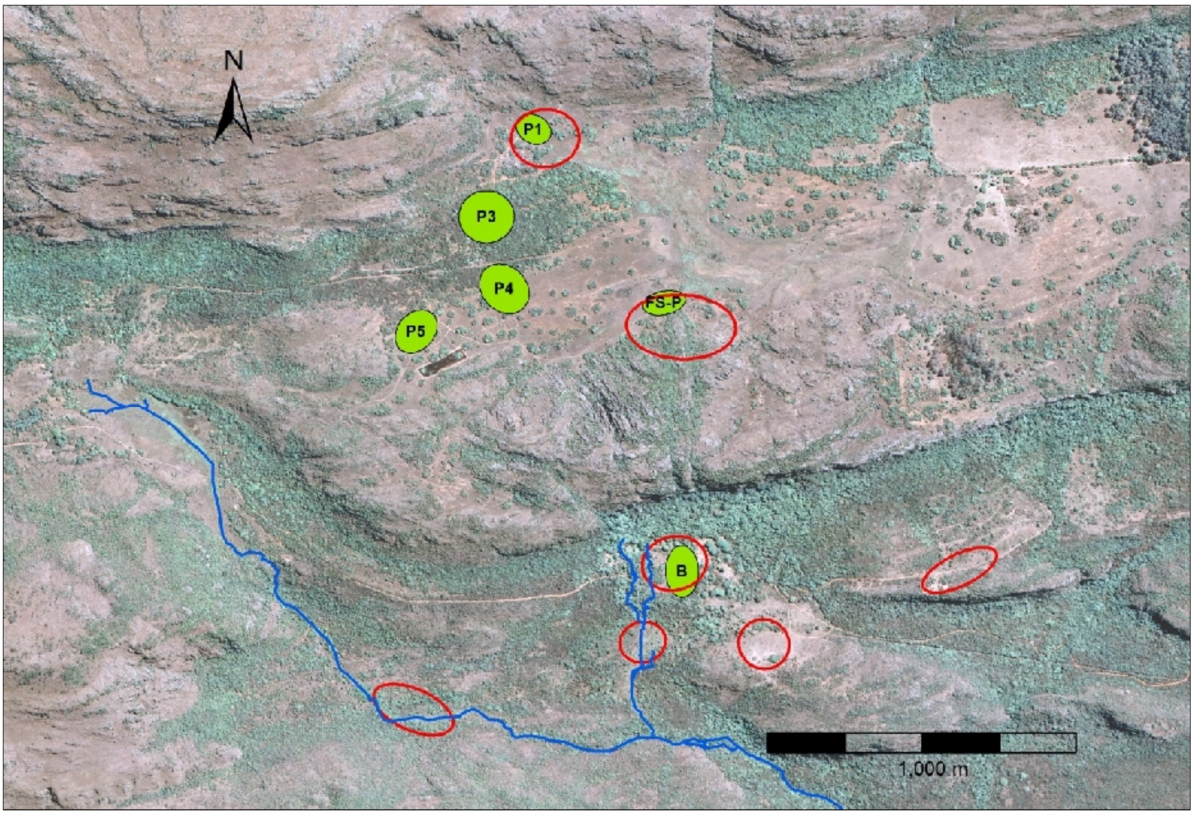

Figure 6.6 Resource hotspots (*green ellipses*) and clusters of important resources (*red outlined*) and water source (*blue line*) running through the study area.

Since some change-points may have been identified due to topological constraints (Byrne *et al*. 2009), it was expected that non-resource decision hotspots may have consequently been identified near topological features that systematically limit travel (*e.g.*, cliffs). Decision hotspots P1 and P2 (Figure 6.5a-b) were identified as N-RH for the year and summer respectively and both were situated near steep cliffs as illustrated by a 3D image of part of the study area in Figure 6.7a. However, although the cliffs were relatively steep, leading to the highest peak in the Soutpansberg mountain range (Letjume 1745m) they did not seem to restrict baboon travel. Figure 6.7b shows all travel paths recorded throughout the study period and although the majority of the travel paths are found at lower altitudes (*green lines*), many travel paths lead into the higher altitude mountain range behind the decision hotspots (*yellow/orange lines*). This indicates that although steep cliffs were present, these were not experienced as a travel constraint by baboons and therefore topology does not explain the identification of decision hotspots at these two locations.

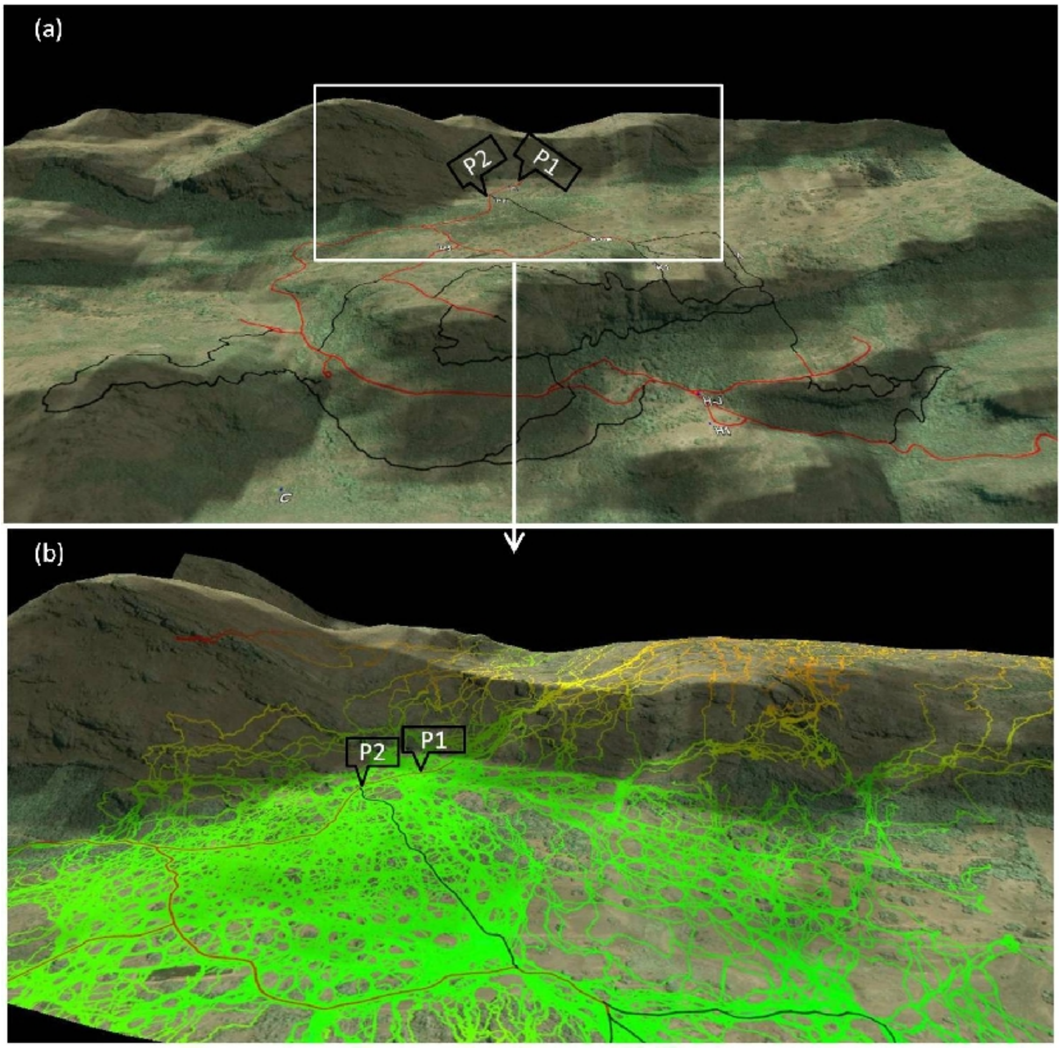

Figure 6.7 (a) Non-resource decision hotspots P1 and P2 were situated at the bottom of steep cliffs, however (b) frequent travel routes (*thin lines* coloured according to altitude: lower altitudes [*green*] to higher altitudes [*red*]) going up and down these cliffs indicate that cliffs are not perceived as a travel constraint.

Instead, the locations of N-RH highly coincided with dirt roads and trails at Lajuma Research Center (Figure 6.8). Although dirt roads in the Lajuma area are man-made, not all of them are used frequently (or at all) by cars nowadays and some sections are severely overgrown. The one-man width trails on the other hand, are all natural game trails. All trails shown in Figure 6.8 (*black dashed lines*) are marked in the field and mapped onto hard-copy maps, to assist people visiting Lajuma Research Center navigate through the Lajuma area and these trails are frequently used. However, there are many other obvious natural game trails crossing through the Lajuma area that intersect with the ‘formal’ (*i.e.*, mapped) trails. Most of the non-resource decision hotspots were identified at junctions in the mapped road/trail network (decision hotspots at locations P1, P2, P5, FS-P, H-J and H1) (Figure 6.8). Although the decision hotspots at locations K1 and A were located on the network, they were not located specifically near junctions. However, at these two locations other natural game trails merged with the mapped trail network, which is likely to account for their identification at these locations.

Only one non-resource decision hotspot was identified distant from the mapped trail network (location 'C' in Figure 6.8). When baboon travel paths and the area surrounding the decision hotspot are investigated in more detail, it becomes clear that the decision hotspot is situated in a forested valley that seems to delineate the edge of the baboons' range (Figure 6.9) and in which several important resources were available throughout the year (Figure 6.10). The mountains surrounding this small valley were not insurmountable (*personal observation*) and should form no constraint in travel for baboons. It thus seems that a decision hotspot is identified at location C, because when the baboons would orient towards new goals after feeding in this valley, they would "turn around" to get to these goals.

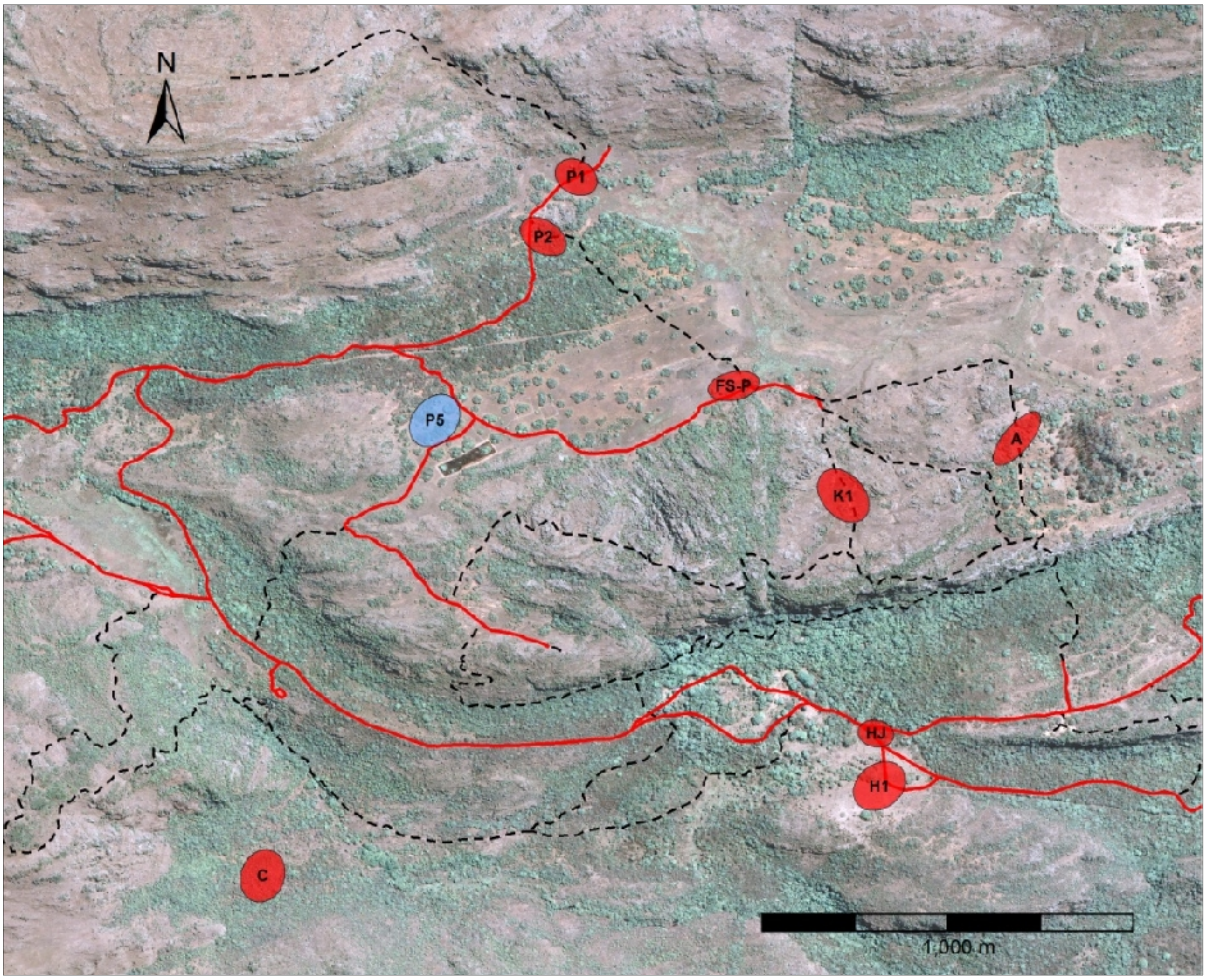

Figure 6.8 Dirt roads (*red lines*), trails (*black striped lines*), non-resource decision hotspots (*red ellipses*) and decision hotspots in category 'both' (*blue ellipses*) at Lajuma Research Center.

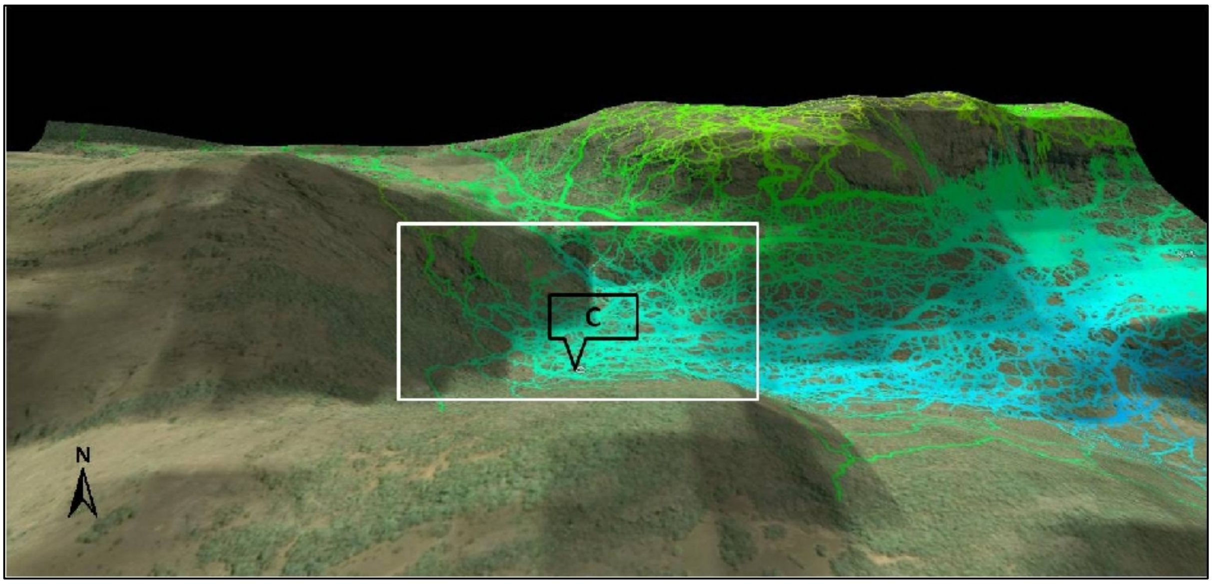

Figure 6.9 Non-resource decision hotspot C is situated in a valley. Travel routes (*thin lines* coloured according to altitude: lower altitudes [*blue*] to higher altitudes [*green/yellow*]) show the decision hotspot is identified at the edge of the baboons' range. The white box displays the extent of Figure 6.10.

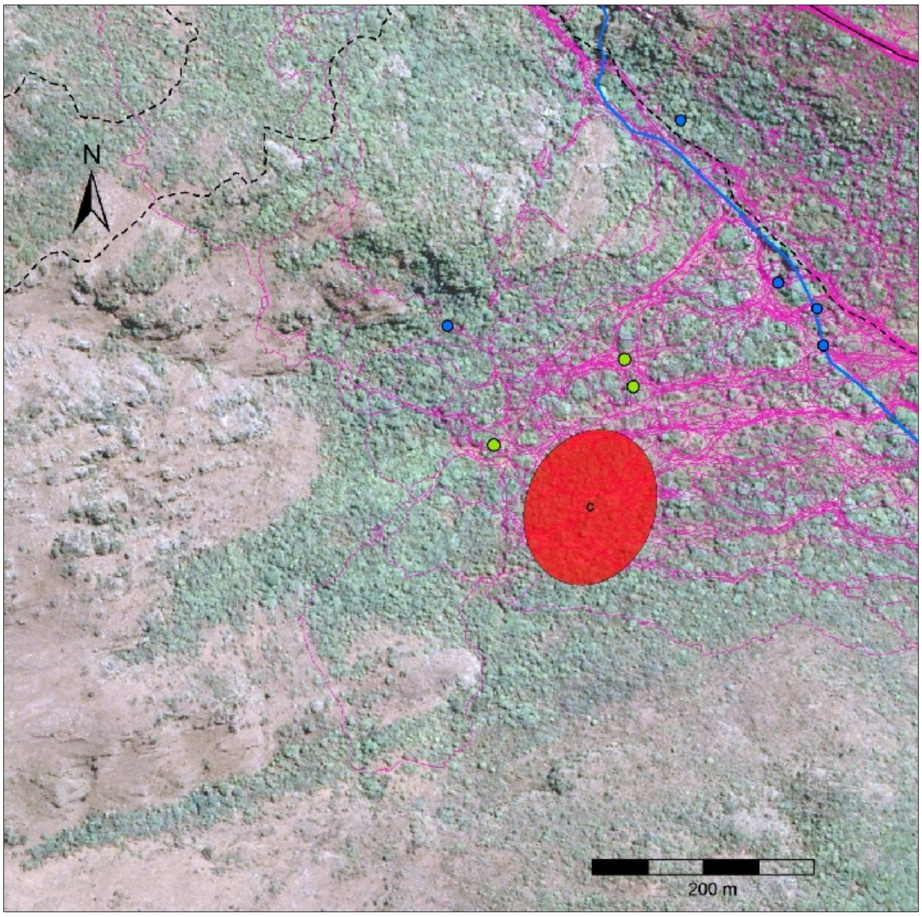

Figure 6.10 The valley surrounding the N-RH (*red ellipse*) is forested and has a river running through (*blue line*) and several important resources were recorded in the area in summer (*green dots*) and winter (*blue dots*). N-RH C was distant from the mapped trails (*black dashed line*) and dirt road (*black line*). Travel paths (*pink lines*) going through the area show that the decision hotspot is identified at the edge of the baboons' range.

6.4 Discussion

In the previous chapter the CPT was shown to successfully identify locations at which animals start orienting towards a goal and therewith to determine locations where travel decisions are being made. In this chapter the utility of the change-point test (CPT) was extended by a novel application of *CrimeStat* (Levine 2009), a spatial statistics program for the analysis of crime incident locations, to provide the first quantitative analysis of the spatial distribution of change-points by identifying clusters of change-points where animals repeatedly change direction on multiple travel days through hotspot analysis (Levine 2009). Change-points were found to be significantly clustered in space and the subsequent hotspot analysis delimited clusters of change-points where the baboons made repeated travel decisions, which are termed ‘decision hotspots’.

Change-points have been shown to be associated with biologically meaningful locations (Byrne *et al.* 2009; Asensio *et al*. 2011). Some change-points however may be identified at landmarks that constrain travel direction (Byrne *et al*. 2009) and it was expected that decision hotspots may have consequently been identified near topological features that systematically limit travel in certain directions (*e.g.*, cliffs). However, there was no evidence that topological features imposed constraints in travel directions and it thus seems unlikely that decision hotspots were identified for this reason. In baboons 70% of change-points coincided with food or water resources (Byrne *et al.* 2009) while in white-handed gibbons (*Hylobates lar*) 78.4% of identified change-points were associated with food sources (Asensio *et al*. 2011). Byrne *et al.* (2009) also highlighted that change-points could be sited at important landmarks, which may aid navigation. The hotspot analysis presented in this chapter provides support for both of these suggestions, since while a significant number of decision hotspots were located at food sources, some were also located near topographical features within the baboons’ home range, particularly at navigational landmarks such as junctions in roads or trails, without the presence of any food or water resource (for example decision hotspot at location H-J in Figure 6.5). Interestingly, certain decision hotspots were consistent across seasons, despite resources only being available for restricted periods (*e.g.*, decision hotspot at location FS-P), suggesting that specific locations may be retained as navigational landmarks even when resources are absent. This reveals an important utility to the method since the identification of decision hotspots that may allow landmarks that delineate the tight network of routes characteristic of network maps to be distinguished (Byrne 2000; Di Fiore & Suarez 2007; Noser & Byrne 2007a), and so removes the subjectivity from previous studies based on manual identification (Di Fiore & Suarez 2007; Presotto & Izar 2010). At the same time, the method offers an objective assessment of keystone resources within the environment without the need for detailed behavioural or phenological observations, since it identifies the high value resources central to the animals’ travel decisions.

A second important application of the identification of decision hotspots may be in studies of group-decision-making. While research into the mechanisms and dynamics of decision-making processes at the individual level is critical to understanding higher-scale collective movements (Petit & Bon 2010), behavioural observations on primates have generally been restricted to examining morning departures from sleeping sites (Stueckle & Zinner 2008). The objective identification of decision hotspots within daily travel paths will increase the ability to study decision-making processes by allowing a range of sites to be selected for detailed observations that would not otherwise have been identified (King & Sueur 2011). As a consequence it should offer greater scope for examining temporal variation in decision processes where factors such as the role of foraging success might also be assessed.

There are several statistical techniques to identify decision hotspots and it was not the aim of this chapter to provide a comprehensive review of all different potential techniques. However, it should be clear that there are several statistical techniques to identify decision hotspots with many criteria that can be used for any particular technique (*e.g.*, the geographical scale of the clusters and the visual display). It should therewith be realized that there is not a single solution to the identification of decision hotspots, but that different techniques may reveal different decision hotspots and patterns among the decision hotspots and one must be aware of this variability and choose techniques that reflect sample size and complement other types of analysis. Nevertheless, objective methods that provide an empirical description of locations where decisions are concentrated are likely to be an invaluable addition to the toolkit of techniques for studying animal spatial behaviour. It is imperative that the underlying causes that link the change-points together are discovered in some systematic way, but delimiting decision hotspots should itself allow observations to be targeted at key locations and thus aid this process. The identification of decision hotspots should thus represent an important second step following the CPT in many studies of spatial cognition and decision-making.

In the next chapter, movement patterns to and from travel goals (change-points) and highly valuable resource locations (resource hotspots) are investigated. In Chapter 8, whether or not baboons use a network of habitually used travel routes to navigate through the landscape will be investigated further and the location and function of non-resource decision hotspots will be examined in relation to this. Characteristics of travel paths leading towards and from change-points and resource decision hotspots are examined to determine whether movement patterns of chacma baboons are more consistent with Euclidean or topological spatial awareness.

CHAPTER 7

GOAL ORIENTED TRAVEL

7.1 Introduction

Studies on spatial memory have provided ample evidence that primates show outstanding large-scale spatial knowledge (Janson 1998), travelling efficiently between resources, often finding the closest ones or the most productive ones (*e.g.*, Menzel 1973; Garber 1988; Janson 1998) and potential food sources are sometimes bypassed in favour of more preferred ones (*e.g.*, Garber 1989; Janson 1998; Noser 2004; Noser & Byrne 2007b; Janmaat 2006; Cunningham & Janson 2007; Valero & Byrne 2007; Normand *et al*. 2009). The routes used by primates when travelling between resources often seem to be highly efficient and goal-directed and in most cases, routes taken between known resources are either approximate straight lines (*e.g.*, Janson 1998; Pochron 2001; Cunningham & Janson 2007; Valero & Byrne 2007) or a succession of a several straight-line segments (Di Fiore & Suarez 2007; Noser & Byrne 2007b, 2010). Although non-linear routes would indeed indicate a lack of goal-directedness, animals may travel using highly linear routes without knowing the locations of goals (Janson & Byrne 2007). Some animals rely on topographic or boundary features of their environment to orient or travel (*e.g.*, Valero & Byrne 2007; Di Fiore & Suarez 2007) and such landmarks are often linear over long distances thus resulting in linear travel (Janson & Byrne 2007). Alternatively, animals could follow simple straight-line-strategies to avoid backtracking, which would be efficient in a habitat rich in resources without the use of any kind of Euclidean map (Janson & Byrne 2007). The need of some animals to monitor their home range on a regular basis may also require relatively long and rapid movements which may result in straight line travel (*e.g.*, Terborgh & Stern 1987). Finally, linear travel may simply arise as a compromise between individuals that want to travel as a group (Janson & Byrne 2007). The use of linear travel routes by itself is thus not evidence for goal-directed travel (Noser & Byrne 2007b; Janson & Byrne 2007) and is not sufficient for identifying the mechanism involved in navigation (Noser & Byrne 2007b; Normand *et al*. 2009).

Travel speed, in combination with linearity, has been proposed to be a more useful quantification of the anticipation of reaching a goal (Janson & Di Bitetti 1997, Pochron 2001, 2005; Janmaat *et al*. 2006; Noser & Byrne 2007a, 2007b). Where constant travel speed and a low linearity would indicate a lack of goal directedness during navigation, variation in travel speed and high route linearity are expected if animals plan ahead of time and goals are in fact anticipated. However, due to the fact that goals may simply become visible at short range or potential olfactory cues may give away the location of goals in advance, travel speed and linearity could increase within a certain range of the goals, even though no planning has occurred. It has also been proposed that travel could slow down due to sensory cues picked up at a certain distance from the goal. These sensory cues can be given off by the resource itself (*e.g.*, olfactory cues), by group members that are already present (*e.g.*, for animals that live in fission fusion societies [Normand & Boesch 2009] or that live in very large social groups where group spread is large and individuals at the front of the group arrive well ahead of those at the rear), or by members of other groups in areas where groups have overlapping home ranges. Sensory cues may thus cause travel to either increase or decrease from a certain distance from the goal without there being any planning involved. Since goals may become visible from varying distances and other sensory cues may also be picked up from different distances, depending on the circumstances (*e.g.*, wind direction, wind speed or ripeness of fruits), the location of the goal, the type of goal and the direction of approach, it is impossible to know from what distance variation in travel speed due to sensory cues may be expected. To overcome the potential effect of goals becoming visible on travel speed and path linearity, it has been suggested that movement patterns should be analyzed as long as goals are out of sight (Noser & Byrne 2007b) and as such linear travel paths to out-of-sight resources have 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 (*e.g.*, Janmaat *et al*. 2006; Janson & Di Bitetti 1997; Noser & Byrne 2007b; Valero & Byrne 2007). Nevertheless, such an approach does not account for the potential effects of non-visual sensory cues, such as olfactory or vocal cues, which may be picked up from further away.

Another challenge in studying goal-directedness lies in the concept of "path segments" and travel "goals". The definition of a "path segment", over which linearity is calculated, has varied greatly. Path segments have for instance been defined as travel between locations at which the animal is stationary (*i.e.*, remains at the same location) for a particular time pre-determined by the researcher (so-called 'stop-sites'), independent of the animal's behaviour at this location (*e.g.*, Valero & Byrne 2007; Bates & Byrne 2009). Path segments have also been defined as travel between the point where an animal stopped to handle food, and the location where the animal was present a certain time period before the food-handling event (Pochron 2001). More commonly, however, a path segment refers to travel between consecutive feeding locations (*e.g.*, Matthews 2009; Normand & Boesch 2009), which may sometimes be limited to particular types of resources (*e.g.*, fruit trees: Janson 1997). Path segment length (*i.e.*, the travel distance between goals) has been highly variable between study species and habitat. For instance Normand & Boesch (2009) found an average distance between food resources of 294m (min distance 124m), considering only those path segments consisting of more than 4 waypoints, for chimpanzees (*Pan troglodytes verus*) in lowland rainforest. Valero & Byrne (2007) report an average beeline distance of path segments of 150m (± 160m), studying spider monkeys (*Ateles geoffroyi yucatanensis*) in subtropical forest. Noser & Byrne (2007b) calculated a median inter-resource distance which they termed "segment distance", of 438m (with a range from

75m to 4,540m) for baboons (*Papio ursinus*) in woodland savannah. As can be seen from these studies, path segment length not only varies with study species and/or habitat, but also greatly varies within studies (thus when study species and habitat are constant). Since path linearity is often computed as the ratio between the beeline distance between two locations and the actual distance travelled between these locations, irrespective of what these locations may represent (*e.g.*, stop sites, feeding sites, sleeping sites), when path segments get very large the corresponding steps are likely to include more and conflicting directional changes (Byrne *et al.*, 2009). As a result path segment length in itself is likely to affect path linearity.

In the primate literature concerning goal directedness, travel "goals" usually refer to food resources, typically individual fruiting trees (Normand & Boesch 2009; Normand *et al*. 2009; Noser & Byrne 2010) or artificial feeding platforms (Janson 2007; Lührs *et al.* 2009), although some studies have additionally included water resources (Noser & Byrne 2007b), resting locations (Valero & Byrne 2007) and sleeping sites (Noser & Byrne 2007b) as goals. Collecting data on such goals requires detailed behavioural and/or phenological observations that can be a highly labour intensive and time consuming, especially when animals live in habitats with high biodiversity. For example, in the Taï National Park in Côte d'Ivoire, data were collected by 4 people for over 3 years to sample a total of 12,299 individual trees in order to create a botanic map of approximately 15km^2, which was "only" about 60% of the territory of the group of chimpanzees under study (Normand *et al*. 2009). It has been suggested that independent evidence on the value of travel goals (*i.e.*, not based on the animal's own behaviour) is required to be able to infer goal-directed travel and hence presumptive knowledge of the location of the goals. If concurrent fast and direct travel towards valuable (large, predictable) resources without detouring to other potential resources along the path is shown, while inferior (smaller, unpredictable and low value) resources are approached at low speed and linearity (Janson & Di Bitetti 1997; Pochron 2001; Pochron 2005; Janmaat 2006), this provides very strong evidence for goal-directed travel (Janson & Byrne 2008). This has been shown, for instance, for white-faced saki monkeys (*Pithecia pithecia*) (Cunningham & Janson 2007). Also chacma baboons show linear travel towards valuable resources, whilst bypassing other food resources. Noser (2004) found that chacma baboons did not feed on different food types in accordance with the food's availability. Instead baboons fed on fruit items more often than on seeds in the early mornings, whereas they fed on seeds in the vicinity of the sleeping site as fall-back foods in the afternoons (Noser 2004). The baboons chose out-of-sight fruit in the presence of the in-sight seeds and travelled towards these valuable resources with high path linearity and travel speed (Noser & Byrne 2007b). During the 3-week fruiting period of the mountain fig (*Ficus glumosa*), baboons made repetitive use of a single 'fig-route' visiting the same 10 fig trees in the same order every morning, approaching them along linear routes and high speeds whilst bypassing other resources (Noser & Byrne 2010). Pochron (2001) showed that yellow baboons (*Papio hamadryas cynocephalus*) travelled more quickly and more directly to foods that provide a relatively high number of grams per minute handling compared to fallback foods, which were approached slowly and indirect. Further study however showed, that resources with a high economic valuable are indeed purposefully encountered, but that the economic value must be compared to other foods, not to the proportion of time feeding, or weight or numbers of grams per minute of preparation time that are obtained (Pochron 2005). For example, baboons purposefully approached baobab fruit (quick and direct) in the dry season, but in the lush wet season baboons travelled to this resource slow and indirect (Pochron 2001). This was explained by the economic value of baobab fruit compared to other foods: in the dry season only one other food provided more grams per minute preparation compared to 7 other foods in the lush season. The baobab is thus more valuable to the baboons in the dry season than in the lush season (Pochron 2005). In his study of baboons' movement patterns, Sueur (2011) also showed that baboons speed up when going to important food locations. Together, these studies suggest that baboons seem to plan at least part of their journeys and actively choose their out-of-sight resources, reaching them in an efficient and goal-directed way.

Unless animals are seen to by-pass detectable, but inferior resources in the route, linear travel paths to out-of-sight resources do thus not necessarily imply that travel goals are anticipated (Janson & Byrne 2007; Asensio *et al*. 2011). As such, it may be inappropriate and arbitrary to identify a potential planned segment from a hypothetical decision point to its corresponding goal, as travel between two biologically relevant locations (*i.e.*, from one feeding location to the next) and it is thus a major challenge to objectively identify the travel goal (if any) for an animal as well as the points at which they supposedly decided to move towards a goal (Byrne *et al*. 2009; Asensio *et al*. 2011). The change-point test (CPT) has been developed to identify so-called change-points at locations where changes in direction occur in travel routes (Chapter 4) and has been shown to identify high value resources central to the animals' travel decisions (Byrne *et al*. 2009, Ascensio *et al*. 2011, Chapter 6). The CPT has therefore been suggested to be an objective alternative to the use of travel between food sources as a window into cognitive mechanisms underlying travel paths (Byrne *et al.* 2009; Asensio *et al*. 2011). Thus, instead of defining path segments as travel between food sources (which may or may not have been the goal of travel), path segments in this study were defined as travel from one change-point to the next (Asensio *et al*. 2011) to study whether baboons' travel paths are goal-oriented. Although visibility was not measured in this study, in the nearby Blouberg mountains (with a woodland savannah habitat very similar to that at Lajuma Research Center) visibility of resources was found to be 82m ± 35m (with an absolute maximum of 219m) (Noser & Byrne 2007b). Given that distances between consecutive change-points ranged from 161m to 3137m (median of 646.0m), it was concluded that the large majority of consecutive travel change-points were likely out of sight from each other.

The CPT has been shown to predominately identify locations that are readily interpreted in biological terms (Byrne *et al.* 2009; Ascensio *et al.* 2011; Joly & Zimmermann 2011) and only for a small minority of change-points, a biologically meaningful reason why animals start orienting towards a new goal may not be detected (3.8% and 13.8% in chimpanzees and baboons respectively: Byrne *et al*. 2009; 6.2% in white-handed gibbons: Ascensio *et al*. 2011). In the previous chapter, the CPT was extended to identify clusters of change-points, termed decision hotspots. Although certainly not all change-points with interpretable events will have been included in decision hotspots, decision hotspots nevertheless highlighted locations with highly important resources and topological features at which baboons repeatedly changed direction on multiple travel days (Chapter 6). At the same time, decision hotspots were likely to exclude change-point locations at which animals changed direction more unintentionally and sporadically, for reasons such as journey disruptions, troop encounters and disruptive social events and exclude change-point locations without interpretable events. However, since the identification of change-points and decision-hotspots were based solely on spatial data and did not include any event data, it remains possible that some change-points without interpretable events were nevertheless included in decision hotspots. Decision hotspots were categorised into a resource hotspot or a non-resource hotspot, where resulting resource hotspots were found to represent highly valuable resources (Chapter 6).

The aim of this chapter is to investigate whether baboons show goal-oriented travel and whether they ‘know’ where they are heading and anticipate reaching their travel goals. In contrast to previous studies (but see Ascensio *et al.* 2011), travel goals in this chapter are those locations identified by change-points (Chapter 5) and resource hotspots are considered to be locations of highly valuable resources and ‘major’ travel goals (Chapter 6). Travel speed and linearity of path segments between travel goals (*i.e.*, travel route between consecutive change-points) and travel trajectories before and after highly valuable resources (*i.e.*, resource hotspots) are investigated to see whether baboons show goal-oriented travel. Where constant speed and a low linearity would indicate a lack of goal directedness during navigation, variation in travel speed and high route linearity are expected if baboons if goals are in fact anticipated. To test whether baboons changed their travel speed before arriving at (major) travel goals, their initial speed (*i.e.*, leaving speed) was compared to their final speed (*i.e.*, approach speed). Furthermore, it is expected that baboons travel more direct and faster towards highly valuable goals (*i.e.*, resource hotspots) than towards other goals (*i.e.*, change-points that fall outside resource hotspots), while controlling for the distance over which travel speed and linearity is measured.

To discriminate the possible effects sensory cues have on travel speed, movement patterns approaching travel goals were investigated at different spatial scales. ‘True’ differences in travel speed, due to goal directedness and advance planning instead of sensory cues, were expected to be evident at larger spatial scales and further away from (major) travel goals. Furthermore, it has been suggested that animals may plan further ahead when foods are limited (Valero & Byrne 2007) and as such that cognitive mechanisms may become more evident during the dry winter season. Byrne & Noser (2007b) indeed found that the degree of linearity in travel routes varied seasonally, with more directed movements during the dry periods when food was most limited. For this reason, movement patterns in this chapter were investigated for summer and winter separately, as well as for the year as a whole.

7.2 Methodology

7.2.1 Path segments and trajectories

Path segments (N=829) were defined as travel between travel goals (*i.e.*, consecutive change-points) as identified in Chapter 5. Since baboons did not visit highly valuable resources (*i.e.*, a resource hotspot) (Chapter 6) on a daily basis, let alone visit two of these major travel goals in one day, it was not possible to investigate "path segments" between two resource hotspots. Instead, trajectories (up to 8 steps) leading to and from resource hotspots were investigated. These trajectories effectively coincided with travel ranging from about 50m to 500m (average step length was 50.2m) before and after resource hotspots (note that beeline distances are smaller). This trajectory length was selected since it encompasses the mean bee line distance between important resources found in the nearby Blouberg (438m) (Noser & Byrne 2007b). Figure 7.1 illustrates the distribution of change-points and resource decision hotspots in the baboons' home range.

Data were analysed for the year as a whole and subsequently analysed for summer and winter separately. For resource hotspots this meant that data for summer RH and winter RH were pooled to provide results for the year as a whole. Note that these pooled data were different from identified "year RH" in Chapter 6 (*e.g.*, Section 6.3.4) (where such "year RH" were decision hotspots identified using both summer and winter change-point data and they had resources available in both summer and winter), which may have been entirely different resource hotspots (*i.e.*, at different locations) than those identified for summer and winter.

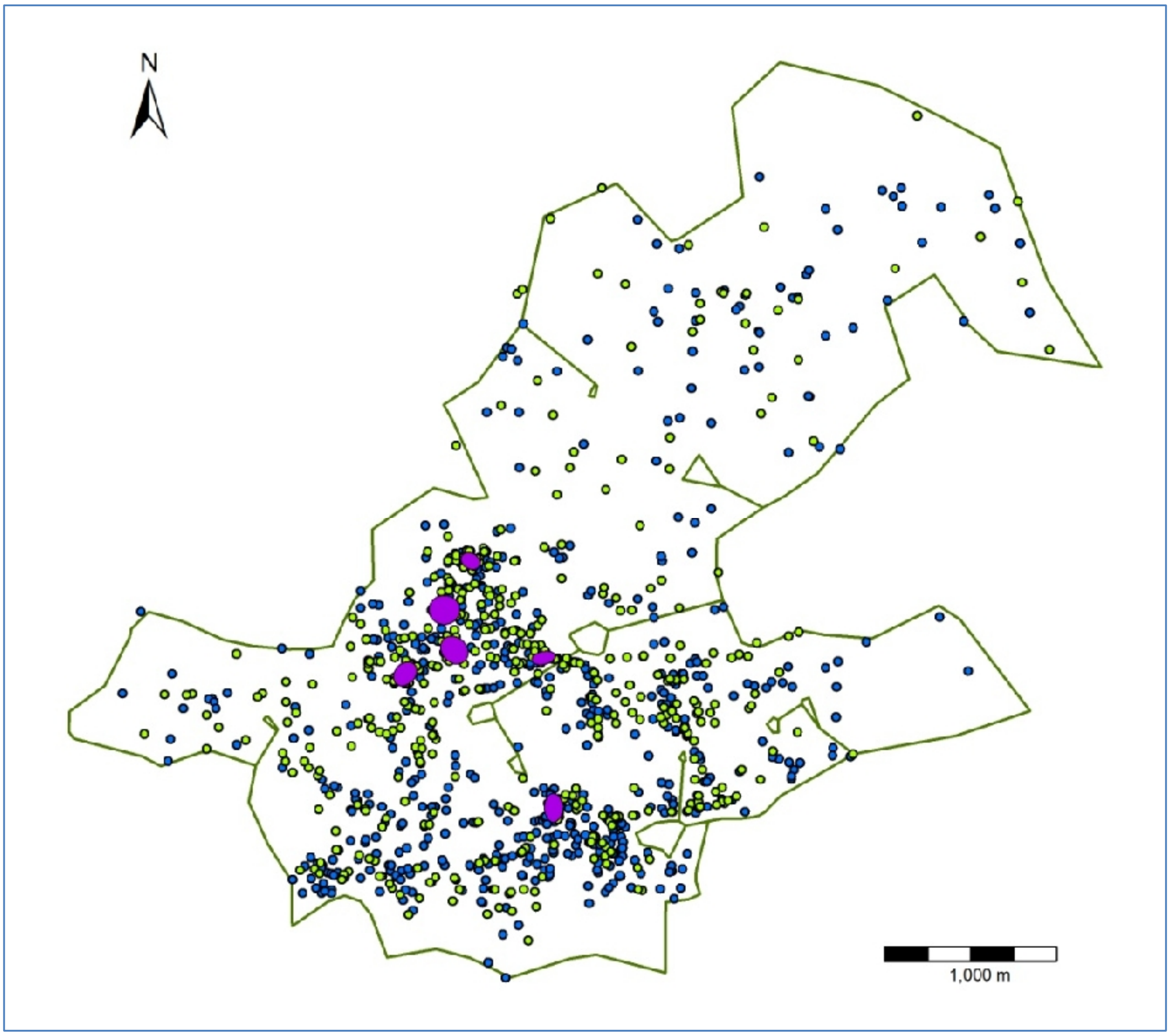

Figure 7.1 Change-points identified in summer (*green dots*) and in winter (*blue dots*) and resource hotspots (*purple ellipses*) identified in the baboons' home range at 99% isopleth level (*green line*).

7.2.1.1 Path linearity

Path linearity was calculated using a linearity index between 0 and 1 (the R value in Barschelet 1981), computed as the ratio between the beeline distance (D) between two consecutive change-points (*i.e.*, the beeline distance of the path segment) and the actual route length travelled (*i.e.*, the sum of individual step lengths) (Figure 7.2): the closer linearity index approaches the value 1, the smaller the angular deviation of the vectors, and thus the more linear the corresponding segment.

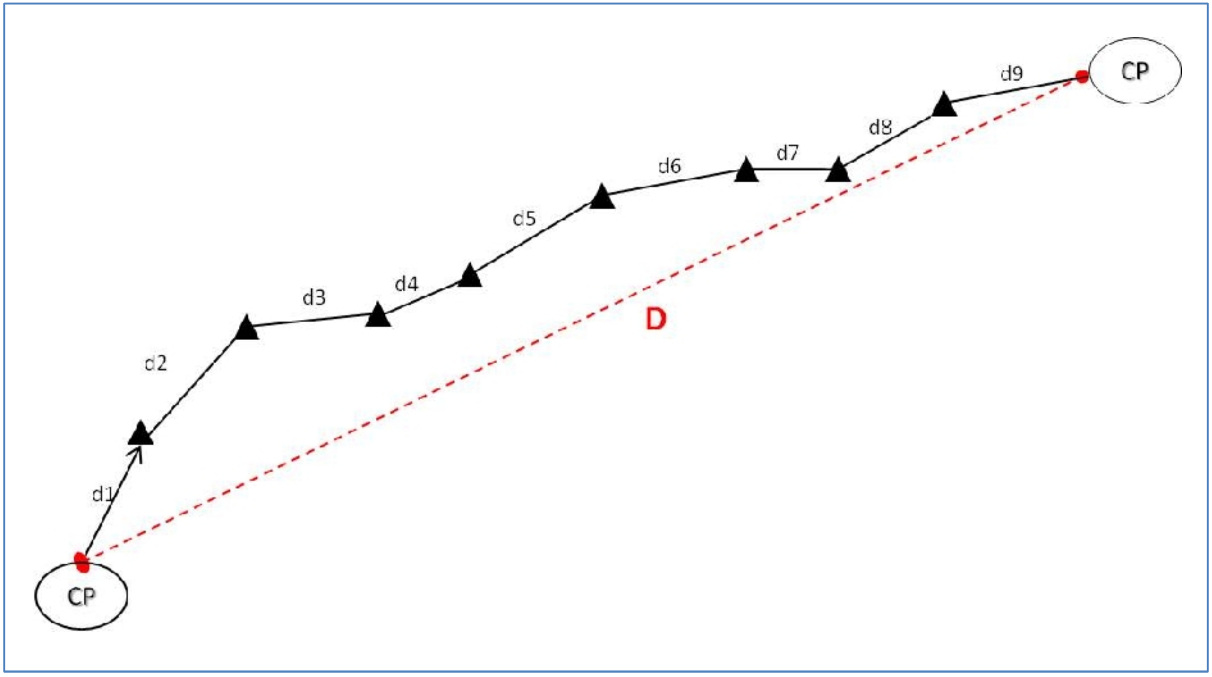

Figure 7.2 Linearity index of path segments were calculated by dividing the direct distance of the segment by the actual distance travelled. Here, the linearity index is calculated as D/(d1+d2+d3+d4+d5+d6+d7+d8+d9).

For resource hotspots the linearity index was computed as the ratio between the beeline distance (D) approaching the resource hotspot (*i.e.*, the beeline distance over the 8-step trajectory) and the actual route length travelled (*i.e.*, the sum of the 8 step lengths) (Figure 7.3).

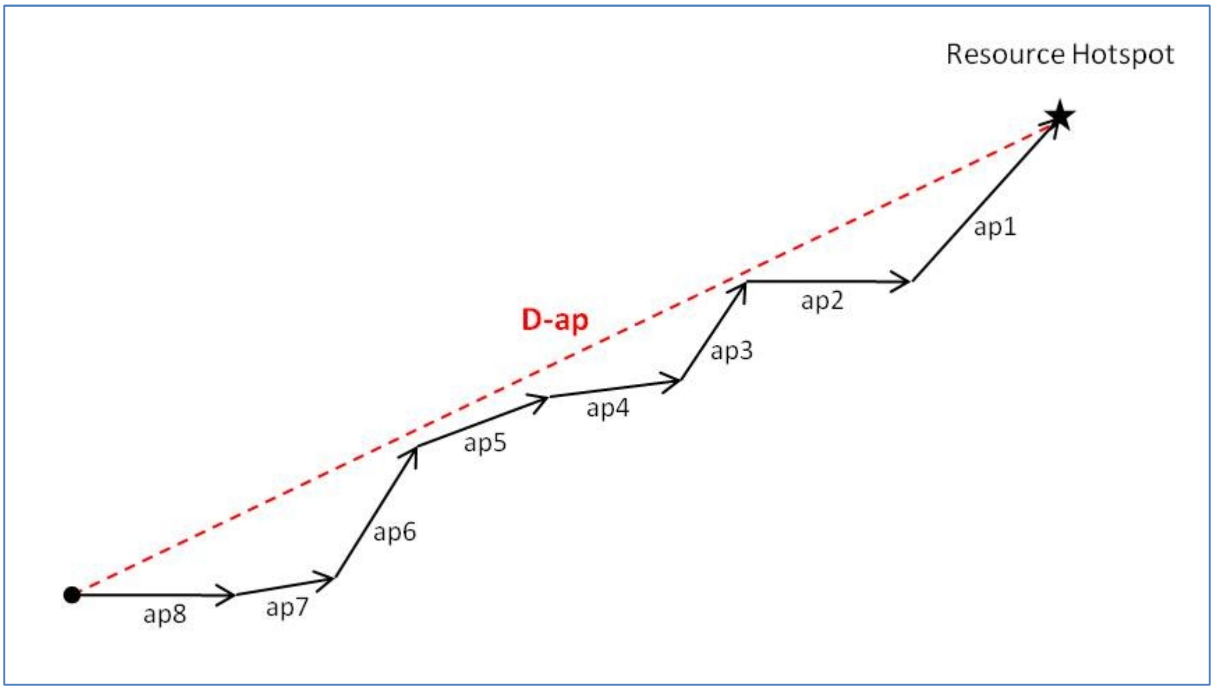

Figure 7.3 Linearity indices of trajectories leading towards (ap) resource hotspots were calculated by dividing the direct distance of the trajectory (D) by the actual distance travelled (sum ap1-ap8).

7.2.1.2 Travel speed

Mean travel speed was calculated over up to 8 steps after leaving travel goals (lv1, M-lv2 to M-lv8) and over up to 8 steps approaching travel goals (ap1, M-ap2 to M-ap8). Mean speeds were calculated by dividing the sum of each individual step lengths (Σd) by the sum of each individual step durations (Σt). For example M-ap2 was calculated as:

M-ap2 = ((distance ap1 + distance ap2) / (time ap1 + time ap2))

Note that for path segments (*i.e.*, travel between consecutive change-points) this meant that the leaving speed from a first change-point was compared to the approach speed to the next visited change-point, while for trajectories (*i.e.*, travel leading to and from resource hotspots) the leaving speed from a RH was compared to the approach speed of that same RH (Figure 7.4a, c). Since travel speed data were significantly different from a normal distribution (Kolmogorov-Smirnov test $p<0.01$), and were not corrected after appropriate transformations, non-parametric tests were applied. To test for differences in travel speed between initial (leave) and final (approach) speeds (up to 8 steps) to change-points, paired Wilcoxon Signed ranks tests were performed (since these speeds were calculated for the same path segment). The pairs compared were thus lv1-lv2, Mlv2-Map2, Mlv3-Map3 and so on until Mlv8-Map8. However, if the path segment was shorter than 16 steps there was ‘overlap’ in steps between the mean leaving speed and mean approach speed. In such cases the number of steps was divided by 2 (rounded down) to determine the maximum numbers of steps over which mean travel speeds were calculated and compared. Such a situation is illustrated in Figure 7.4b, which shows a path segment containing 13 steps between two consecutive change-points for which mean travel speeds were thus calculated for up to only 6 steps instead of 8. For resource-hotspots Mann-Whitney U tests were performed to test for differences in travel speed between initial (leave) and final (approach) speeds (up to 8 steps).

To investigate whether resource hotspots were approached at higher speeds than other goals (*i.e.*, change-points outside resource hotspots), approach speeds averaged over 2 steps (M-ap2) and over 8 steps (M-ap8) were compared between change-points and resource hotspots using Mann-Whitney U tests. M-ap2 represents the approach to goals on a small scale, at which potential sensory cues might affect travel speed, while M-ap8 represents the approach to goals on a large scale, at which potential sensory cues were unlikely to affect travel speed.

Finally, to discriminate potential effects of sensory cues on the approach speed to travel goals, travel speeds approaching (major) goals were investigated at different scales. To do so, travel speeds were calculated for 8 steps approaching goals individually (ap1 to ap8). First a Kruskal-Wallis test was used to test for differences in approach travel speed between all 8 steps at the same time.

Subsequently, paired Wilcoxon Signed Rank tests were used to test for differences in travel speed approaching (major) goals. However, sample sizes of approach speeds (ap1 to ap8) were not always consistent, because if a resource was encountered at the start of a travel day, and the baboons travelled only a short distance before reaching their first travel goal, approach speed could not be calculated for steps further away. Moreover, for path segments shorter than 16 steps the maximum number of approach steps was determined as described above (Figure 7.4b) to prevent overlap in what was considered "leave" and "approach". Thus, more data were available for the final step (ap1) than for the 8th step before approaching a goal (ap8) and thus some 'pairs' in the paired Wilcoxon Signed Rank test were excluded due to a lack of data. Therefore, Mann-Whitney U tests were used additionally to compare approach speeds between the different steps. For all tests, the null hypothesis of no difference in travel speed between samples, was rejected at a significance level of p<0.05.

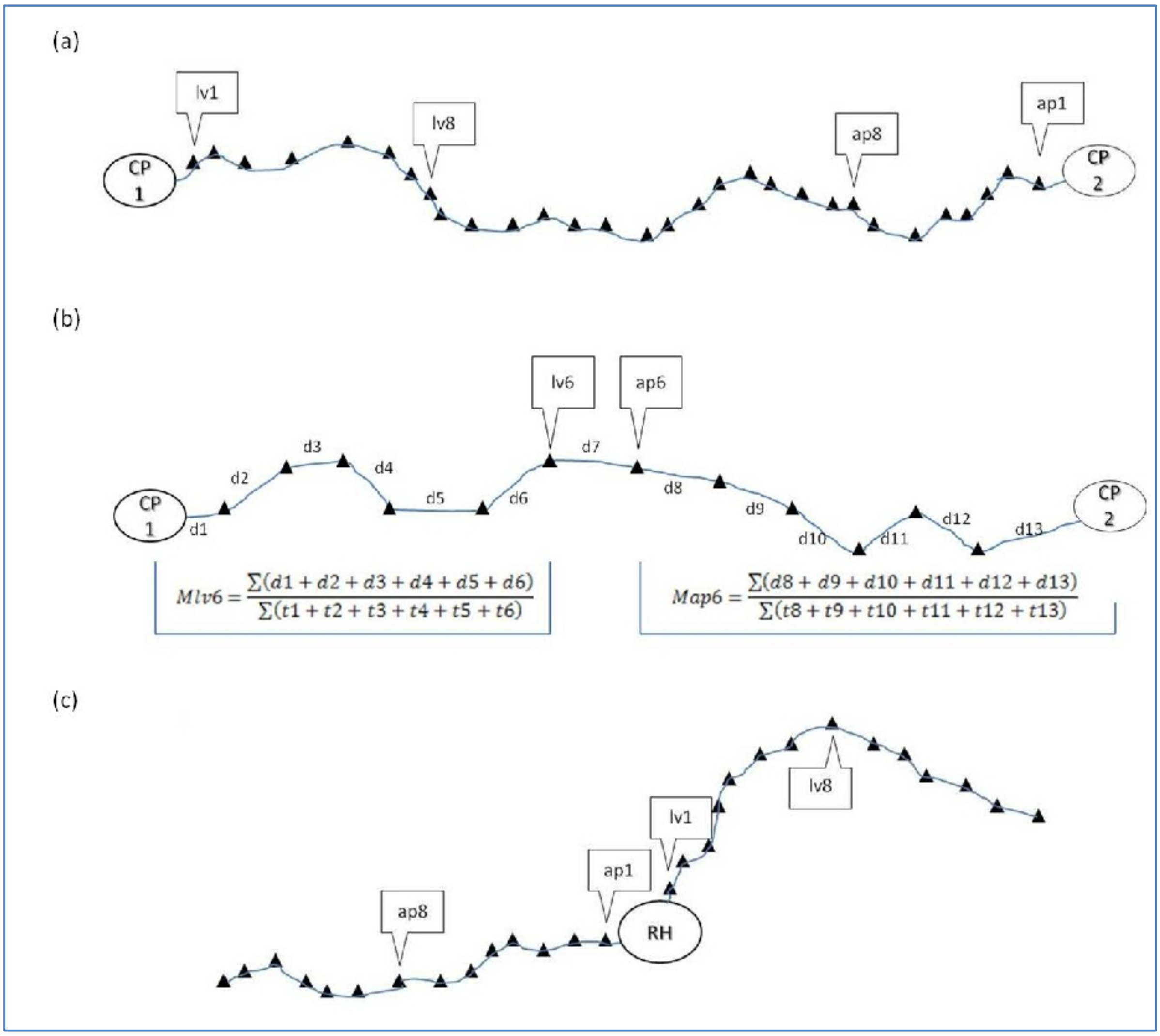

Figure 7.4 Initial (leaving) speeds were compared to final (approach) speeds at 8 different scales for (a) change-points (CP) and (c) resource hotspots (RH). If path segments were shorter than 16 steps (b), then the number of steps was divided by 2 (here 13/2=6.5) and mean travel speed was calculated up to this number (rounded down) so that there was no 'overlap' of steps in calculating final and initial travel speed (*i.e.*, steps were only included in the leave or approach segments). Mean travel speeds were calculated by the sum of step distances (Σd) divided by the sum of the time it took to travel this distance (Σt).

7.3 Results

7.3.1 Path linearity

Since linearity indices were not normally distributed, median linearity indices are reported. Baboons travelled rather directly between consecutive change-points throughout the year with distances travelled close to the 'bee-line' distances (N=829, LI=0.816). Baboons did show significantly more direct travel in winter (N=467, LI=0.830) than in summer (N=362, LI=0.800) (Mann-Whitney U test: U=77274, Z= -2.121, p<0.05) (Table 7.1). For 88.3% (N=732) of the path segments linearity ratios were above 0.6 and for 54.3% (N=450) of the path segments linearity ratios were above 0.8.

Resource hotspots were approached along highly linear routes throughout the year (N=247, LI=0.860) and there was no significant difference in the degree of linearity of the trajectories between summer (N=159, LI=0.863) and winter (N=88, LI=0.853) (Mann-Whitney U test: N=267, Z= -1.251, p=0.211) (Table 7.1). For 84.6% (N=226) of the trajectories, linearity ratios were above 0.6 and for 63.0% (N=168) of the trajectories, linearity ratios were above 0.8. Moreover, the trajectories leading towards resource hotspots were significantly more linear than the path segments between change-points throughout the year (Mann-Whitney U test: U=96276, Z= -3.200, p=0.001) and in summer (Mann-Whitney U test: U=25529, Z= -3.740, p<0.001), but not in winter (Mann-Whitney U test: U=20384, Z= -0.614, p=0.539) (Table 7.1).

Table 7.1 Median linearity indices (LI) for path segments (travel between consecutive change-points [CP]) and for trajectories leading towards resource hotspots (RH) for summer, winter and the year as a whole. The percentage of paths with linearity indices higher than 0.8.

	summer (N)	winter (N)	year (N)	LI > 0.8 (N)
between CP	0.800 (362)	0.820 (467)	0.816 (829)	54%
RH approach	0.863 (159)	0.853 (88)	0.860 (247)	63%

Baboons thus seem to travel more directly towards resource hotspots than between change-points. However, trajectories leading towards resource hotspots were by definition limited to 8 steps, whereas path segments between consecutive change-points consisted of 5 to 187 steps. The distances travelled towards resource hotspots that were investigated here (*i.e.*, sum of the 8 individual step lengths of trajectories) were consequently significantly shorter (403.4m ±94.6m) than distances travelled between consecutive change-points (1006.8m ±707.9m) (Mann-Whitney U test: U=22299.5, Z= -18.681, p<0.001). In turn, this also placed an upper limit on the bee-line distances. Therefore, further analyses were conducted to determine whether baboons truly travelled more directly towards key resources than towards other goals or that this result was the consequence of differences in distance over which linearity was measured. Path segments smaller than 500m (N=182), with travel distances similar to those of the trajectories leading towards resource hotspots (397.6m ±63.7m and 403.4m ±94.6m respectively), were selected. The linearity ratios of these path segments (N=182, LI=0.850) were not significantly different from the linearity ratios of the trajectories leading up to resource hotspots (N=247, LI=0.860) (Mann-Whitney U test:U=22376.5, Z= -0.079, p=0.973). This shows that baboons did not travel significantly more directly to key resources than to other goals, but instead this result was an artefact of the shorter distance over which linearity was measured.

7.3.2 Travel speed

To test whether baboons change their travelling speed before arriving at resources, the initial (approach) and final (leaving) speeds were compared to one another at 8 different scales. For travel between change-points the paired Wilcoxon Signed rank tests (Table 7.2) showed a significant deceleration when approaching resources, regardless of scale (*i.e.*, approach speed is slower than leaving speed).

The results for the trajectories approaching and leaving resource hotspots were somewhat less consistent (Table 7.3). Nevertheless two main conclusions are drawn. Foremost, the speeds at which baboons left RH were lower than the speeds at which RH were approached and this trend was consistent across scale and season. This is in sharp contrast to the findings for travel between change-points where the initial leaving speed was consistently higher than the final approach speed (Table 7.2). Secondly, the trend of a fast approach and slow leave speed to and from RH is only significant at smaller scales (up to 4 steps) after which no significant difference between approach and leaving speed were found (Table 7.3).

Furthermore, baboons travelled significantly faster in summer (0.273 ± 0.178 m/s) than in winter (0.230 ± 0.194 m/s) overall (Mann-Whitney U test: N=829, Z= -6.444, p<0.001).

Table 7.2 Initial leaving speeds (lv) of path segments were significantly higher than their final approach speeds (ap) at different scales, both in summer and winter. Sample size (N), Z and p value from paired Wilcoxon Signed Rank tests are shown.

	Summer					**Winter**				
	N	**lv**	**ap**	**Z**	**p**	**N**	**lv**	**ap**	**Z**	**p**
Lv1-Ap1	441	0.500	0.402	-5.623	<0.001	616	0.402	0.337	-4.431	<0.001
Mlv2-Map2	441	0.443	0.344	-5.490	<0.001	616	0.338	0.288	-4.494	<0.001
Mlv3-Map3	441	0.416	0.324	-5.574	<0.001	616	0.303	0.271	-3.262	<0.01
Mlv4-Map4	441	0.391	0.307	-5.411	<0.001	615	0.295	0.260	-3.284	<0.01
Mlv5-Map5	432	0.365	0.302	-4.310	<0.001	605	0.289	0.250	-3.978	<0.001
Mlv6-Map6	413	0.352	0.279	-4.799	<0.001	580	0.282	0.241	-4.086	<0.001
Mlv7-Map7	379	0.344	0.274	-4.328	<0.001	522	0.273	0.236	-3.307	<0.01
Mlv8-Map8	327	0.324	0.269	-3.230	<0.01	457	0.261	0.234	-2.385	<0.05

Table 7.3 Leaving (lv) and approach speeds (ap) for RH trajectories were compared at 8 scales using a Mann-Whitney U test (Z, U and p values are shown). Significant differences between leaving and approach speeds are highlighted.

		N	lv	N	ap	U	Z	p
year	lv1-ap1	390	0.273	386	0.346	67431	-2.511	.012
	Mlv2-Map2	355	0.254	379	0.267	64185	-1.076	.282
	Mlv3-Map3	339	0.213	341	0.260	50697	-2.773	.006
	Mlv4-Map4	381	0.197	366	0.233	62257	-2.532	.011
	Mlv5-Map5	374	0.201	363	0.216	63460	-1.530	.126
	Mlv6-Map6	368	0.198	351	0.216	59745	-1.738	.082
	Mlv7-Map7	361	0.201	347	0.211	58291	-1.596	.110
	Mlv8-Map8	354	0.199	345	0.213	56415	-1.742	.081
summer	lv1-ap1	235	0.399	231	0.420	24778	-1.627	.104
	Mlv2-Map2	223	0.321	229	0.325	24165	-.986	.324
	Mlv3-Map3	216	0.271	215	0.321	20554	-2.062	.039
	Mlv4-Map4	235	0.247	226	0.269	23520	-2.123	.034
	Mlv5-Map5	234	0.244	226	0.264	24207	-1.568	.117
	Mlv6-Map6	232	0.239	224	0.266	23918	-1.469	.142
	Mlv7-Map7	232	0.239	222	0.262	23173	-1.846	.065
	Mlv8-Map8	231	0.230	221	0.264	22434	-2.227	.056
winter	lv1-ap1	155	0.155	155	0.241	10252	-2.231	.026
	Mlv2-Map2	132	0.121	150	0.153	9131	-1.125	.260
	Mlv3-Map3	123	0.110	126	0.179	6367	-2.432	.015
	Mlv4-Map4	146	0.106	140	0.137	8791	-2.045	.041
	Mlv5-Map5	140	0.116	137	0.120	8860	-1.095	.273
	Mlv6-Map6	136	0.111	127	0.124	7768	-1.409	.159
	Mlv7-Map7	129	0.117	125	0.120	7567	-.846	.397
	Mlv8-Map8	123	0.112	124	0.120	7203	-.754	.451

7.3.3 Approach speed towards valuable resources and other goals

To investigate whether valuable goals were approached at higher speeds than other goals, the approach speed averaged over 2 steps (M-ap2) and over 8 steps (M-ap8) were compared between change-points and resource hotspots. Over the year as a whole baboons approached resource hotspots significantly faster than they did change-points at both scales (Mann-Whitney U test: U=171881.0, Z= -4.103, p<0.001 and U=139467.5, Z= -2.612, p=0.009 for M-ap2 and M-ap8 respectively).

However, there were pronounced seasonal differences when approach speed was investigated at smaller scales. M-ap2 was significantly higher for resource hotspots than for change-points in summer (Mann-Whitney U test: U=39099.0, Z= -4.975, p<0.001), but not in winter (Mann-Whitney U test: U=43594.0, Z= -1.072, p=0.284). M-ap8 was significantly higher for resource hotspots than for change-points both in summer (Mann-Whitney U test: U=39011.5, Z= -4.150, p<0.001) and winter (Mann-Whitney U test: U=25803.0, Z= -3.430, p=0.001). Baboons thus travel significantly faster towards resource hotspots than towards change-points, but at a smaller scale this difference is only significant in summer. Furthermore, the approach speed towards resource hotspots averaged over 2 steps (M-ap2) was significantly higher than when measured over 8 steps (M-ap8) (Mann-Whitney U test: U=59352.0, Z= -2.144, p=0.032). Baboons thus seem to accelerate when approaching highly valuable resources.

7.3.4 Effect of sensory cues

When the approach to change-points was investigated in more detail, paired Wilcoxon Signed Rank tests (Table 7.4) showed that the speed of the final two steps approaching (ap1-ap2) change-points were significantly slower still than the previous approach steps (ap3-ap8) (Figure 7.5). However, in approaching resource hotspots, there was no significant difference in travel speed between the 8 approach steps in summer (Kruskal-Wallis test: N=166, df=7, χ^2=12.361, p=0.089) or winter (Kruskal-Wallis test N=87, df=7, χ^2=7.843, p=0.347).

Table 7.4 Paired Wilcoxon Signed Rank tests (sample size N, Z and p values are shown) showed that travel speeds of the final 2 steps(ap1-ap2) approaching change-points were significantly slower than the previous approach steps (ap3-ap6).

	year			summer			winter		
	N	Z	p	N	Z	p	N	Z	p
ap1-ap2	1057	-4.073	<0.001	441	-3.116	0.002	616	-2.660	0.008
ap1-ap3	1057	-7.195	<0.001	441	-4.283	<0.001	616	-5.817	<0.001
ap1-ap4	1056	-6.296	<0.001	441	-3.737	<0.001	615	-5.141	<0.001
ap1-ap5	1047	-7.661	<0.001	438	-5.627	<0.001	609	-5.251	<0.001
ap1-ap6	1029	-6.237	<0.001	432	-3.163	0.002	597	-5.555	<0.001
ap1-ap7	999	-6.600	<0.001	422	-4.404	<0.001	577	-4.888	<0.001
ap1-ap8	947	-7.156	<0.001	400	-4.456	<0.001	547	-5.720	<0.001
ap2-ap3	1057	-4.694	<0.001	441	-2.378	0.017	616	-4.161	<0.001
ap2-ap4	1056	-3.319	0.001	441	-1.252	0.211	615	-3.347	0.001
ap2-ap5	1047	-5.057	<0.001	438	-3.973	<0.001	609	-3.235	0.001
ap2-ap6	1029	-3.244	0.001	432	-1.093	0.274	597	-3.384	0.001
ap2-ap7	999	-4.171	<0.001	422	-2.485	0.013	577	-3.334	0.001
ap2-ap8	947	-4.383	<0.001	400	-2.849	0.004	547	-3.286	0.001

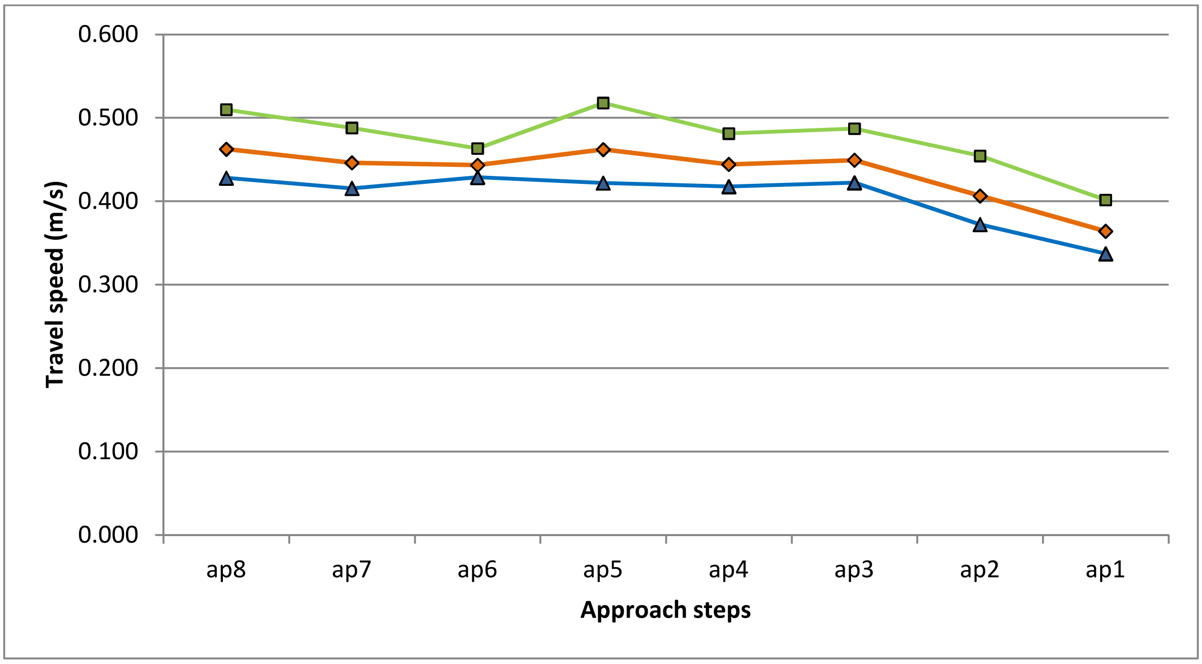

Figure 7.5 Travel speeds up to 8 steps before reaching goals (*i.e.*, change-points) are shown for year (*orange line with diamonds*), summer (*green line with squares*) and winter (*blue line with triangles*). Note that the goal is "located" on the right side of the graph and that the approach (*i.e.*, travel direction) is from left to right.

7.4 Discussion

Baboons travelled along rather linear paths with distances travelled close to the direct, bee-line distances, although they did not seem to travel more directly towards highly valuable goals. Baboons also changed their travel speed when approaching travel goals and showed significantly faster travel towards highly valuable goals than towards other travel goals. It thus seems that baboons 'knew' when they were nearing their goals and adapted their speed accordingly.

There was, however, dissimilarity in movement patterns between highly valuable resources and the other travel goals. The change in travel speed observed when approaching goals was due to significantly higher leaving speed than approach speed and baboons therefore showed a significant *deceleration* over path segments. Moreover, the travel speeds over the final two steps approaching travel goals were significantly slower still than those of previous approach steps. Thus when baboons got close to their travel goals (within 93.9 ± 28.9m) they slowed down even further. In contrast, baboons approached highly valuable goals at significantly higher speed than that at which they left these valuable goals. Furthermore, the average travel speed over the final two steps before reaching highly valuable resources were significantly higher than the average travel speed calculated over the final eight steps. Movement patterns for highly valuable resources were thus the opposite of movement patterns towards other, less valuable goals.

These findings may be explained by the dual function of the travel goals identified by the CPT. Although the CPT predominately identifies locations associated with food resources, change-points are also located at topological features, such as junctions in roads or trails (Byrne *et al*. 2009), where no resources may be present. The CPT thus identifies travel goals at the end of feeding bouts, but also places from where new travel directions and routes towards the next travel goal are taken (Asensio *et al*. 2011) and some locations may be identified at which group routes deviate for no apparent reason other than the group made a decision to do so (King & Sueur 2011). There is much debate on how travel decisions are made (*e.g*., Conradt & Roper 2003; Rands *et al.* 2003; Couzin *et al*. 2005; Seeley *et al.* 2006; King & Cowlishaw 2009a; Lusseau & Conradt 2009; Petit & Bon 2010). Many species have shown some sort of 'voting' to seemingly come to a 'consensus', including hamadryas baboons (*Papio hamadryas*) (Kummer 1968), mountain gorilla (*Gorilla berengei berengei*) (Watts 2000) and Tonkean macaques (*Macaca tonkeana*) (Sueur & Petit 2008; Sueur *et al.* 2010, 2011). In contrast, it has been argued that in leaving their morning sleeping site baboons follow a simple rule "follow a friend" rule that results in collective movement and that they show no sign of voting behaviours (King *et al.* 2011). Studies on group decision-making come from decisions to 'make the move' (King & Sueur 2011), studied in the context of departure from morning sleeping sites (*e.g.*, Sigg & Stolba 1981; Stueckle & Zinner 2008; King *et al.* 2011) or departure after significant resting/stop periods (*e.g.*, Boinski 1993; Watts 2000; Sueur *et al*. 2009, 2010) (but see Pyritz 2011). Yet very little is known about travel decision 'on the move' (King & Sueur 2011), because researchers generally do not know when or where such decisions are made (Byrne *et al.* 2009) and individuals are synchronized in their behaviours to varying degrees (King & Cowlishaw 2009b). Nevertheless, it is likely that the decision-making process takes some time and when conflicts of interest emerge between troop members, the need to negotiate terms of acceptance slows decision processes (Conradt & Roper 2005). At change-points baboons may thus have to come to a consensus on where to travel next, and since they live in relatively large social groups conflicts may arise. Baboons may thus slow down their travel speed during the process of decision-making in approach to change-point locations.

Furthermore, the CPT has also been shown to identify change-points at locations with troop encounters (Byrne *et al*. 2009; Asensio *et al.* 2011). Baboons typically respond to the presence of other troops by 'long waiting periods' (Noser & Byrne 2007a pp: 338), which may have contributed to the decrease in travel speed when approaching change-points.

Hotspot analysis was likely to exclude most locations where animals changed direction more unintentionally and sporadically, for reasons such as troop encounters, journey disruptions and social events and also was likely to exclude most change-points that were not associated with interpretable events. Resource hotspots were associated with key resources, which were shown to be highly valuable travel goals (see Chapter 5), which were approached significantly faster than other goals. Moreover, the average travel speed over the final two steps before reaching highly valuable resources was significantly higher than the average travel speed calculated over the final eight steps. It is likely that the visibility of resources was comparable to that found in the nearby Blouberg mountains (82m ± 35m) (Noser & Byrne 2007b), since the woodland savannah habitat at Blouberg is highly similar to that at Lajuma Research Center (*personal observation* suggests that visibility is likely to be far less in many places of the study area). So when baboons got in close range of highly valuable travel goals it may be expected that visual (and possibly olfactory) cues revealed the location of those resources, which resulted in a further increase of travel speed at short distance. Moreover, it is possible that the first individuals to arrive at a resource give off vocal cues that are picked up by individuals at the back of the troop. Rapid travel in close range of resources is suggested to be an effect of indirect or scramble competition, because the first individuals to arrive at the resource may obtain more food or feed more quickly than those arriving later (Janson 1985; 2007).

Due to pronounced seasonal differences in rainfall and biomass production at the study site it was predicted that there would be a greater emphasis on efficient ranging during the dry, cold winter season when food was least abundant. Indeed baboons travelled significantly more directly from one goal to the next in winter than in summer, but this was not accompanied by a higher travel speed. In fact, baboons travelled significantly slower in winter than in summer. It has been argued that low ambient temperatures at the study site demand high thermoregulation which may force animals to minimize energy expenditure in winter by reducing day journey length (Willems 2009; Harrison 1985). This may also explain why baboons travel more efficiently, but slower in winter. However, since there was no concurrent higher speed and directness in winter, it cannot be concluded that baboon travel routes were more goal oriented in winter than in summer.

In fact, trajectories leading towards highly valuable resources were travelled faster and were more direct in summer than in winter. It may be argued that since the majority of food trees produced flowers and fruits in summer, it is possible that visual and olfactory cues played a bigger role in summer than in winter. However, the differences in both speed and linearity were consistent over large trajectories leading up to resources. The average bee-line distance to resources of the trajectories investigated was 317m (±99m), which is much larger than the maximum visibility measured in the nearby Blouberg (104m) (Noser & Byrne 2007b) and visual cues were thus likely to be excluded in the majority of cases. It is also unlikely that baboons smelled the resources over these large distances, "given that baboons have small olfactory bulbs and show no signs of relying on olfaction during foraging" (Fleagle 1988 and Garber & Hannon 1993 in Noser & Byrne 2007b pp: 264). Thus although at short range valuable resources may become visible and also olfactory cues may occasionally play a role, potentially stronger sensory cues in summer than in winter do not explain that the trajectories leading to value resources were traversed more directly and at faster speed by baboons. It is likely that baboons anticipated higher resource values during summer months in which most trees provided highly preferred foods and as such travelled towards highly valuable resources in a more goal-directed manner during summer than winter.

The results suggest that baboons anticipate some properties of resources they are going to visit, well before they perceive them, and thus plan ahead at least some part of their travel. They travelled significantly faster towards highly valuable goals than towards other goals, and showed more goal-directed travel to highly valuable resources during summer than winter, when the next goal was likely to be out-of-sight in the majority of cases. Travel speed increased only at very close proximity to travel goal, when goals were likely to come into sight and so this increase in speed is most likely the effect of sensory cues. In summary, the data provided evidence of goal-directed travel of baboons at the research site and they suggested that baboons seemed to ‘know’ when they were nearing their goals and adapted their speed accordingly, indicating goal-directed and mental map processes. Nevertheless, the results do not shed light on the navigational mechanism used by baboons. To investigate what mechanisms baboons may use in navigating efficiently between travel goals, Chapter 8 explores the concept of spatial representation. Whether or not baboons use route-based travel in navigating through the landscape is investigated and predictions from the hypothesized use of a Euclidean map and a topological map are tested.

CHAPTER 8

SPATIAL REPRESENTATION

8.1 Introduction

Many wild primates occupy large home ranges and travel long distances every day to reach resources, which makes them ideal subjects to study spatial cognition. Remembering the locations of resources and travelling efficiently between them, directly impacts primates' survival and reproductive success and this distinct selective advantage has been hypothesized to have influenced the evolution of intelligence (Milton 1981, 1988, 1993; Clutton-Brock & Harvey 1980; Gibson 1986; Byrne 2000; Platt 2006). Studies often rely on the assumption that efficient travel between goals resembles straight-line travel paths and path linearity is frequently used to establish the presence of efficient, goal-directed travel (Janson & Byrne 2007). Primates have been observed navigating efficiently between food resources, often finding the closest ones (*e.g.*, Boesch & Boesch 1984; Garber 1988, 1989; Janson 1998) or the most productive ones (*e.g.*, Janson 1998; Valero & Byrne 2007; Normand *et al*. 2009; Noser & Byrne 2010; Asensio *et al*. 2011). Yet, these findings give little insight into the orientation mechanism that the animals may use during navigation.

Animals can navigate towards goals using different mechanisms, some of which are now well understood. For example, ants and bees monitor direction primarily by means of a celestial compass that measures the horizontal position of the sun or the polarised pattern in the sky caused by Raleigh scattering of the sun's rays (Wehner & Rossel 1985; Wehner 1992; Dyer & Dickenson 1996; Collet & Zeil 1998). Although animals can navigate using this type of orientation mechanism, known as *path integration*, to rely on it solely results in navigational errors which become amplified the further along the path the animal travels (Wehner 1992; Bennet 1996; Collet & Zeil 1998). So while most animals use path integration in their movements (Etienne *et al.* 1998), they may also possess additional spatial cognitive abilities.

Path integration is often supplemented by route-based navigation that uses the topological relation between objects (Collet & Zeil 1998). This type of spatial representation is known as a *topological map*. Navigating the environment using such a topological map envisions that an animal's mental representation of locations and features in its environment consist of a set of interconnected, learned travel routes among sites (Milton 2000; Poucet 1993; Di Fiore & Suarez 2007). Topological maps thus represent the connectivity of the environments in a graph-structured network where intersections (also called vertices, nodes or junctions) represent well-defined locations in the environments, such as food trees, at which animals make decision about where to travel next (Di Fiore & Suarez 2007). Alternatively, animals may possess highly detailed information about the spatial relationships among landmarks, which allows them to compute distance and direction from any one place to any other known place, based on a Euclidian representation of space. True angles and distances between landmarks are represented within some kind of coordinate system, which allows an animal to compute routes between points that are out of view and thus to bridge informational gaps. This quantitative representation of the environment is known as a *Euclidean map*. Animals using a Euclidean spatial representation will thus travel by 'computing' a relatively straight or direct route to reach travel goals and have the ability to take novel routes and short cuts, whereas animals using a topological-based representation, are expected to re-use the same set of travel paths to reach travel goals that are located in the same part of their home range and to re-orient travel at frequently used nodes or 'decision-points' (Suarez 2003).

Over the last couple of decades, questions regarding spatial orientation and the mental representation of space have drawn particular attention from primate ecologists (Boinski & Garber 2000). Although numerous studies on spatial cognitive abilities in primates have been conducted under controlled conditions, in small-scale and simplified environments of captivity (*e.g.*, Menzel 1973; Gibeault & MacDonald 1994; Cramer & Gallistel 1997; MacDonald & Agnes 1999; Poti 2000), the study of primates' navigational skills in their natural habitat has been relatively neglected (Janson & Byrne 2007). Crucial characteristics of a Euclidean map are the ability to take novel short cuts (Tolman 1948, but see Noser & Byrne 2007a), make detours and path innovations (Bennet 1996), all of which are very difficult to show in a natural condition where animals would rarely face a new environment (Janson 2000). Moreover, a topological map with a very high number of landmarks is thought to be just as precise as a Euclidean map (Byrne 2000; Janson & Byrne 2007). Discrimination between the different kinds of spatial representation becomes even more difficult, because a given species could use several mechanisms simultaneously (Lührs *et al*. 2009). Despite these serious challenges to study navigational skills of primates in their natural habitat there is some evidence from studies in the wild that is consistent with a Euclidean spatial awareness (*e.g.*, Gould 1986; Normand & Boesch 2009; Presotto & Izar 2010). However, the existence of Euclidean mental maps has been seriously challenged (*e.g.*, Poucet 1993; Benhamou 1996; Bennett 1996; Byrne 2000; Janmaat *et al.* 2011) and there is a growing body of evidence to support the use a topological map in primates (*e.g.*, Sigg & Stolba 1981; Milton 1980, 2000; Noser & Byrne 2007a, 2010; Di Fiore & Suarez 2007; Erhart & Overdorff 2008). The topological map has been argued to be an efficient system for storing environmental spatial information (Poucet 1993; Di Fiore & Suarez 2007) and is considered a less cognitively demanding representation of the environment than a Euclidean map because instead of remembering where resources are, animals have only to associate the resources along familiar routes and memorise this association between landmarks and the nearby food source (Bennet 1996; Garber 2000; Poti *et al.* 2005; Presotto & Izar 2010).

Researchers have reported repeated use of the same non-linear pathways or network of pathways for a wide variety of taxonomic groups (*e.g.,* orang-utans (*Pongo pygmaeus*) Mackinnon 1974; howler monkeys (*Alouatta palliata*) Milton 2000, Hopkins 2011; spider monkeys (*Ateles belzebuth*) and woolly monkeys (*Lagothrix poeppigii*) Di Fiore & Suarez 2007; lemurs (*Propithecus diadema edwardsi, Eulemur fulvus rufus*) Erhart & Overdorff 2008; black capuchin monkeys (*Cebus nigritus*) Presotto & Izar 2010; proboscis monkeys (*Nasalislarvatus*) Boonrata 2000 and baboons (*Papio hamadrayas*) Sigg & Stolba 1981; (*Papio Anubis*) Byrne 2000; (*Papio ursinus*) Noser & Byrne 2007a, 2010). Such repeated use of particular travel paths may be less linear, but still have several advantages over straight line travel. For instance, repeated use of pathways could facilitate energy conservation by routing the primate according to particular landscape features (Di Fiore & Suarez 2007; Presotto & Izar 2010). The use of habitual routes would allow animals to forage efficiently, since it brings animals into contact with many potential feeding sources for monitoring or visitation (Di Fiore & Suarez 2007). Furthermore, since eaten and defecated seeds are deposited more frequently along habitual used travel paths, over generations, route-based travel may strongly influence the structure and composition of the habitat, “raising the fascinating possibility that primate frugivores are active participants in constructing their own ecological niches” (Di Fiore & Suarez 2007 p.317).

Although findings of repeatedly used travel routes are generally considered evidence that primates possess a topological map, it is not necessarily evidence that primates navigate (solely) using a topological map or lack a Euclidean spatial representation (Noser & Byrne 2007a; Presotto & Izar 2010). For instance Presotto & Izar (2010) showed black capuchin monkeys (*Cebus nigritus*) did travel using habitual routes, but that they also travelled far from these habitual routes, and were thus not limited to a route-based network. Moreover, the monkeys could reach the same location from different starting points using different paths, even when they could not see a prominent landmark associated with that location and thus do not require continued sight of visible landmarks (Presotto & Izar 2010). Presotto & Izar (2010) conclude that depending on the quality and distribution of the food resource they find, black capuchin monkeys possess topological spatial awareness, but also some kind of Euclidean spatial awareness.

In the previous chapter, baboons were shown to navigate efficiently between travel goals. Baboons changed their travel speed when approaching travel goals and showed significantly faster travel towards highly valuable goals than towards other travel goals. Baboons seemed to ‘know’ when they were nearing their goals and to adapt their speed accordingly. Other studies also showed that baboons used the shortest linear route to travel from one location to another and that they speeded up as they approached out-of-sight water or food source, indicating goal-directed and mental map processes (Pochron 2001, 2005; Noser 2004; Noser & Byrne 2007b, 2007b, 2010; Sueur 2011). However, these findings do not allow discriminating between the types of orientation mechanism that baboons may use during navigation.

The primary aim of this chapter is to determine whether movements of chacma baboons are more consistent with topological spatial awareness or Euclidean spatial awareness. First, baboon travel routes are investigated to whether or not baboons use a network of routes to navigate through the landscape. However, in light of arguments that the use of habitual routes does not necessarily exclude a Euclidean map-like awareness (Presotto & Izar 2010), three predictions resulting from the hypothesized use of Euclidean maps and topological maps were tested to discriminate between Euclidean and topological map-like awareness. Although these predictions are unable to 'prove' a Euclidean map, each prediction is able to provide strong support for a topological map. Furthermore, although each prediction by itself might not conclusively discriminate between the two different kinds of spatial representation, the three predictions combined can provide a clear support for one alternative.

Since it is difficult to test wild animals in a new environment, an alternative way to differentiate between different kinds of spatial representation is to delineate the areas where animals are less frequently present (Normand & Boesch 2009). If animals navigate using Euclidean spatial awareness, their navigation should remains highly efficient even in lesser known, peripheral areas of the home range (Normand & Boesch 2009). On the other hand, when animals navigate using a topological map, differences in movement patterns between an animal's core area and the peripheral area might be expected, as the further they move from the core area, the fewer available familiar landmarks they have to guide their movement (Normand & Boesch 2009). Thus if navigation is less linear in the periphery than in the well known core area, this would provide evidence for the use of a topological map. However, if no variation in movement patterns is detected between the core area and the periphery, this does not give conclusive evidence for the use of a Euclidean map, since it could alternatively suggest that animals have accumulated a similar knowledge of the periphery as of the core area (Normand & Boesch 2009). Therefore the use of a topological map does not necessarily result in less efficient travel in terms of linearity between the periphery and the core area. The first prediction tested was:

- There is no difference in travel route linearity between the periphery and the core area [supports both the use of a Euclidean map and topological map].
- Movement patterns between the periphery and the core area differ with less linear navigation in the periphery than in the core area [supports only the use of a topological map].

It has been suggested that as a consequence of the use of a Euclidean map in a less well known area, animals forage between travel goals that are closer to one another than in the core area (Normand & Boesch 2009). Therefore, the actual distance travelled and the straight-line distance between travel goals in the core area and the periphery was investigated.

Secondly, directions from which travel goals were approached were examined to help distinguish between the use of a Euclidean and a topological map. If animals navigate by a Euclidean map this allows them to arrive at known goals from all possible directions, whereas if navigating using a topological map, they would be more likely to approach a travel goal from the same direction(s), that is, from the same landmarks or routes every time. However, if there are a sufficient number of landmarks present, or if animals are familiar with approaching a goal from all directions, it would not be possible to distinguish between the mechanisms of navigation. It is also possible that animals that possess Euclidean map spatial awareness approach certain resources from the same direction. The second prediction tested was:

- Travel goals are approached from all directions [supports the use of a Euclidean map, but does not exclude the use of a topological map].
- Travel goals are approached from the same direction using the same landmarks and/or travel routes [supports the use of a topological map, but does not exclude the use of a Euclidean map].

In addition to examining the direction at which goals were approached, the initial direction when leaving a goal was compared to the general direction adopted to reach the next goal. If animals are using a Euclidean map to navigate through the landscape, the difference between these two directions should be negligible since animals would know the exact direction in which to travel towards the next goal and would be able to do so in a goal-directed manner (Normand & Boesch 2009). In contrast, if animals travel using landmarks the difference between these two directions is expected to be higher because animals would have to reorient along the way when encountering landmarks or nodes (Di Fiore & Suarez 2007). However when many landmarks are available, animals may be able to minimize the difference between the two directions even when making use of a topological map. This leads to the final prediction:

- There is no difference between the initial direction when leaving a travel goal and the general direction towards the next goal [supports both the use of a Euclidean map and a topological map].
- The initial direction when leaving a travel goal is different from the general direction towards the next goal [supports the use of a topological map only].

It has been suggested that animals may plan further ahead when foods are limited and as such that cognitive mechanisms may become more evident during the dry winter season (Valero & Byrne 2007). For this reason, the predictions described above were tested for summer and winter separately.

8.2 Methodology

8.2.1 Route based network

Recent studies have attempted to delineate potential networks of repeatedly used travel routes (Di Fiore & Suarez 2007; Presotto & Izar 2010; Hopkins 2011). In doing so however, there has not been a consistent definition of a 'repeatedly used travel route' and different criteria have been used. For instance Di Fiore & Suarez (2007) created habitual route networks for spider monkeys (*Ateles belzebuth*) and woolly monkeys (*Lagothrix poeppigii*) by overlaying all recorded daily travel paths and then identifying, by eye, all paths that appeared to have been used more than once. These 'initial routes' were then permanently included in the habitual route network, when "segments of the individual travel routes were clearly concordant with the proposed initial routes (*i.e.*, they followed the same trajectory as the proposed route for about 100m and lay within 25m of the proposed route)" (Di Fiore & Suarez 2007 p. 320). Presotto & Izar (2010) adapted this method by separating all travel paths in layers and plotting these together by months and then comparing layers between pairs of months for each year. Subsequently pairs of months and all months were combined together and all travel paths repeated within 50m (based upon the visual field) were visually identified (Presotto & Izar 2010). To create habitual route networks for black capuchin monkeys (*Cebus nigritus*) Presotto & Izar (2010) used two criteria: (1) by connecting all paths that were repeated at least two times (*i.e.*, as Di Fiore & Suarez 2007) and (2) by connecting all paths that were repeated at least four times. Although the more demanding criterion of four repetitions did not affect their conclusion that black capuchin monkeys were using habitual routes that they were able to travel far from using novel paths, it did affect the size of the route network and the proportions of location records and feeding trees falling outside the visual detection distance from the route network (*i.e.*, a smaller route network and a higher proportion of location records and out-of-sight feeding trees were found with the more demanding criterion) (Presotto & Izar 2010). To discriminate between the hypotheses that the monkeys are repeating a path because it is part of a topological map or because it leads to memorized feeding locations, Presotto & Izar (2010) used the additional criterion that repeatedly used paths in the same month should be independent of feeding sources. Both these studies identified habitual route networks using vector data in ArcView. In contrast, Hopkins (2011) overlaid all travel paths of mantled howlers (*Alouatta palliata*) upon a grid and categorised each grid cell as containing no pathway, an arboreal pathway, or a repeatedly used arboreal pathway (some cells were classified as containing both an arboreal pathway and a repeatedly used arboreal pathway) using Matlab software (Mathworks 2008) (Hopkins 2011). Repeatedly used arboreal pathway cells were those through which mantled howlers travelled ≥ 45m (based upon the visual field) in length that were used on two or more different days (Hopkins 2011) and this study thus used the same “two times” criterion as Di Fiore & Suarez (2007) and Presotto & Izar (2007). When paths fell within 5m of one another, they were considered to be the same path and a mean path was generated (Hopkins 2011). The result of this method is therefore a grid in which neighbouring cells (5mx5m) categorised as repeatedly used pathways represent path segments (in a range of 45m – 200m in “length”), and the ‘route network’ contained more smaller disconnected “segments” compared to the route networks of the previous two studies (Figure 8.1).

Locational data were recorded as described in Chapter 2 Section 2.3.1. Original paths were ‘cleaned’ up for the purpose of these analyses. All data were filtered so that consecutive track points were separated by a distance of exactly 20m to (1) reduce the errors in the representation of baboon movements caused by observer movement within the troop while recording other behavioural data and (2) remove standstill GPS errors and (3) remove clumps of track points at locations where the troop was more or less stationary for long periods of time, such as near sleeping sites. To do so, all original track points were imported in ArcMap 9.3 and using the “Convert Locations To Paths” function of Hawth’s Analysis Tool, successive records were then joined to create travel paths (N=478), representing daily paths for full follow days (N=234) or partial daily paths for less than full-day samples (N=137). Note that if the troop was lost for any period of time during a (partial) follow day a second path for that same day was created, hence the total number of paths (N=478) exceeds the number of follow days (N=371). These polylines were subsequently smoothed using the “Smooth Line” function (Data Management Toolbox » Generalization) in ArcMap 9.3. The default PAEK smoothing algorithm (Polynomial Approximation with Exponential Kernel) was used with a 50m smoothing tolerance and endpoints for closed lines were preserved. After this, the smoothed polylines were converted back to points with a 20m interval using the “Convert Paths to Locations” function of Hawth’s Analysis Tool. An example of the result of the process of cleaning up track is shown in Figure 8.2.

To determine whether the study animals travelled through a network of habitual routes within their home range, the method devised by Di Fiore & Suarez (2007) was applied. Initial identification of repeatedly used routes was done by overlaying all recorded paths and then identifying, by eye, all paths that appeared to have been used multiple times. These initial routes were sketched and digitized using the Editor Tool in ArcMap 9.3 and were then confirmed by superimposing, one at a time, the individual tracks. Two habitual route networks were created. In the first habitual route network, a route was permanently included in the network when sections of the track followed by the troop were clearly concordant with the proposed route, *i.e.*, they followed the same trajectory as the proposed route for at least 100m and lay within 25m of the proposed route, on at least two different days (Di Fiore & Suarez 2007). In accordance with Presotto & Izar (2010), the probability that the baboons would use the same path twice just by chance, and not because they were constricted to that path, was considered high and as such a more demanding criterion of four repetitions was also adopted.

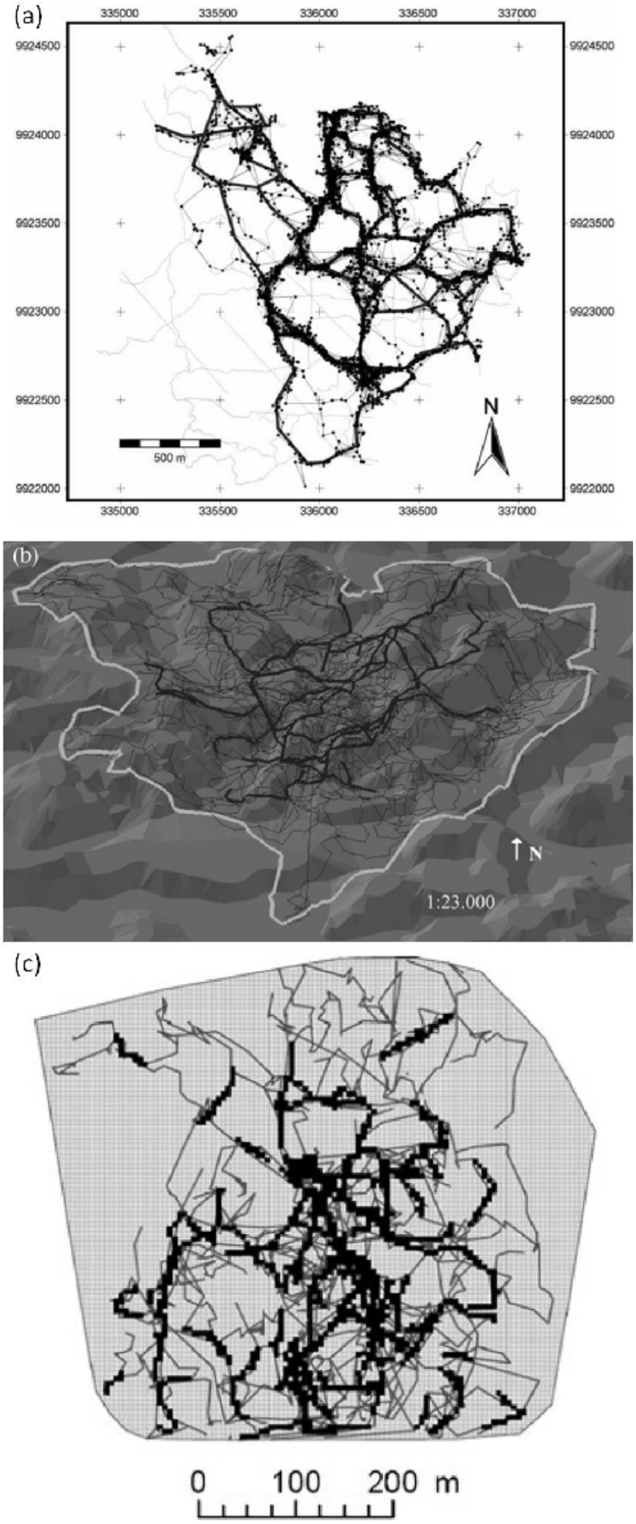

Figure 8.1 Habitual route networks of (a) spider monkeys (Figure 1a in Di Fiore & Suarez 2007) (b) black capuchin monkeys (Figure 3b in Presotto & Izar 2010) and (c) manled howler monkeys (Figure 2a in Hopkins 2011) with daily travel paths (*fine grey lines*) and repeatedly used paths (*think grey lines / black cells*) based on the criterion of two repetitions.

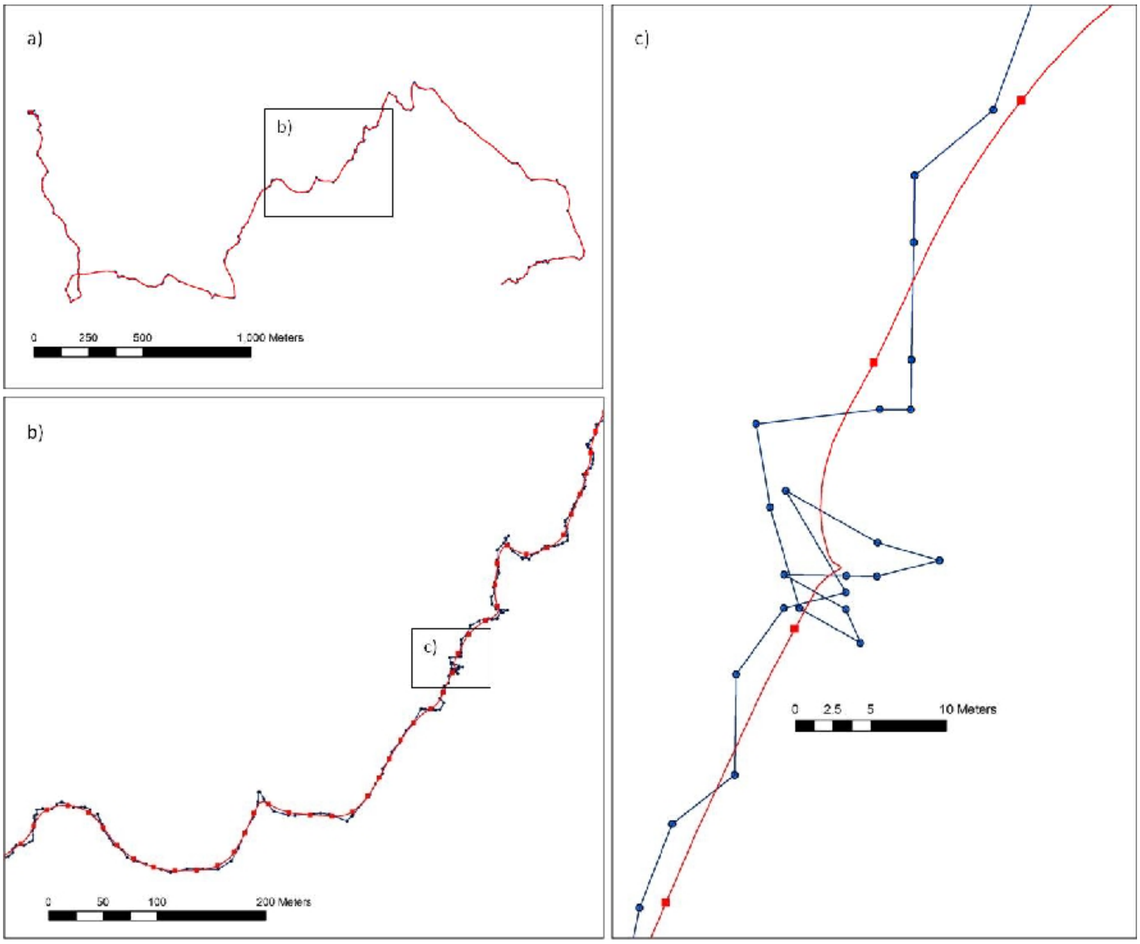

Figure 8.2 Baboon travel route with the original track (*blue line*) with track points (*blue dots*) and the smoothed track (*red line*) with new track points (*red squares*) created after applying the smooth function and converting lines back to points at a regular 20m distance interval. Insets (b) and (c) show the process in more detail.

The second route network was therefore created in which a route was permanently included in the route network when sections of the track followed by the troop were clearly concordant with the proposed route on at least four different days. The resulting two habitual route networks were superimposed on the actual daily routes followed by the baboons. Then, buffer analyses were conducted to estimate the proportion of track points (those with a distance interval of 20m) that fell within 5m, 10m, 15m, and 25m bands around the two habitual route networks, which were defined using the Multiple Ring Buffer tool in ArcMap 9.3.

Where two or more paths within the networks crossed (or joined), the location was defined as an intersection. Intersections may simply be an arbitrary junction of two travel paths, or they could be decision points where the baboons make decisions about where to travel next, being free to choose to turn down any of the intersecting routes, as suggested by Di Fiore and Suarez (2007). To test whether route intersections were decision points, two approaches were used. First the method of Di Fiore and Suarez (2007) was followed and each track was overlaid on the route map one at a time and the approach and leaving directions at each intersection was tallied. When at least two alternate paths were selected at a single intersection from any single approach direction (type 1), or when the same path was taken at an intersection following approaches from different directions (type 2), the intersection was scored as a decision point (Figure 8.3). The second approach to investigate whether route intersections were decision points, was to examine the spatial proximity or overlap between route intersections and change-points identified in Chapter 5. Moreover, the locations of non-resource decision hotspots (Chapter 6) in the network were reviewed.

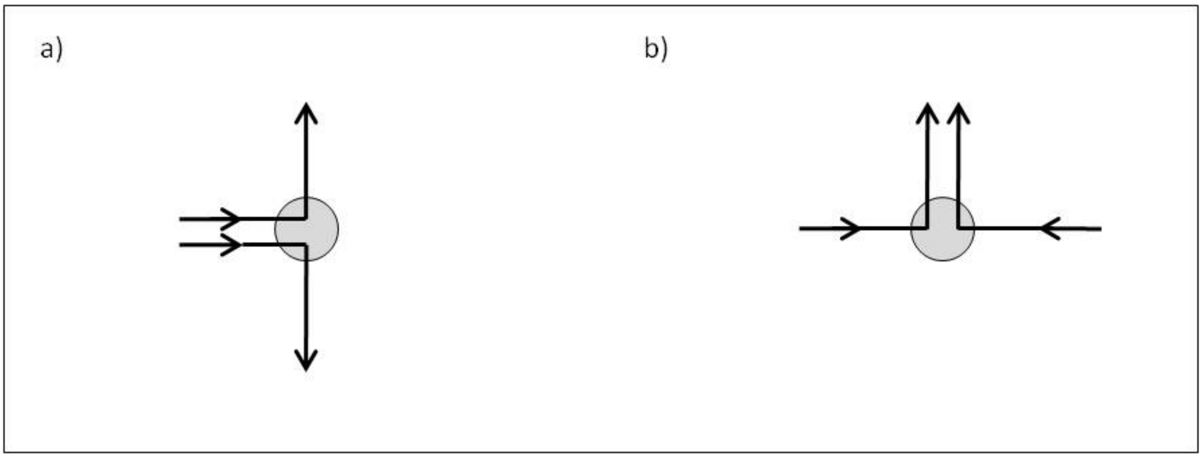

Figure 8.3 Intersections (*grey circles*) were identified as a decision point when (a) at least two alternate paths (*black lines*) were selected at a single intersection from any single approach direction or (b) when the same path (*black lines*) was taken at an intersection following approaches from different directions.

8.2.2 Travel goals

As in the previous chapter, travel goals are those locations identified by change-points (Chapter 5) and resource hotspots are considered to be locations of highly valuable resources and therewith 'major' travel goals (Chapter 6). Predictions resulting from the hypothesised use of Euclidean maps and topological maps were tested for both individual change points as well as for resource hotspots (but see section 8.2.3).

8.2.3 Travel route linearity between core area and periphery

To discriminate between the two navigational mechanisms, linearity of travel routes in the core area and periphery is investigated. The adaptive Local Convex Hull (LoCoH) method (Getz *et al.* 2007) was used to estimate the baboons' home range and core area (Chapter 3 Section 3.2.1). Home range boundaries were delimited by 99% volume isopleths and the core area was defined as that area in which the animals spend 75% of the time (Normand & Boesch 2009) and subsequently travel goals that fell within the core area and within the periphery were identified (Figure 8.4). Note that although some goals fell outside the 99% isopleth home range boundary, these goals were still considered to be within the peripheral area. Since all resource hotspots fell within the core area, this prediction was tested only for change-points.

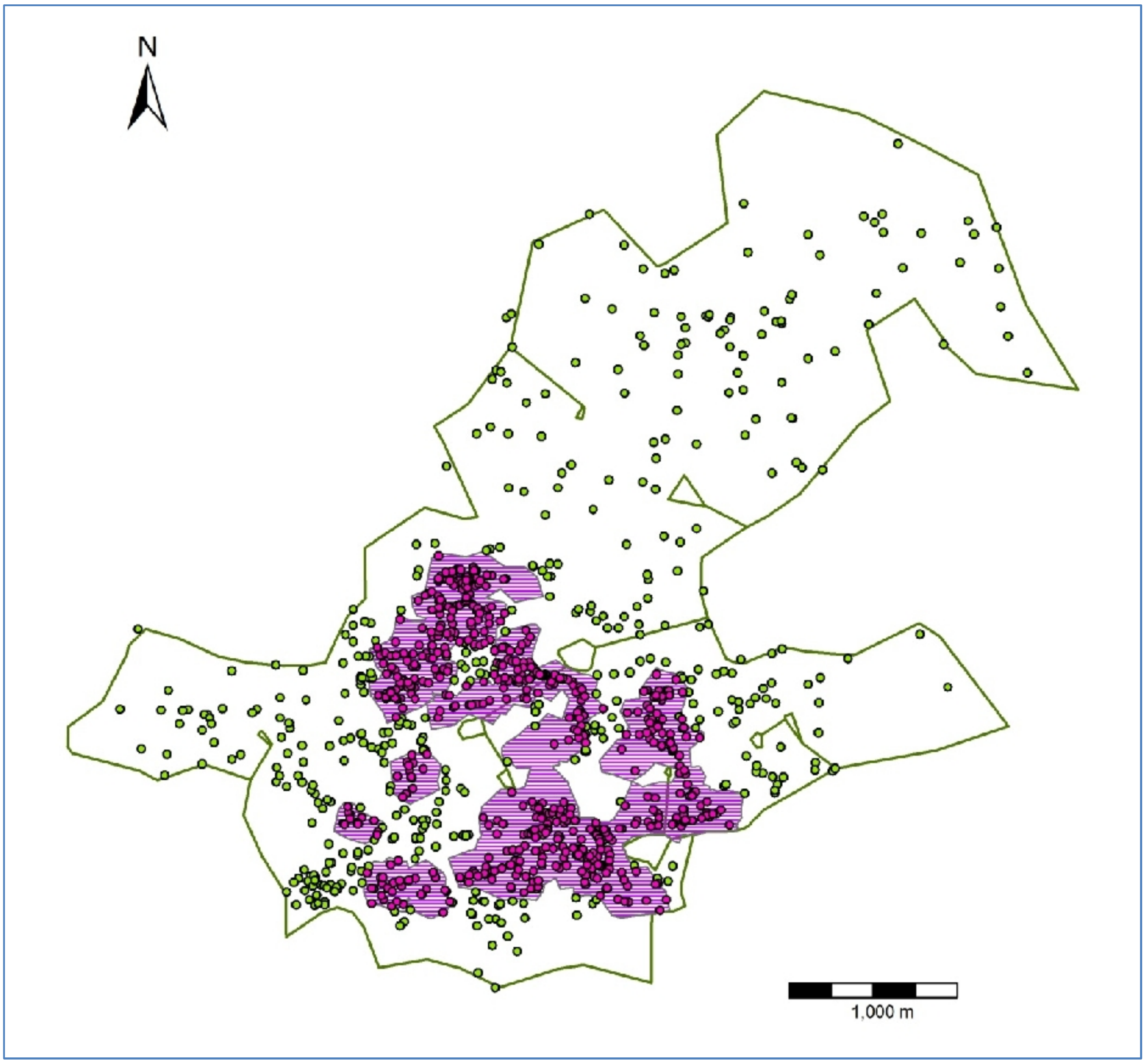

Figure 8.4 Home range boundary (*green line*) and core area (*purple striped area*) delineated by 99% and 75% isopleths respectively, estimated using the adaptive Local Convex Hull (LoCoH) method (Getz *et al*. 2007). Travel goals in the core area (*purple dots*) and in the periphery (*green dots*) are shown.

Path segments were defined as travel between consecutive travel goals and only those path segments that fell entirely within the one or other area (*i.e.*, core area or periphery) were included. Thus, if a change-point was located within the periphery but the next change-point was located within the core area (or vice versa) this path segment was excluded (N=328). A total of 501 segments were included for this analysis, of which 200 in the core area and 301 in the periphery. Path segments consisted of a minimum number of steps of 5 (with a bee-line distance between change-points 162.0m and an actual distance travelled of 246.7m), which was considered to be large enough to avoid the bias of short steps which would, in the case of a topological map, be linked to too few landmarks (Normand & Boesch 2009).

Path linearity was calculated for each path segment using a linearity index between 0 and 1 (the R value in Batschelet 1981), computed as the ratio between the beeline distance (D) between two consecutive change-points (*i.e.*, the beeline distance of the path segment) and the actual route length travelled (*i.e.*, the sum of individual step lengths) (see Chapter 7 Figure 7.2): the closer linearity index approaches the value 1, the smaller the angular deviation of the vectors, and thus the more linear the corresponding segment.

8.2.4 Approach direction

For each travel goal the direction of approach was analysed every time a travel route intersected with the goal location in that season, regardless of the time spent at the location or whether a possible resource at the location was used or not, since these factors do not influence the prediction for the different map types used. First, travel routes that intersected with the locations of change-points and resource hotspots were identified using spatial joins between travel routes (represented by waypoints) and resources created in ArcMap 9.3 [Analysis Tools toolbox > Overlay > Spatial Join] using "closest" as match option. Convex hulls identified the location of resource hotspots, while the locations of change-points were represented by the point location of the change-point buffered by 10m buffer using Hawth's Analysis Tool, an analytical add-in for ArcMap 9.3. An additional distance field was created for each waypoint, showing the distance to the closest resource hotspot and when waypoints were located within the resource location (*i.e.*, within the convex hull for RH) distance was zero. Change-points and resource hotspots identified for summer were joined only to summer routes and change-points and resource hotspots identified for winter only to winter routes.

Final steps approaching travel goals were subsequently identified as travel between the waypoint with a distance value of zero (*i.e.*, the waypoint fell within the resource hotspot convex hull or within the change-point buffer) and its previous waypoint. Note that travel within resource hotspots was not considered as an 'approach'. Thus, if multiple subsequent waypoints fell within resource hotspots (*i.e.*, subsequent waypoints with a distance value of zero), the final approach step was calculated between the "first" waypoint that fell within the resource hotspot and its previous waypoint as illustrated by Figure 8.5. Due to the small buffer around change-points and to the 35m distance filter that was applied to the data beforehand, this situation did not occur for change-points.

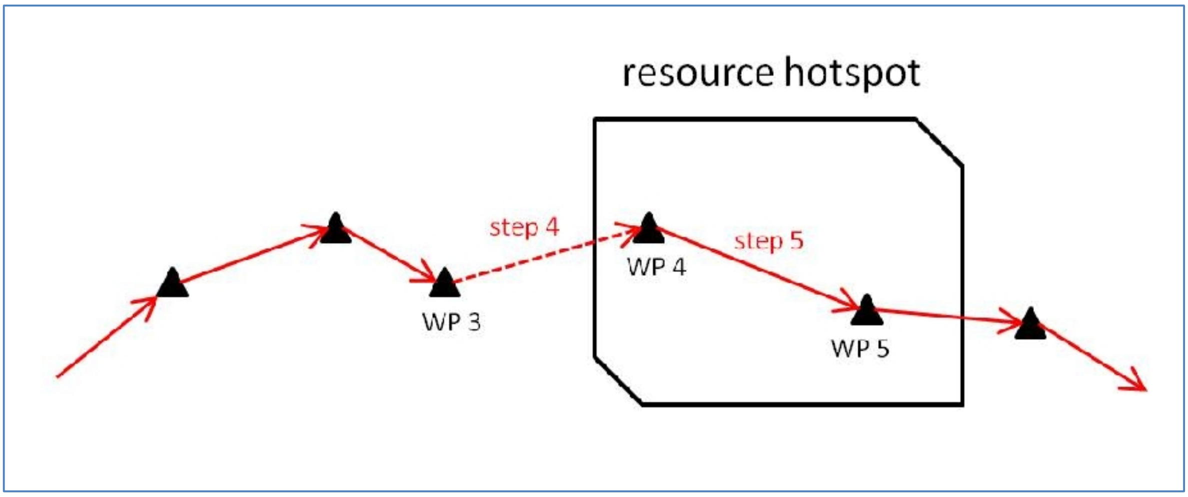

Figure 8.5 If multiple waypoints (WP) fell within resource hotspots (*black rectangle*) (WP4 & WP5) the final step (*dashed red line*) was determined as travel between the "first waypoint" that fell within the resource hotspot (WP4) and its previous waypoint (WP3). Thus step 5 is not included in the analysis.

The direction of each final step approaching a resource was calculated using the circular statistics software program *Oriana* (Kovach Computing Services 2009). Coordinates of waypoints with distance value of zero (which represents the end point of the final step: XY end) and coordinates of its previous waypoint (which represents the start point of the final step: XY start) were entered in Oriana and were converted to an angle. In the conversion process the starting point is translated to the origin of the circular graph, so the angle is the direction towards which the end point is pointing. Hence, directions of the final step approaching resources were calculated as a compass direction (deviation from the True North) between 0° and 360°.

Approach directions of the final steps approaching change-points and hotspot resources were analysed per resource hotspot and per 'change-point location'. Change-points were highly clumped and when at the same location represented the same travel goals. For example, a large fruiting fig tree could be an important goal of travel for an extended period of time and thus a change-point would be identified for each day that the baboons oriented towards this fig tree. Therefore, approach angles were grouped (per season) over change-points with overlapping buffer areas (*i.e.*, that were closer than 20m together) and analysed per change-point 'location'. This situation is illustrated in Figure 8.6 in which change-points 59, 62 & 65 and change-points 94, 101 and 110 are grouped together, resulting in 6 unique change-point locations for which approach angles were analysed. For summer, 79 change-points were grouped into 45 change-point locations. Together with the remaining 335 change-points make a total of 380 separate summer change-point locations. For winter, 172 change-points were grouped into 71 change-point locations, which together with the remaining 444 change-points for that season make a total of 514 separate winter change-point locations (totalling to 894 change-point locations throughout the year). Each change-point location (*i.e.*, travel goal) was given a unique ID based on the season during which the (grouped) change-points were identified, followed by a number (*e.g.*, SUM-783 and WIN-11).

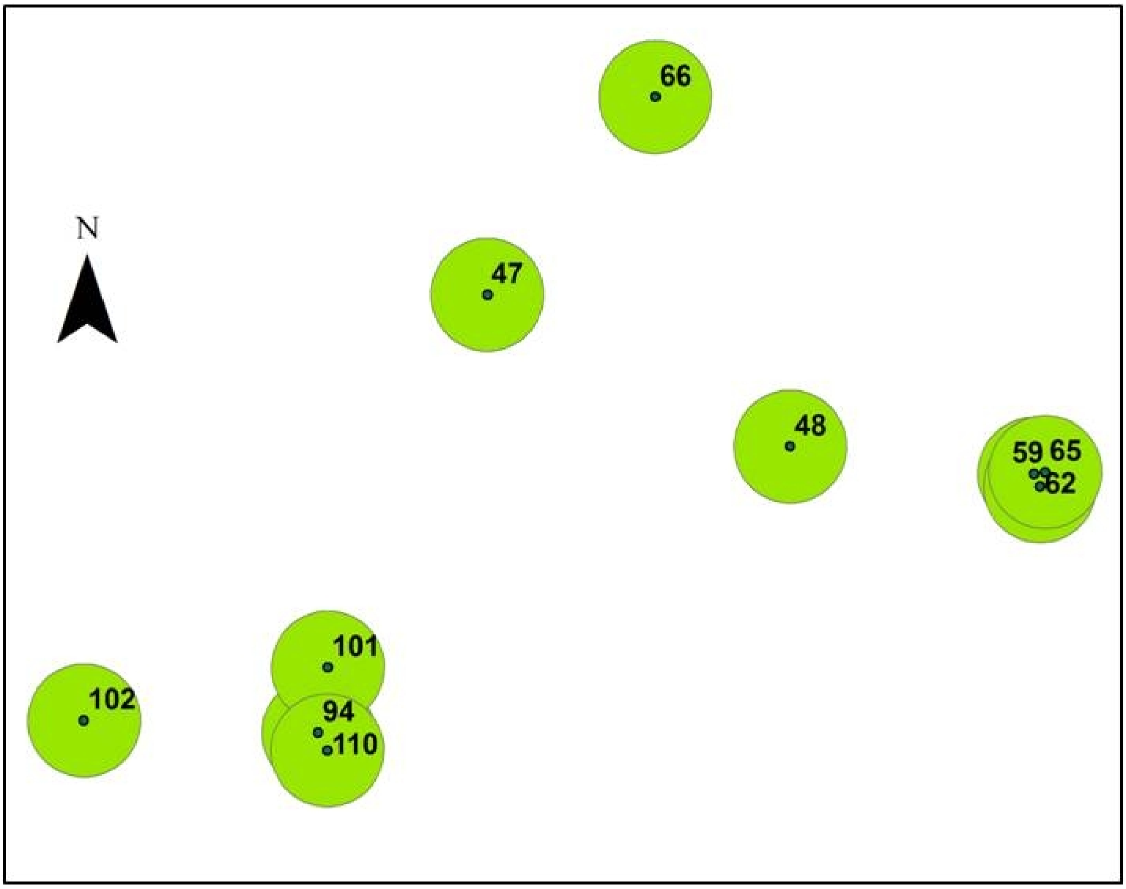

Figure 8.6 Change-points (*points*) were buffered with a 10m buffer (*polygons*) and subsequently grouped into unique change-point locations when buffer areas overlap (change-points 101, 94 & 110 and change-points 59, 62 & 65 were grouped into 2 unique locations). Approach angles were subsequently grouped for each change-point location and analysed per location (here 6 unique locations).

To examine the distribution of final approach directions around the circle, one parametric and two non-parametric tests were performed for each change-point location and each resource hotspot (*i.e.*, for each [major] travel goal) separately. The parametric Rao's spacing test takes as its null hypothesis that the data are uniformly distributed. This is tested by looking to see if the spacing between adjacent points is roughly equal around the circle. For uniform distribution the spacing between points should be roughly 360°/n. If the actual spacings deviate too much from this value then the likelihood that the data are uniformly distributed is reduced. This test can be more powerful than the commonly used Rayleigh test (*e.g.*, Valero & Byrne 2007), especially when the data are bimodal (Kovach 2009). The Rayleigh test is another measure of circular spread to determine departure from uniformity, based on the length of the mean vector. When the length of a mean vector is very small, this indicated a uniform distribution, whereas if the length of a mean vector is very large this indicates a clumped distribution. However, when data are bimodal, this also results in a small vector length and as a result the Rayleigh test wrongly gives non-significant results. This situation is illustrated in Figure 8.7

where the hypothetical data do not seem to be uniformly distributed around the circle, but instead appear to be bimodal. Since the length of the mean vector is very small (note the short arrow from the centre), the Rayleigh test gives a non-significant test result (*i.e.*, concludes that the data is not significantly different from a uniform distribution). Rao's Spacing test however, gives a probability less than 0.01 for these hypothetical data, and the null hypothesis of uniformity can be rejected.

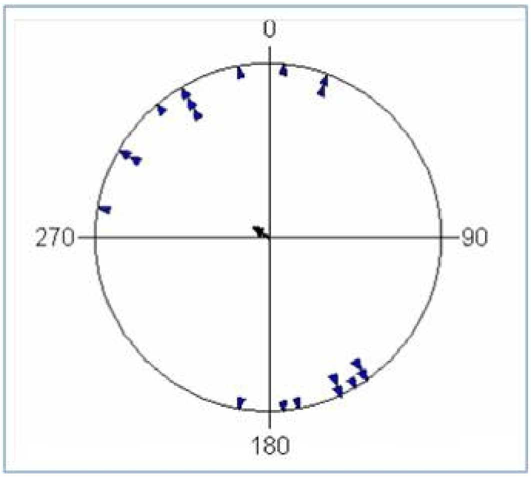

Figure 8.7 Circular raw data plot (Kovach 2009) with example data appearing to be bimodal (non-uniform).

The Watson's U^2 test (Fisher 1993 p. 84; Mardia & Jupp 2000 p. 104; Zar 1999 p. 657; Batschelet 1981 p. 79) performs a goodness-of-fit test against a uniform distribution. It does this by calculating the mean square deviation for the fitted distribution. If the deviation is too high (resulting in a high U^2 and a low probability), then the null hypothesis that the data fit the uniform distribution is rejected. The modified statistic is used, as shown in Fisher's (1993) formula 4.36 or Mardia & Jupp's (2000) formula 6.3.36.

Finally, Kuiper's test (Fisher 1993 p. 66; Mardia & Jupp 2000 p. 99; Batschelet 1981 p.76), which takes the alternative approach of directly comparing the distribution of the data to the uniform distribution, was performed. This test is comparable to the Kolmogorov-Smirnov test in linear statistics, which is based on the maximum deviation of the observed distribution from the expected. In *Oriana* the uniform distribution is represented graphically in distribution plots by a diagonal line and Kuiper's V statistic is based on the largest vertical deviations above and below the diagonal line. Too great a deviation, giving a high V and low probability, leads to rejection of the null hypothesis that the data fit the distribution. The formula used incorporates the correction factor shown in Fisher's (1993) equation 4.12 and Mardia & Jupp's (2000) equation 6.3.30.

Since the number of approach angles varied greatly per change-point location (range: 1 – 41) and per resource hotspot (range: 42 – 114), initially the influence of the number of approach angles on the distribution was investigated. Four change-point locations with sample sizes greater than 20 were randomly selected and 4 sub-samples with sample sizes 5, 10 and 15 were created for each change-point location with randomly selected approach angles. Selections of change-point locations and approach angles were both carried out using the “Create Random Selection” sampling tool of Hawth’s Analysis Tools. The distributions of the different subsamples were compared.

Distributions of approach angles were illustrated by circular diagrams. These graphs are similar to rose diagrams, but they are made up of parallel-sided bars that show the number of observations within each class range. The actual width of the bars (equal to the width of the class range) was set to 10°. The mean of the data was represented by (black) straight lines from the centre of the circle and the arcs extending to either side represent the 95% confidence limits of the mean. Confidence limits can be unreliable when the combination of the sample size and the concentration is low, in which cases the confidence limit arc was displayed in red instead of black.

8.2.5 Leaving directions

Initial leaving steps (lv1) were identified as travel between the first waypoint that fell outside the travel goal location (*i.e.*, outside the resource hotspots or change-point buffer) and its previous waypoint. Travel within resources (*i.e.*, travel between two consecutive waypoints with a distance value of zero) was not considered a ‘leaving’ step as illustrated by Figure 8.8.

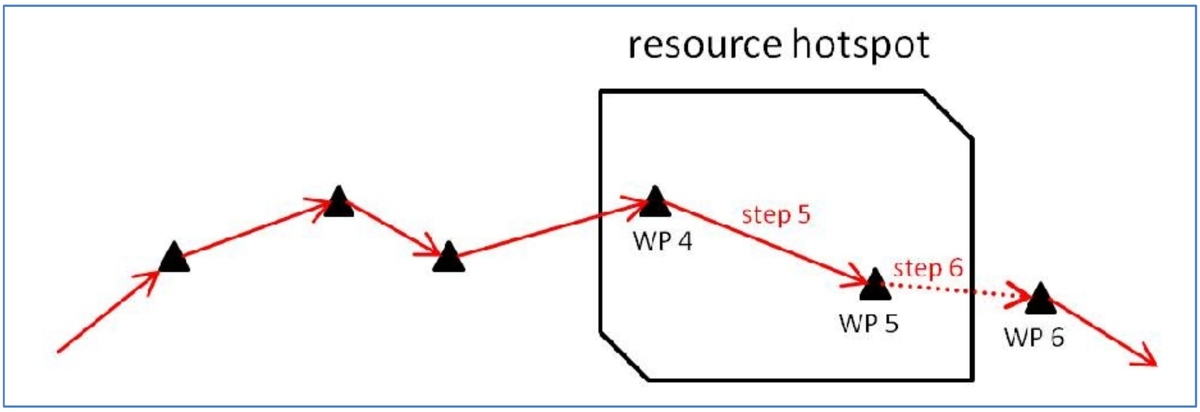

Figure 8.8 If multiple waypoints (WP) fell within resource hotspots (*black rectangle*) (WP4 & WP5) the initial leaving step (*dotted red line*) was identified as travel between the first waypoint that fell outside the resource hotspot (WP6) and its previous waypoint (WP5). Thus step 5 is not included in the analysis.

Coordinates of waypoints that fell within goal locations represented start points of initial leaving steps (with XY start initial) and subsequent waypoints represented end points of initial leaving steps (with XY end initial). General directions were calculated as the direction to the next change-point. Since baboons did not visit resource hotspots every full-day follow, and even less frequently visited multiple resource hotspots in one full-day day, it was not possible to investigate general direction from one resource hotspots to the next, as done for change-points. For resource hotspots therefore, the general direction was measured as the direction to the 8th waypoint recorded after leaving the resource hotspot (Figure 8.9). A trajectory of 8 steps to measure general direction was selected, since the travel distance of these trajectories (403m ± 94.6m) was similar to the mean bee line distance between important resources (438m) and much larger than the visibility (82m ± 35m) in the nearly Blouberg mountains (Noser & Byrne 2007b). Moreover, trajectories of 8 steps were selected to avoid the bias of shorter trajectories which may, in the case of a topological map, be linked to too few landmarks (for this same reason did Normand & Boesch [2009] select only resources with more than 4 steps [mean segment length of 294m] between them). Coordinates of the waypoint that fell within the goal location represented the start point (with XY start general) and the coordinates of either the next change-point or, for resource hotspots, the 8th waypoint, were the end point of the general direction vector (with XY end general). The coordinates were then converted to an angle in *Oriana* representing the initial direction and general direction that the baboons left travel goals. In the conversion process the starting point is translated to the origin of the circular graph, so the angle is the direction towards which the end point is pointing. Hence, initial and general leaving directions were calculated as a compass direction (deviation from the True North) between 0° and 360° (Di Fiore & Suarez 2007; Normand & Boesch 2009) (Figure 8.9).

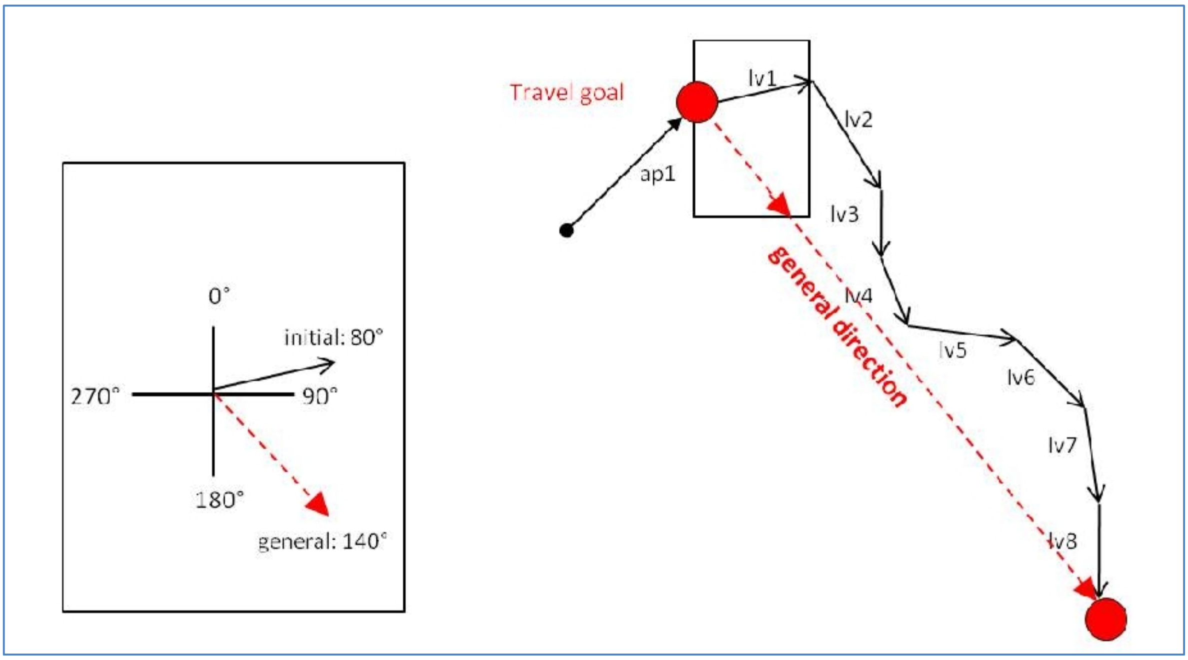

Figure 8.9 Initial direction (80°) when leaving a travel goal (*red circle*) (*i.e.*, direction of the first leaving step [lv1]), measured as the angle deviation from True North between 0° – 306°, see inset) was compared to the general direction (140°) adopted to eventually reach a next goal (*red circle*) using a pairwise circular statistical test. Moreover, the deviation between initial leaving direction and general direction (60°) was compared to a straight line, taking GPS error into account (15.82°). Note that travel between consecutive change-points can be smaller or larger than 8 steps, but that for resource hotspots the general direction was consistently calculated over 8 steps.

Initial directions and general directions were first directly compared to one another using two circular pairwise multisample tests. Since neither the distribution of initial or general directions per season and per step fitted the Von Mises distribution (Watson's U^2 Test and Kuiper's Test: $p<0.01$), the non-parametric Chi-Squared test (Batschelet 1981 p.109) and Mardia-Watson-Wheeler test were applied in *Oriana*. The Chi-Squared test determines whether general directions differ significantly from each other in some unspecified way. The data were grouped into classes with a class width manually set to 10°. In order to obtain reliable test results and classes without any observations were ignored (which is particularly useful if observations are clustered fairly closely around the mean, with the result that a large portion of the circle will not have any data) (Kovach 2009). The Chi-Squared statistic was then calculated based on the differences between the observed frequencies of the samples. The p value calculated for each test is the probability associated with the null hypothesis that the samples are drawn from the same population and if this probability was less than the chosen significance level of 0.05, then the null hypothesis was rejected in favour of the hypothesis that the samples are from different populations that differ in some way. The difference may be in the distribution, mean direction, or other parameter; further investigation is then needed to determine the precise difference is between the two samples.

The second pairwise multisample test was the Mardia-Watson-Wheeler Test (Fisher 1993 p.122; Mardia & Jupp 2000 p.147; Batschelet 1981 p.101; Zar 1999 p. 633), also called the Uniform Scores Test, which is a non-parametric test for determining whether two or more distributions are identical. The basic premise is that the samples are pooled together, sorted into increasing angles, which are then evenly distributed around the circle by calculating a uniform score (or circular rank). If the distributions of the samples are identical, then the new uniform scores for the samples should be evenly interspersed around the circle, and their resultant vector lengths R should be short and similar. Any significant difference between the Rs will lead to a large W test statistic and rejection of the null hypothesis of identical distributions.

The second way to investigate whether initial directions significantly differed from general leaving directions was to examine the deviation between the two directions (Figure 8.9). If baboons know the precise direction to travel towards the next goal, their travel route is expected to resemble straight line travel and so under the Euclidean map hypothesis the deviation between the initial and general leaving directions was expected to approach zero. Potential error in GPS accuracy had to be taken into account since this may influence the expected deviation from a straight line. Although GPS error was almost always less than 8 meters (*personal observation*), it was not systematically determined in this study. However, the inaccuracy of the GPS model used in this study was determined under lowland rainforest circumstances where it was found to be ± 14.2m (Normand & Boesch 2009). For example, for a distance travelled of 50m (which represents the mean distance between two consecutive waypoints), the consequences of the inaccuracy of the GPS (14.2m) to measure the correct angle would be 15.82° and the linearity index would become 0.9619 instead of 1 theoretically for a straight line (Normand & Boesch 2009). Therefore, deviation was considered to be significantly different from a straight line if it was larger 15.82°.

To ensure that all deviation values lay between 0° and 180° the deviation between the initial and general leaving direction was calculated as follows:

| Initial direction – General direction |

When | Initial direction – General direction | > 180:

360 - | Initial direction – General direction |

Since deviation was calculated between 0° and 180° it could be treated as a linear variable and as such was analysed using linear statistics. A one-sample Kolmogorov-Smirnov test showed that the data were significantly different ($p<0.01$) from a normal distribution and that deviation data were highly skewed towards zero for the year, summer and winter separately at all scales over which the general direction was measured (2-8 steps) (Skewness values ranged from 1.145 to 2.947). To ensure the data approximated to a normal distribution, a third-root transformation was applied ($[\text{deviation}]^{1/3}$) (Zar 1999). Subsequently, one-sample T-tests were performed in PASW Statistics release version 17.0.0 (SPSS Inc. 2008), with an expected value of 2.51 ($[\text{GPS error}]^{1/3}$).

8.3 Results

8.3.1 Route-based network

Tracing of habitual paths using the two repetitions criterion revealed a dense network of repeated routes almost spread entirely over the troop's total range (Figure 8.10a). When the four repetitions criterion was used to trace the habitual routes network, the spatial range of the created network was not so much more limited, but it was clearly less dense than route network based on tracks using the two repetitions criterion (Figure 8.10b).

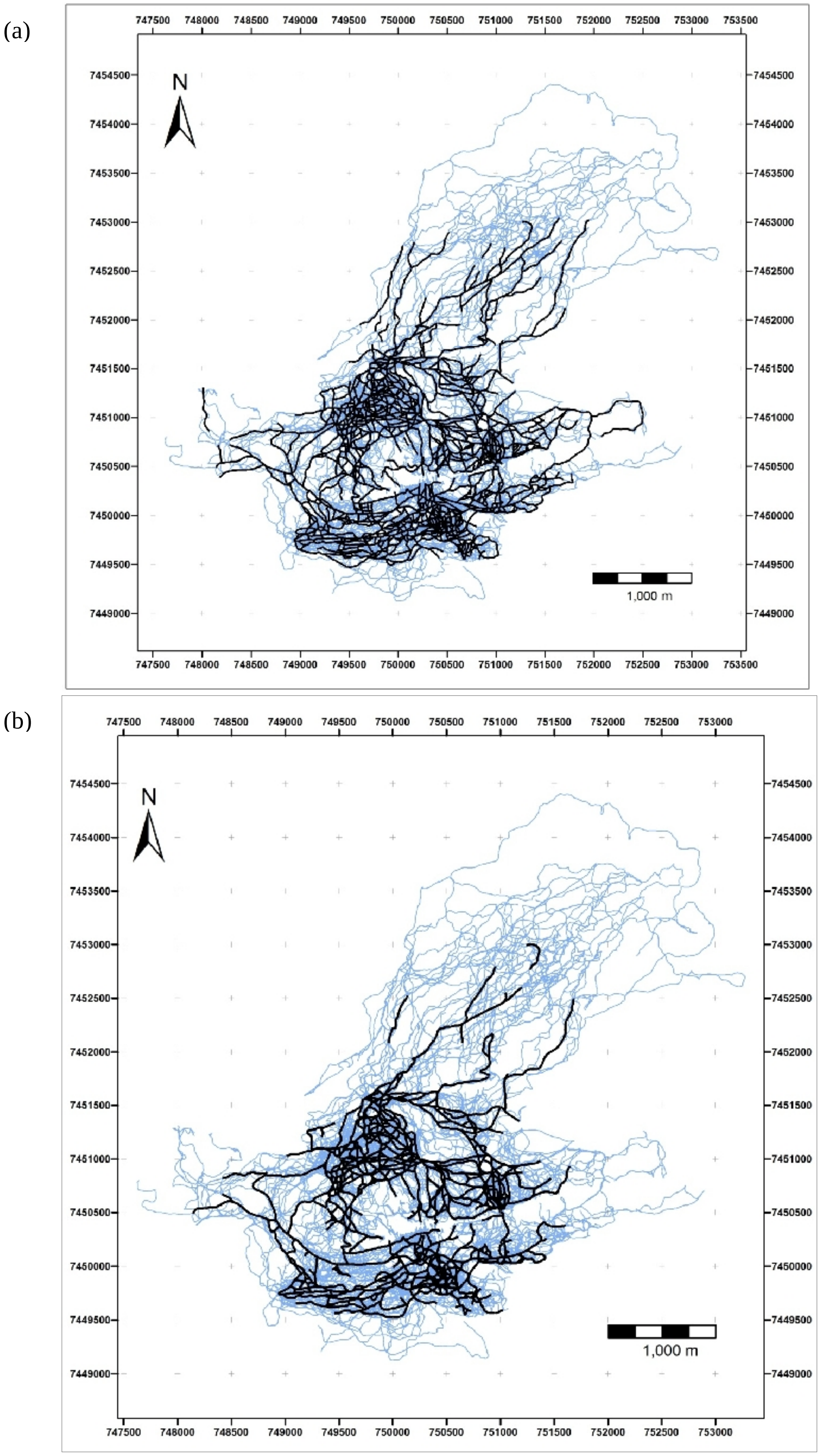

Figure 8.10 Travel paths (N=478) (*fine blue lines*) of baboons at Lajuma research centre, South Africa with the network of travel paths used (a) ≥ 2 times and (b) ≥ 4 times (*thicker black lines*) superimposed.

The numbers of location records did not fall equally within the 5, 10, 15, 20, 25 bands around the habitual network created using the criterion of two repetitions (total location records: df=4, χ^2 =137116.5, p<0.001) or four repetitions (total location records: df=4, χ^2 =113593.6, p<0.001) (Table 8.1). This suggests that baboons range significantly more in the vicinity of the route network than further away from the route network.

Table 8.1 Percentage of all location records (N=97,734) that fell within the different bands around the habitual route networks using the two and four repetitions criteria.

Buffer	2 x network	4 x network
5	60.7%	53.6%
10	13.7%	13.3%
15	6.4%	5.9%
20	3.6%	3.9%
25	2.2%	2.7%

The percentage of location records fell within 25m of the habitual route networks was 86.5% for the network using the two repetitions criterion and 79.5% for the network using the four repetition criterion (Figure 8.11). Moreover, for both networks more than 50% of all location records fell within 5m of the network routes (Figure 8.11).

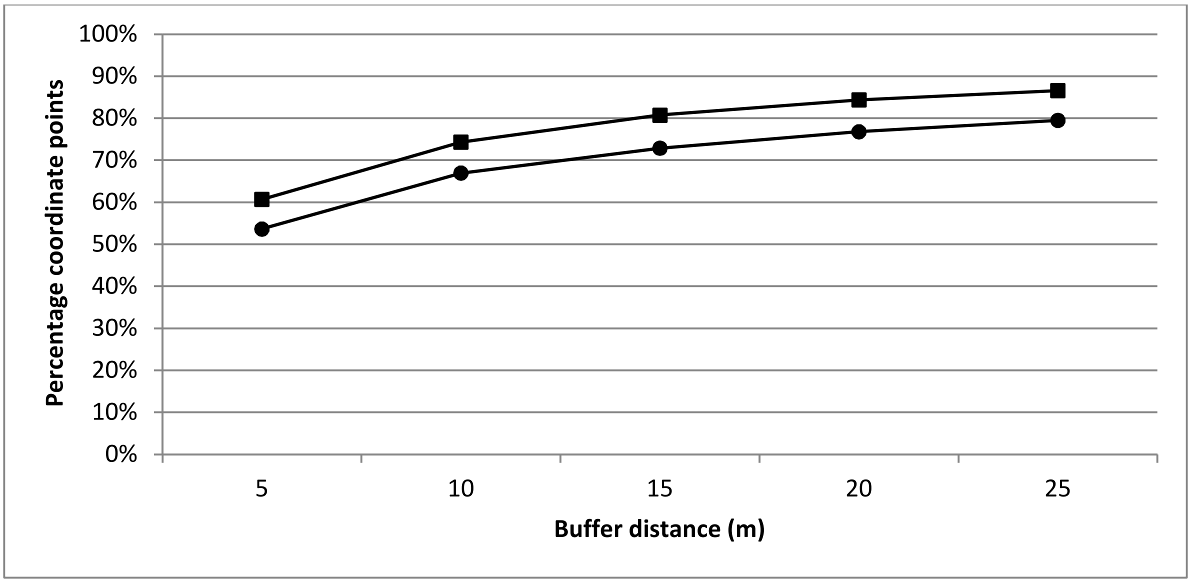

Figure 8.11 Cumulative proportion of location records that fell within successive 5m distance bands around habitual routes based on two repetitions (*squares*) and four repetitions (*dots*).

In total 657 intersections were identified in the habitual route network based on four repetitions. Consistent with the idea of a topological map, 86% (N=565) of intersections were also confirmed as decision points. Moreover, 42% (N=268) of all intersections were found at the same location as a change-point and 92% (N=589) of intersections were located within 50m of a change-point.

In fact, many of the network route segments were used repeatedly on more than 10 days and some on more than 50 days. When a much more demanding criterion of 10 or more repetitions was applied to the baboons' travel routes, to identify the routes that are used more intensively, this revealed a route network of 'highways' (Figure 8.12). Under this stringent criterion, 56% of all location records still fell within 25m of the highway network. Interestingly, decision hotspots identified in Chapter 6 coincided with intersections in the highway network (Figure 8.12). This confirms the idea that baboons repeatedly make travel decisions at these locations.

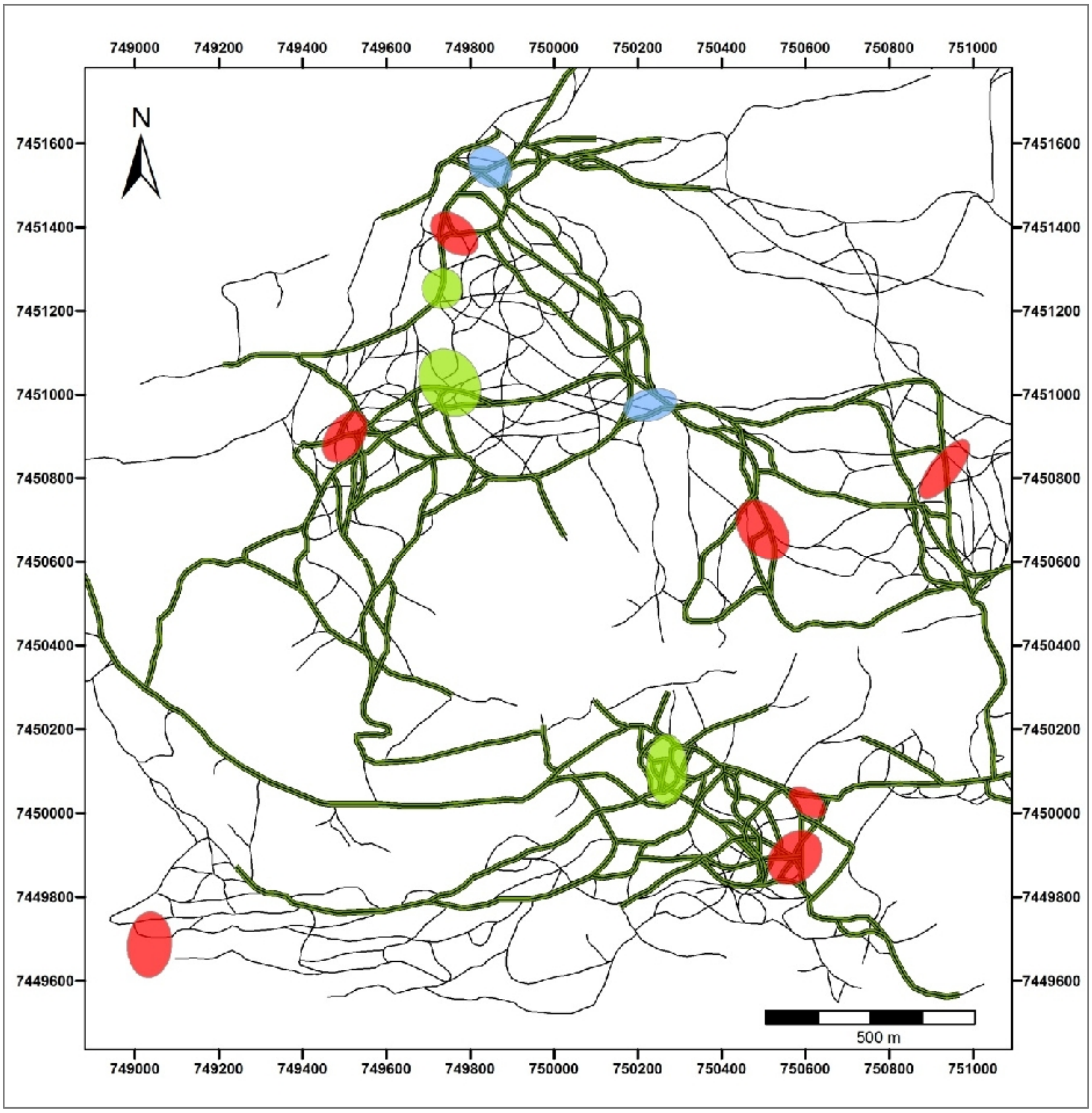

Figure 8.12 Habitual route network (*thin grey lines*) created based on the 4 repetition criterion and the highway network created based on 10 repetition criterion (*thick green lines*), with non-resource decision hotspots (*red ellipses*), resource decision hotspots (*green ellipses*) and both decision hotspots (*blue ellipses*) as categorised in Chapter 6 Section 6.3.5.

8.3.2 Travel route linearity between core area and periphery

The linearity of travel segments in the core area (N=200, median LI=0.815) was not significantly different from the linearity of path segment in peripheral areas (N=301, median LI=0.808) (Mann-Whitney U test: U=29352.0, Z= -0.471, p=0.637), which does not support the use of a topological map. Furthermore, no significant difference in distance travelled or straight-line distance between goals between the core area and the periphery was found (Mann-Whitney U test: U=29051.0, Z= -0.661, p=0.509 and U=28888.0, Z= - 0.764, p=0.455 respectively).

8.3.3 Approach angles

8.3.3.1 Effect of sample size

For all four selected travel goals, the distribution of approach angles (all with a sample sizes of 22) were significantly different from a random (Rao's Spacing Test p<0.05) and uniform (Watson's U^2 Test and Kuiper's Test p<0.05) distribution (Table 8.2). Thus, approach directions were significantly clumped and baboons did not approach goals from all directions but instead used a subset of potential direction(s). This is confirmed when looking at the distribution of approach angles in a circular diagram (Figure 8.13).

Table 8.2 Four travel goals (*i.e.*, change point locations) (with N>20) were selected to test whether the observed distribution could be influenced by the number of approach angles.

	SUM-783	SUM-877	WIN-11	WIN-235
Number of Approach Angles	22	22	22	22
Mean Vector (µ)	213.3°	290.4°	303.7°	56.3°
Length of Mean Vector (r)	0.218	0.148	0.399	0.275
Rao's Spacing Test (U)	227.5	225.7	171.0	239.0
Rao's Spacing Test (p)	< 0.01	< 0.01	< 0.05	< 0.01
Watson's U^2 Test (Uniform, U^2)	0.306	0.215	0.267	0.383
Watson's U^2 Test (p)	< 0.005	< 0.05	< 0.025	< 0.005
Kuiper's Test (Uniform, V)	2.233	1.972	1.956	2.424
Kuiper's Test (p)	< 0.01	< 0.025	< 0.025	< 0.01

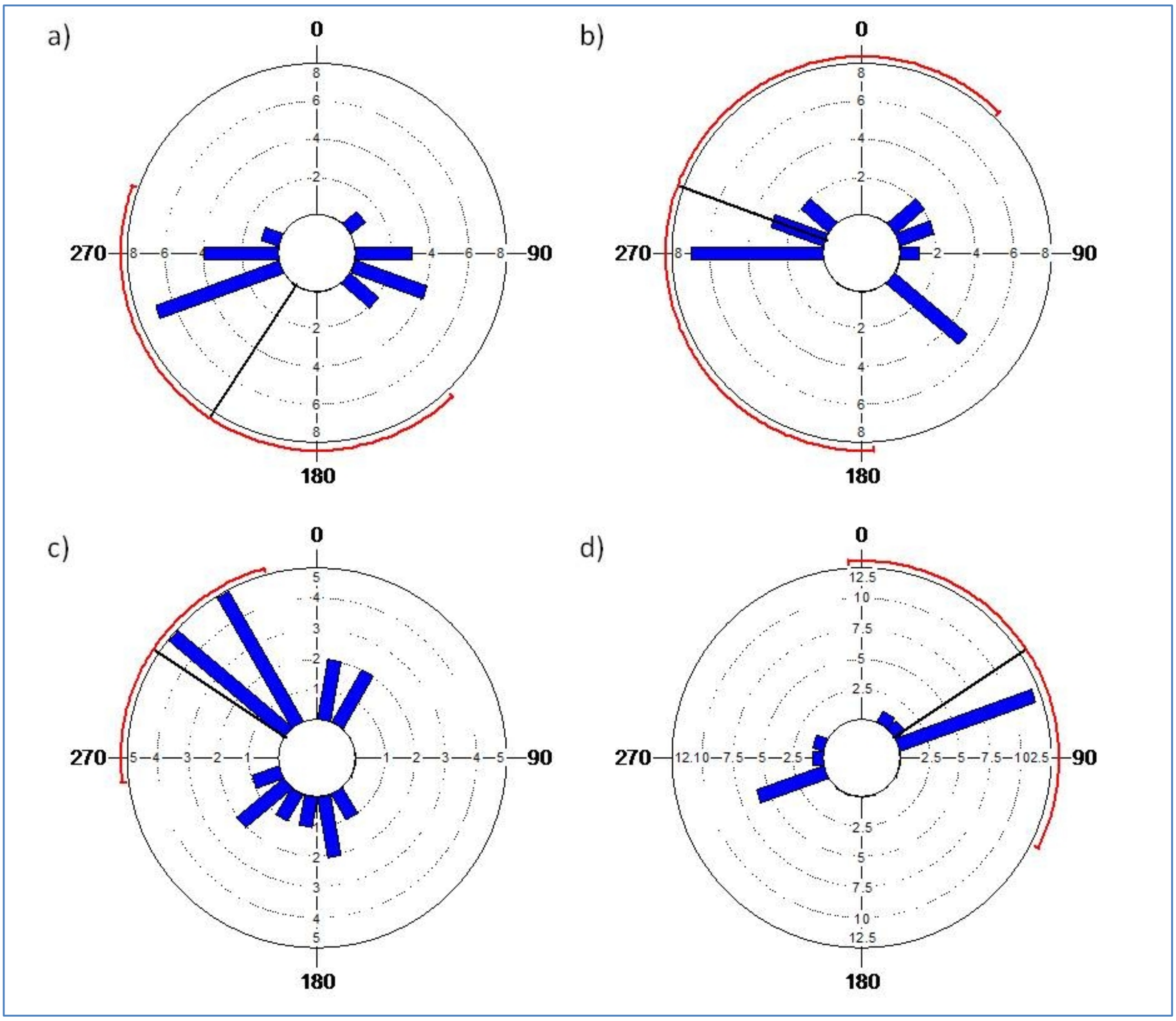

Figure 8.13 Distribution of 2 selected goals for summer (SUM-783 and SUM-877) and 2 selected goals for winter (WIN-11 and WIN-235) (a-d respectively). Note that the parallel side bars (10° width) show the number of observations within each class range (width of class range is 10°), but that the linear scale of the axis varies between resources (for a-b each dotted circle represents 2 observations, for d each dotted circle represents 1 observation and for d each dotted circle represents 2.5 observations).

Sub-sampling the number of approach angles to a sample size of 5 affected the results of all three tests (Table 8.3). Watson's U^2 test was unable to calculate any results due to the low sample size, while Kuiper's test now showed a non-significant result ($p<0.05$) when sub-sampling to 5 approach angles for all goals, indicating a uniform distribution of approach angles. A similar trend was observed for Rao's Spacing test, which showed that the distribution of approach angles for SUM-783 was still significantly clumped (N=5, U= 199.1, $p<0.05$), while for the other 3 goals non-significant results ($p>0.05$) were found, indicating a random distribution of approach angles.

Table 8.3 Sub-sampling the original number of approach angles from 22 to 5 greatly affected the tests results. Stars indicate test results that could not be calculated due to small sample size. Only Rao's Spacing test showed that the approach angles to goal SUM-783 were significantly different than a uniform distribution.

	SUM-783	SUM-877	WIN-11	WIN-235
Number of Approach Angles	5	5	5	5
Mean Vector (μ)	219.5°	276.8°	322.1°	273.5°
Length of Mean Vector (r)	0.412	0.596	0.596	0.269
Rao's Spacing Test (U)	199.1	172.3	144.1	154.6
Rao's Spacing Test (p)	< 0.05	> 0.05	> 0.10	> 0.10
Watson's U^2 Test (Uniform, U^2)	*****	*****	*****	*****
Watson's U^2 Test (p)	*****	*****	*****	*****
Kuiper's Test (Uniform, V)	1.491	1.696	1.5	1.402
Kuiper's Test (p)	> 0.15	> 0.05	> 0.15	> 0.15

When sample size was increased to 10 approach angles, results were somewhat inconsistent between tests and between goals (Table 8.4). For SUM-783, Rao's Spacing test again showed that the distribution of approach angles was significantly clumped (N=10, *U*= 176.0, p<0.05), although both Watson's U^2 test and Kuiper's test showed that the distribution was uniformly distributed (p>0.15) around the circle. For SUM-877, Rao's Spacing test showed a significantly clumped distribution of approach angles (N=10, *U*= 182.0, p<0.05), as did both Watson's U^2 test and Kuiper's test show a uniform distribution (N=10, p>0.15). For WIN-11 all three tests showed that that approach angles were not significantly clumped (N=10, p>0.10), while for WIN-235 all three tests showed that approach angles were significantly clumped (Rao's Spacing test: N=10, U=255.0, p<0.01; Watson's U^2 test: N=10, U^2=0.206, p<0.05; Kuiper's test: N=10, *V*=1.944, p<0.025).

Table 8.4 Sub-sampling the original number of approach angles from 22 to 10 affected test results for all four travel goals (see text for more detail).

	SUM-783	SUM-877	WIN-11	WIN-235
Number of Approach Angles	10	10	10	10
Mean Vector (μ)	197.1°	43.1°	278.6°	79.2°
Length of Mean Vector (r)	0.095	0.232	0.34	0.205
Rao's Spacing Test (U)	176.0	182.0	138.1	254.9
Rao's Spacing Test (p)	< 0.05	< 0.05	> 0.10	< 0.01
Watson's U^2 Test (Uniform, U^2)	0.104	0.102	0.092	0.206
Watson's U^2 Test (p)	> 0.25	> 0.25	> 0.25	< 0.05
Kuiper's Test (Uniform, V)	1.316	1.438	1.289	1.944
Kuiper's Test (p)	> 0.15	> 0.15	> 0.15	< 0.025

When sub-sampling the original number of approach angles from sample sizes of 22 to 15, the results for the four goals were no different than those for the original sample sizes and all three tests consistently showed that for all change-points distributions of approach angles were significantly clumped (Table 8.5).

Table 8.5 Sub-sampling the original number of approach angles from 22 to 15 did not affect tests results and approach angles to the four goals were significantly clumped for all three tests.

Column1	SUM-783	SUM-877	WIN-11	WIN-235
Number of Approach Angles	15	15	15	15
Mean Vector (μ)	174.8°	283.7°	287.3°	67.0°
Length of Mean Vector (r)	0.27	0.254	0.434	0.327
Rao's Spacing Test (U)	248.5	222.3	201.1	251.3
Rao's Spacing Test (p)	< 0.01	< 0.01	< 0.01	< 0.01
Watson's U^2 Test (Uniform, U^2)	0.237	0.197	0.253	0.329
Watson's U^2 Test (p)	< 0.025	< 0.05	< 0.025	< 0.005
Kuiper's Test (Uniform, V)	2.031	1.967	1.914	2.302
Kuiper's Test (p)	< 0.01	< 0.025	< 0.025	< 0.01

The minor differences in how sub-sampling affects the distribution of approach angles are explained when examining the original distributions of approach angles (*i.e.*, with the original sample sizes) in more detail (Figure 8.13). The original distribution of approach angles (N=22) for WIN-235 (Figure 8.13d) was highly bi-modal, which explains why after sub-sampling test results still show that the distribution is significantly different from a uniform distribution (with a sample size of 10, all three tests indicated that approach angles were significantly clumped). On the other hand for WIN-11 the original distribution of the 22 approach angles seemed less clumped (Figure 8.13c), as is confirmed by lower U values for Rao's Spacing test, lower V values for Kuiper's Test and lower U^2 values for Watson's U^2 Test (Table 8.2). This which explains why all three tests showed that the distribution of approach angles were uniformly distributed around the circle, when sub-sampled to 10,

In conclusion, sub-sampling to 5 approach angles greatly affected the results that in some cases could not even be calculated at all. Sub-sampling to a sample size of 10 affected those distributions more, which had less clumped original distributions to start with, whereas sub-sampling to 15 approach angles, did not affect the results for any of the four selected goals. It seems that if distributions of approach angles are in fact (highly) clumped, distributions will be flagged as significantly clumped, even at very low sample sizes. However, when distributions with small sample size do fit a uniform distribution, this may just be the result of the small sample size. To therefore ensure both significant and non-significant test results are reliable, only goals with 15 or more approach angles were analysed.

8.3.3.2 Approach direction

Only change-point locations with a minimum sample size of 15 were included in this analysis (*i.e.*, the change-point location was approached at least 15 times) (Table 8.6). Four resource hotspots (P3, P4, P5 and FS-P) were identified for the summer season and two resource hotspots (P1 and B345) were identified for the winter season (see Chapter 6). Sample sizes ranged from 41 for P1 to 114 for B345, with an average of 65 approach angles per RH and as such, distribution of approach angles for all six RH were analysed.

Table 8.6 Change-points [CP] were grouped into unique CP locations and the distribution of approach angles for those CP locations with sample sizes greater than or equal to 15 were analysed. The number of CP locations with only 1 change-point is shown between brackets.

	sum	win
Number of CP	414	617
Total CP locations	380	514
CP locations with ≥15 approaches (individual, ungrouped CP)	17 (5)	17 (5)

Distributions of approach angles for each resource hotspot are shown in Figure 8.14. On visual inspection of the circular diagrams, approach angles for FS-P, P3 and P1 appear to be clumped, but the distributions for P4, P5 and B345seems more likely to fit a uniform distribution. The results of the three tests to examine whether distributions of approach angles were considered uniformly distributed around the circle or significantly clumped are presented in Table 8.7. Examining the results of Rao's spacing test, Watson's U^2 test and Kuiper's test, these confirm that directions from which resources FS-P, P3 and P1 were approached, were clumped and do not fit a uniform distribution. The values U^2 and V (for Watson's U^2 test and Kuiper's test respectively) were higher for FS-P than for P3 and P1, indicating a higher deviation from the uniform distribution. The distribution of approach angles for resource hotspot P5 was not significantly clumped and the distribution fits a uniform distribution. Results for P5 and B345 were inconsistent between tests. For P5 Rao's spacing test showed that the distribution did not fit a uniform distribution, but both Watson's U^2 test and Kuiper's test indicated the opposite suggesting the distribution is significantly clumped. Approach angles for B345 were significantly clumped according to Kuiper's test, but both Rao's spacing test and Watson's U^2 test showed the distribution was not significantly different from a uniform distribution.

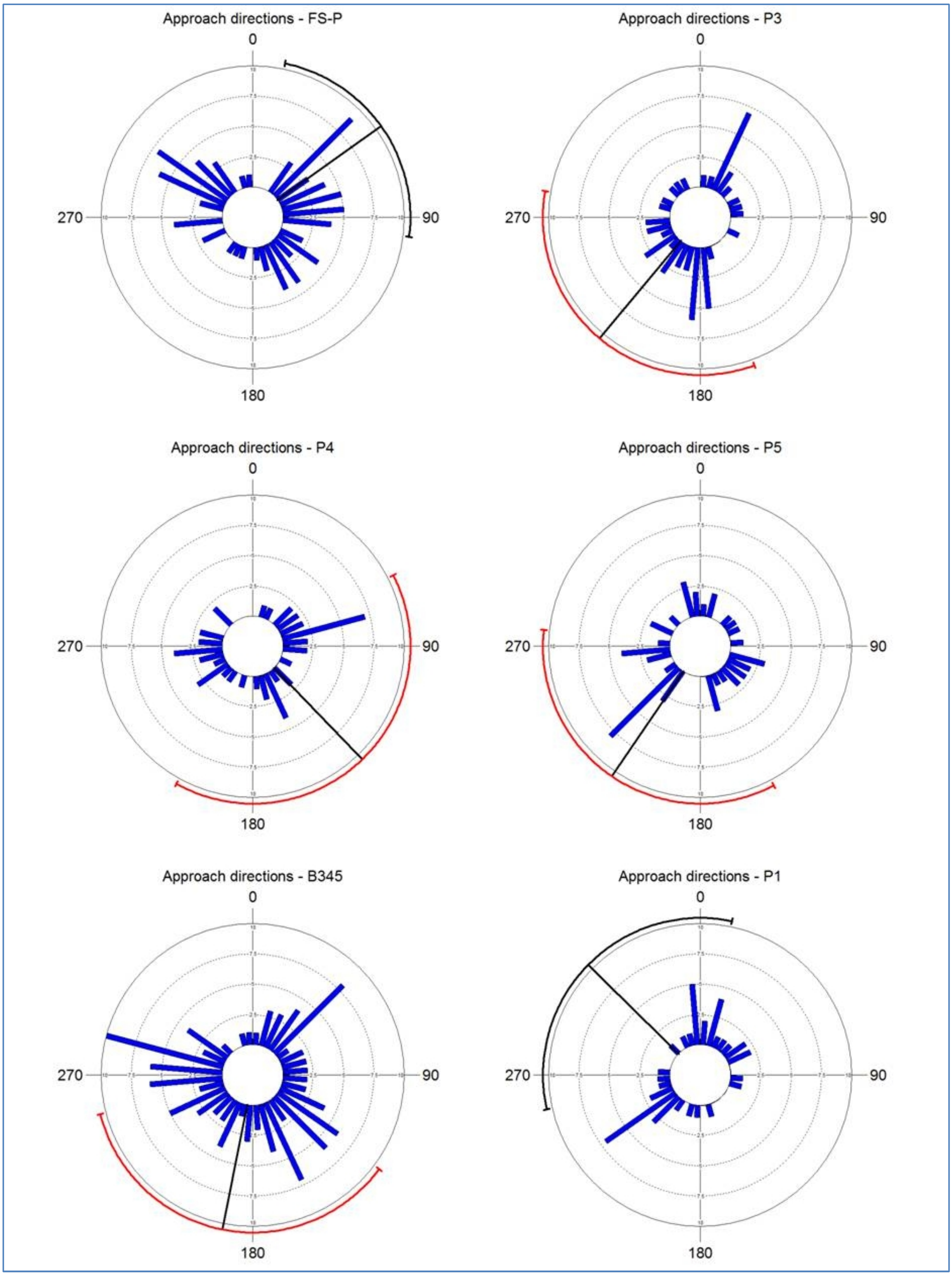

Figure 8.14 Circular distributions of approach angles for summer and winter resource hotspots (RH). The mean approach directions are 54°, 218°, 136° and 214° for the 4 summer RH (for FS-P, P3, P4 and P5 respectively) and 194° and 315° for the 2 winter RH (B345 and P1 respectively), which are represented by black thin lines from the centre of the circle and the arcs extending to either side represent the 95% confidence limits of the mean. Unreliable confidence limits due the combination of the sample size and concentration of the data and are coloured in red.

Table 8.7 Distribution of approach angles were analysed for four summer RH (FS-P, P3, P4 & P5) and two winter RH (B345 & P1) with sample sizes ranging from 42 to 85.

	FS-P	P3	P4	P5	B345	P1
Number of approach angles	85	49	49	48	114	42
Mean Vector (µ)	54.4°	219.8°	136.0°	214.2°	191.2°	314.5°
Length of Mean Vector (r)	0.200	0.188	0.155	0.183	0.115	0.212
Median	51.0°	184.2°	153.3°	223.7°	161.3°	340.1°
Concentration	0.408	0.383	0.313	0.373	0.232	0.435
Circular Variance	0.800	0.812	0.845	0.817	0.885	0.788
Circular Standard Deviation	102.8°	104.8°	110.7°	105.5°	119.2°	100.9°
Standard Error of Mean	21.8°	30.5°	37.2°	31.6°	32.9°	29.1°
Rao's Spacing Test (U)	160.62	158.77	147.07	158.83	132.27	163.02
Rao's Spacing Test (p)	< 0.01	< 0.05	ns	< 0.05	ns	< 0.01
Watson's U^2 Test (Uniform, U^2)	0.321	0.250	0.170	0.146	0.176	0.239
Watson's U^2 Test (p)	< 0.005	< 0.025	ns	ns	ns	< 0.025
Kuiper's Test (Uniform, V)	2.215	2.119	1.734	1.714	1.810	1.927
Kuiper's Test (p)	< 0.01	< 0.01	ns	ns	< 0.05	< 0.025

For change-point locations the results of the three tests to examine whether distributions of approach angles were considered uniformly distributed or significantly clumped are presented in (Table 8.8). For two change-point locations in winter (WIN-440 and WIN-454) all three statistical tests had p values greater than 0.05 and approach angles were thus randomly distributed around the circle. Furthermore, for three change-point locations in summer (SUM-647, SUM-654 and SUM-556), test results were somewhat inconsistent. For SUM-647 and SUM-654, both Watson’s U^2 test and Kuiper’s test showed a uniform distribution of approach angles, whereas Rao’s Spacing tests showed that approach angles were significantly clumped. For SUM-556, only Watson’s U^2 test indicated a uniform distribution of approach angles, while both Rao’s Spacing tests and Kuiper’s test showed that approach angles were significantly clumped. Nevertheless, all three statistical tests consistently showed that the distribution of approach angles for the remaining 29 change-points, and therewith the great majority (85.3%) of approach angle distributions were significantly clumped (Table 8.8).

In total the distribution of approach angles of 40 travel goals (6 RH and 34 CP) were analysed. Of the 8 travel goals (3 RH and 5 CP) for which the data failed to show departure from uniformity, test results were consistent between tests only for 3 travel goals and even here, significance levels fell between 0.25 - 0.05. For 80% of the travel goals examined approach angles were shown to be significantly clumped by all three tests. Thus in the great majority of cases, baboons did not approach the travel goals from all directions, but instead approach them from consistent direction(s) providing strong support for the topological map hypothesis.

Table 8.8 The distributions of approach angles were analysed for 17 summer and 17 winter goals using Rao's Spacing test (with U and p values shown), Watson's U^2 test (with U^2 and p values shown) and Kuiper's test (with V and p values shown). For each resource, sample size (N), mean approach angle (μ) and length of the mean vector (r) are shown. Non-significant results, indicating that approach angles were randomly distributed around the circle, were highlighted.

	N	μ	r	RS-U	RS-p	W-U^2	W-p	K-V	K-p
SUM-526	19	129.4	0.10	274.3	< 0.01	0.325	< 0.01	2.02	< 0.01
SUM-532	15	243.3	0.47	196.4	< 0.01	0.304	< 0.01	2.10	< 0.01
SUM-556	15	224.9	0.20	193.2	< 0.01	0.154	ns	1.84	< 0.05
SUM-566	18	315.8	0.37	299.1	< 0.01	0.481	< 0.01	2.88	< 0.01
SUM-611	15	51.8	0.25	196.2	< 0.01	0.197	< 0.05	2.09	< 0.01
SUM-647	16	253.1	0.09	195.7	< 0.01	0.166	ns	1.52	ns
SUM-654	27	225.3	0.12	201.1	< 0.01	0.117	ns	1.68	ns
SUM-656	15	267.4	0.22	250.2	< 0.01	0.198	< 0.05	1.82	< 0.05
SUM-672	16	280.3	0.62	288.8	< 0.01	0.675	< 0.01	3.21	< 0.01
SUM-676	24	300.7	0.47	176.7	< 0.01	0.317	< 0.01	1.96	< 0.05
SUM-717	20	287.3	0.63	216.5	< 0.01	0.555	< 0.01	2.91	< 0.01
SUM-741	20	104.1	0.21	242.0	< 0.01	0.346	< 0.01	2.27	< 0.01
SUM-754	20	329.9	0.51	229.5	< 0.01	0.525	< 0.01	2.92	< 0.01
SUM-783	22	213.3	0.22	227.5	< 0.01	0.306	< 0.01	2.23	< 0.01
SUM-804	24	356.2	0.36	228.5	< 0.01	0.387	< 0.01	2.45	< 0.01
SUM-805	16	239.5	0.70	220.2	< 0.01	0.600	< 0.01	2.84	< 0.01
SUM-877	22	290.4	0.15	225.7	< 0.01	0.215	< 0.05	1.97	< 0.05
WIN-11	22	303.7	0.40	171.0	< 0.05	0.267	< 0.05	1.96	< 0.05
WIN-34	39	185.8	0.15	220.5	< 0.01	0.276	< 0.01	1.90	< 0.05
WIN-75	15	84.3	0.33	266.1	< 0.01	0.325	< 0.01	2.35	< 0.01
WIN-76	25	348.5	0.30	245.4	< 0.01	0.407	< 0.01	2.60	< 0.01
WIN-94	23	301.7	0.12	273.6	< 0.01	0.371	< 0.01	2.27	< 0.01
WIN-157	15	315.9	0.31	224.7	< 0.01	0.257	< 0.05	2.10	< 0.01
WIN-206	15	65.7	0.53	239.6	< 0.01	0.423	< 0.01	2.59	< 0.01
WIN-208	41	178.2	0.52	182.4	< 0.01	0.635	< 0.01	3.00	< 0.01
WIN-222	15	256.0	0.45	202.9	< 0.01	0.277	< 0.01	2.16	< 0.01
WIN-235	22	56.3	0.28	239.0	< 0.01	0.383	< 0.01	2.42	< 0.01
WIN-252	16	37.9	0.11	250.1	< 0.01	0.225	< 0.05	1.88	< 0.05
WIN-295	18	316.2	0.22	240.6	< 0.01	0.240	< 0.05	2.07	< 0.01
WIN-306	15	6.0	0.10	259.5	< 0.01	0.243	< 0.05	1.93	< 0.05
WIN-424	15	289.3	0.31	284.2	< 0.01	0.329	< 0.01	2.30	< 0.01
WIN-426	17	241.2	0.43	219.1	< 0.01	0.289	< 0.01	2.19	< 0.01
WIN-440	16	269.6	0.31	138.3	ns	0.104	ns	1.49	ns
WIN-454	15	262.0	0.35	164.5	ns	0.169	ns	1.64	ns

8.3.4 Leaving directions

To test whether the initial direction significantly differed from the general direction taken after leaving travel goals, paired Mardia-Watson-Wheeler tests and paired Chi-Square tests were conducted. Results are presented (per season and for the year as a whole) in Table 8.9 for change-points (CP), for which general directions were measured from one change-point to the next and for resource hotspots (RH), for which general directions were measured from the RH to 8th waypoint after leaving the RH.

The initial direction did not differ significantly from the general direction measured from one change-point to the next for either season or the year as a whole. When baboons left resource hotspots, their initial direction differed significantly from the general direction in winter according to test results of the paired Chi-Squared test. The probability level is only just significant and the paired Mardia-Watson-Wheeler test concludes that the initial and general directions are not significantly different from one another in winter. For summer and the year as a whole test results were consistent and no significant differences between the initial direction and general direction taken when leaving resource hotspots were found.

Table 8.9 Test results of Mardia-Watson-Wheeler (MWW) tests and paired Chi-Square (χ^2) tests showing sample size (N), test values W and χ^2, significance levels (p) and the degrees of freedom (df) for the Chi-Square test. Note that for RH summer and RH winter, class width was set to 20° instead of 10° (hence df=16 instead of 35) in order to obtain reliable test results (smaller class widths resulted in more than 20% of the classes with expected frequencies less than 5). Significant results are highlighted.

Travel goal	N	W	MWW-p	χ^2	χ^2-p	df
RH year	273	3.409	0.182	46.28	0.096	35
RH summer	178	2.052	0.358	16.06	0.519	16
RH winter	95	5.515	0.063	26.72	0.045	16
CP year	828	0.950	0.622	36.77	0.387	35
CP summer	361	0.320	0.852	38.33	0.321	35
CP winter	467	1.079	0.583	33.21	0.555	35

The results were confirmed by performing linear statistics on the same datasets. Conducting linear statistics on circular data leads to higher probabilities of finding significant differences (since 0° and 360° are the same direction, but are viewed as opposite sides of the scale by linear statistics) and as such if no significant differences are found using linear statistics, non-significant test results found using circular statistics indicating that initial and general directions are not significantly different from one another are confirmed. Paired Wilcoxon Signed Rank tests showed no significant difference between the initial and general direction taken for all comparisons (Table 8.10).

Table 8.10 Results of paired Wilcoxon-Signed Rank test (sample size N, test value Z and the probability level p are shown) confirmed that there are no significant differences between the initial direction taken and the general direction taken when leaving travel goals.

Travel goal	N	Z	p
RH year	273	-0.261	0.794
RH summer	178	-0.204	0.838
RH winter	95	-0.768	0.442
CP year	828	-0.837	0.402
CP summer	361	-0.494	0.621
CP winter	467	-1.572	0.116

It can thus be concluded that baboons tend to leave travel goals in the same direction as the general direction in which lies their next goal. Nevertheless, the deviation between the initial and general direction was significantly different than expected from straight line travel when taking GPS error into account (Table 8.11). Finally, there were no seasonal differences in deviation for change-points (unpaired t-test: t=0.369, df=780, p=0.712) or resource hotspots (unpaired t-test: t=0.309, df=215, p=0.757).

Table 8.11 Paired t-test showed that the deviation between the initial and general direction taken was significantly different than expected under a straight line when taking GPS error into account.

Travel goal	t	df	Sig. (2-tailed)
CP year	8.666	827	<0.001
CP summer	5.491	360	<0.001
CP winter	6.703	466	<0.001
RH year	6.911	272	<0.001
RH summer	5.509	177	<0.001
RH winter	4.193	94	<0.001

8.4 Discussion

8.4.1 Route-based network

Two route networks of repeatedly used travel routes were delineated and 87% and 80% of location records fell within 25m of the network based on the two repetitions criterion and four repetitions criterion respectively. This percentage is higher than observed for woolly and spider monkeys (*Lagothrix poeppigii* and *Ateles belzebuth*) (60% and 82% respectively) that were found to travel through a system of habitual routes (Di Fiore & Suarez 2007). The numbers of location records did not fall equally within the 5, 10, 15, 20, 25 bands, which indeed suggested that baboons range significantly more in the vicinity of the route network than further away from the route network. Consistent with the idea of a topological map, 86% (N=565) of the intersections in the route network were also confirmed as decision points and 92% (N=589) of intersections were located within 50m of a change-point.

Although these results strongly imply that baboons at Lajuma travel through a system of habitual routes, a note of caution must be made. A very high number of travel routes were analysed (234 full day and 137 partial follow days) compared to previous studies that investigated route-based travel in primates. For example, Presotto & Izar (2010) analysed 100 full day travel routes and Hopkins (2011) analysed 89 full day travel routes. Di Fiore & Suarez (2007) did not specifically state the number of travel routes they analysed, but the highest number of location records used to create a single route network, collected at 5 minute intervals, was 15,103 for “the first spider monkey data set” (Di Fiore & Suarez 2007 p. 319). In comparison, when the travel routes analysed in this chapter are represented by data points at 5 minute intervals, the data set contains 37,912 data points, more than twice as many. Many route segments were traversed two or more times and also four of more times. It is however possible that the baboons used the same path two or four times just by chance, and not because they were restricted to that path. The route networks created based on 2 and 4 repetitions were very dense and as such, the “holes” in the network (*i.e.*, distances between repeatedly used routes) were very small and often completely filled when a 25m band around the network was applied. Therefore, to create habitual route networks based on the criteria that repeated travel routes are those that are repeated two or four times, may have been too relaxed.

The baboons frequently ranged across a relative flat area in the baboons’ home range that is referred to as ‘the patches’ and the habitual route networks were especially dense in this area. Many travel routes intersected this entire area and the route network based on 4 repetitions is especially dense compared to other areas in the baboons’ home range (Figure 8.15). Most of this flat area that has a savanna like habitat with dispersed tree patches and has a very high visibility compared to other parts of the baboons’ home range. Moreover, situated north-east to this area is the highest peak of the Soutpansbergen (Letjume), is visible from nearly everywhere in the patches (Figure 8.16). It is thus likely, that while the baboons had continuous sight of such a prominent landmark, they were able to navigate and orient themselves efficiently, possibly allowing them to reach the same locations using different paths.

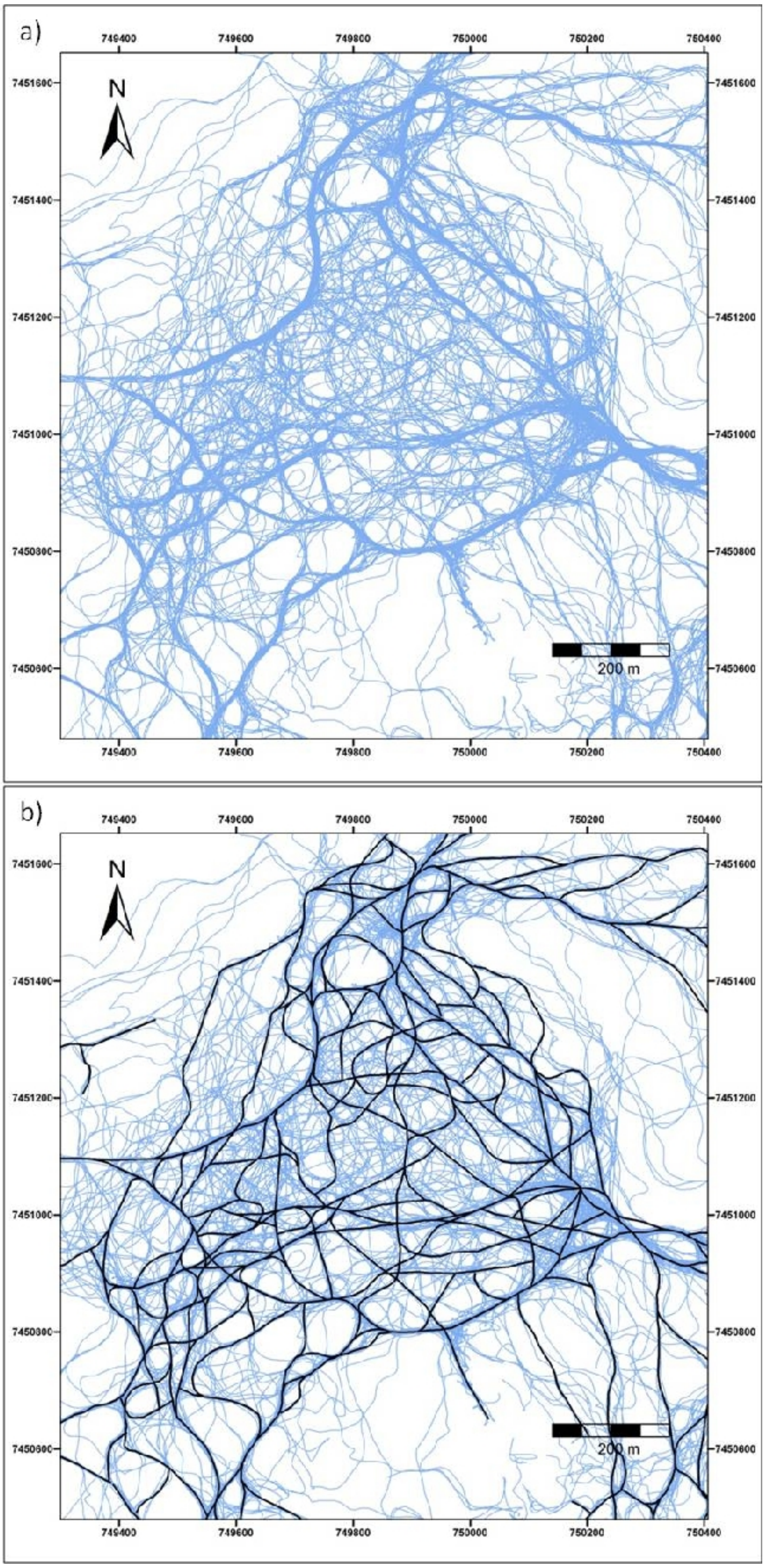

Figure 8.15 (a) Baboon travel routes (*thin blue lines*) in the patches (extend of the white rectangle in Figure 8.16) superposed on (b) the habitual route network (*thick black lines*) created by the connection of segments traced after at least four repeated segments of actual routes.

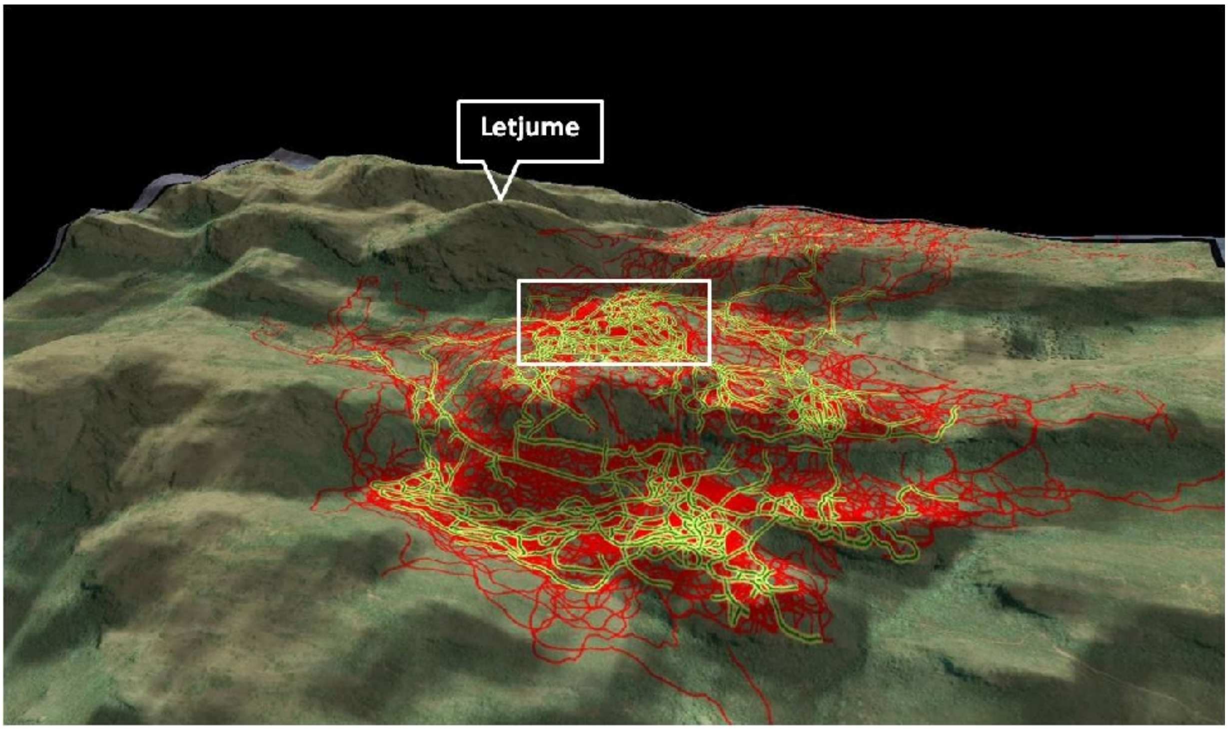

Figure 8.16 Baboons travel routes (*red lines*) and the route network created based on 4 repetitions (*yellow lines*). The *square white rectangle* (extend of Figure 8.15) indicates the relatively flat area of the study area, termed 'the patches', which is located in the vicinity of the highest peak of the Soutpansbergen named 'Letjume'.

Several man-made tracks and natural game trails crossed the baboons' home range and these tracks seemed to be frequently used by the baboons. This notion was confirmed when the highway network and the trail map were plotted together (Figure 8.17). Chapter 6 (Section 6.3.6) showed that junctions in the existing network of many man-made tracks and natural game trails seemed to be used as navigational landmarks. Decision hotpots coincided with junctions in the existing trail network (Chapter 6 Figure 6.9) and consequently with intersections in the baboons' highway network (Figure 8.12).

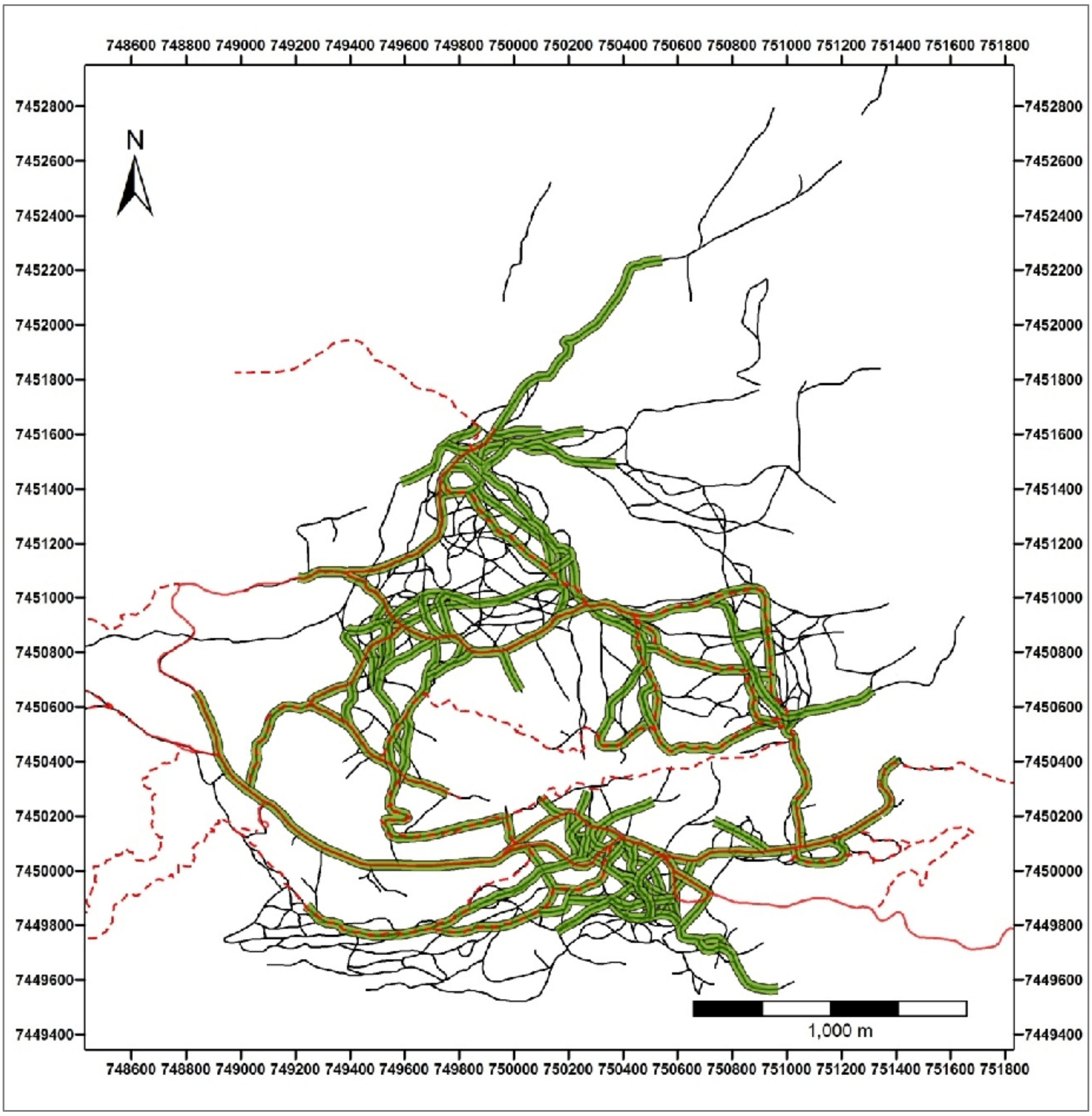

Figure 8.17 Overlap between the existing man-made track (*red lines*) and game trail (*red dashed lines*) network and the baboons' habitual route network created based on the 4 (*thin black lines*) and 10 (*thick green lines*) repetition criterion.

8.4.2 Travel between periphery and core area

To discriminate between the two mechanisms used for navigation, the linearity of travel segments in the core area, where baboons are completely familiar with the area, were compared to the linearity of path segment in peripheral areas, in which baboons only range 25% of the time. Contrary to the predictions for the topological map, the linearity index was not significantly different between the two regardless of distance travelled between consecutive travel goals. However, the linearity of the travel routes in the core area and the periphery was not particularly high (median linearity ratio: 0.815 and 0.808 respectively) compared to other studies on primate travel routes. 78.5% and 72.4% of the path segments in the core area and periphery respectively were considered 'highly linear', *i.e.*, with linearity ratios above 0.7 (Valero & Byrne 2007 p. 310). In comparison, Noser & Byrne (2007b) found a median r value of 0.879 and 44% of segments reached an r value between 0.9 and 1.0 and Valero & Byrne (2007) reported 78% of route segment had linearity rations above 0.8. Normand & Boesch (2009), who argued that chimpanzees possess Euclidean-based spatial awareness, found an average linearity ratio of 0.962. In conclusion, although baboons did not travel more directly in the core area than in the periphery, linearity throughout the home range was not particularly high as one might expect under the hypothesized use of a Euclidean map. It is thus likely that the baboons have accumulated a similar knowledge of the periphery as of the core area which allowed them to navigate with a similar efficiently through both areas.

8.4.3 Approach direction

If baboons were using a Euclidean map rather than a topological map, it was predicted that they would be able to approach goals from all different directions, whereas when using a topological map, they were predicted to approach their travel goals from the same direction(s). Approach directions of 80% of the travel goals were significantly clumped, indicating that baboons do not approach their travel goals from all directions, but instead approach them from the same direction(s), which is more consistent with the hypothesized use of a topological map that than of a Euclidean map. There is evidence that some primate species approach resources from different directions. For instance Garber (1986) showed that saddle-back and moustached tamarins (*Saguinnus fuscicollis* and *Saguinnus mystax*) approached 15 preferred trees (average of 8.6 ± 3.2 revisits per tree) from all directions and Normand & Boesch (2009) found that the mean deviation angle was significantly higher than simulated deviation of revising a resource using one, two or five different routes and that chimpanzees thus do not use routes to approach food trees. However, it must be noted that neither of these studies employed circular statistics that are specifically designed for directional data and should thus be preferred over linear statistics (see also Chapter 5 Section 5.2.3). It has been previously shown in this chapter that even when using circular statistics, some tests are more sensitive to distinguish bi-model distributions (*i.e.*, routes coming from opposite directions) than others (*e.g.*, the Rao's Spacing test employed in this chapter outperforms the Rayleigh test in this respect) (Section 8.2.4). Thus the type of statistical analysis should be noted and conclusions based on linear statistical analysis of angular data should be interpreted with caution.

8.4.4 Leaving direction

Finally, if baboons are using a Euclidean map rather than a topological map, baboons were expected to know in which direction to travel and it was therefore predicted that baboons initiate navigation to a resource with the same direction as when they reached that resource. However, if baboons would be using landmarks to orient themselves, a greater difference between the two was expected. When the initial direction adopted when leaving resources was directly compared to the general direction taken, no difference between the initial and general directions were found and the results are therewith less consistent with the topological spatial representation. On the other hand, when the deviation between initial directions and general directions were compared to straight line travel, taking GPS error into account, the deviation was significantly larger than expected from straight line travel, indicating a possible lack of a Euclidean spatial awareness. Metric characteristics of Euclidean navigation have recently been found in chimpanzees (Normand & Boesch 2009). Chimpanzees initiated navigation to a resource with the exact same direction as when they reached that resource (*i.e.*, the deviation did not differ from straight line travel) (Normand & Boesch 2009). The use of a topological map in an environment with sufficient landmarks may also result in highly efficient and direct travel without the need for Euclidean spatial awareness (Byrne 2000) and it is thus likely that in a mountainous area with many prominent landmarks, the baboons were able to navigate efficiently without using Euclidean navigation.

8.4.5 Conclusion

In this chapter four different approaches were used to determine whether movements of chacma baboons are more consistent with topological spatial awareness or Euclidean spatial awareness. First, baboons were shown to use habitual travel routes to navigate through their home range and that they range significantly more in the vicinity of the route networks than further away. Although the large number of travel routes analysed in this chapter may have increased the probability that route segments were used repeatedly by chance and not because the baboons were restricted to that path, even when adopting a far more stringent criterion of 10 repetitions, 56% of all location records fell within the created ‘highway’ network. The size of the route network and the proportion of location records falling inside the vicinity of the route network varied according to the criterion (two, four or ten repetitions) used to consider a route as habitual. In contrast to Presotto & Izar (2010), a less restrictive criterion did not so much result in a larger network, but rather in a denser route network. Regardless of the criterion used to consider a route habitual, the route networks were denser in relative flat areas where prominent landmarks were visible.

The use of habitual routes does not, however, necessarily exclude Euclidean navigation (Presotto & Izar 2010). Therefore, three predictions resulting from the hypothesized use of Euclidean maps and topological maps were tested to provide support for one alternative. However, each prediction by itself did not conclusively discriminate between the two different kinds of spatial representation, because in an environment with ample visible landmarks, navigation using a topological map is thought to be just as precise as when animals possess a Euclidean spatial representation (Byrne 2000; Janson & Byrne 2007). Baboons were shown to travel as efficiently in the periphery as in the core of their home range, which may be considered an indication of Euclidean spatial awareness, but alternatively the baboons could have accumulated a similar knowledge of the periphery as of the core area which allowed them to navigate using landmarks with a similar efficiently through both areas. The latter explanation for the lack of difference in movement patterns between the core and periphery of the home range seems more favourable, since the linearity ratios were relatively low throughout the home range, compared to those of species which are thought to use a Euclidean map (chimpanzees: Normand & Boesch 2009) and even to those which are thought to use a topological map (baboons: Noser & Byrne 2007a; spider monkeys: Valero & Byrne 2007).

If baboons would be using a Euclidean map rather than a topological map, they were expected to know in which direction to travel and it was therefore predicted that baboons initiate navigation to a resource with the same direction as when they reached that resource. There was no significant difference between the initial and general direction when they were compared to one another directly. However, in contrast to chimpanzees, which are believed to possess Euclidean spatial awareness (Normand & Boesch 2009), the deviation between the initial and final direction did significantly differ from straight line travel as did travel between resources (Chapter 7 Section 7.3.1). It thus seems that since the study area contains many prominent landmarks that the use of a topological map allowed the baboons to navigate from one travel goal to the next efficiently, but that the lack of Euclidean spatial representation restricted this efficiency.

Finally, baboons did not approach their travel goals from all directions as was predicted under the hypothesized use of a Euclidean map. Instead baboons approached travel goals from the same direction(s), which is more consistent with the use of a topological map, although it must be noted that this finding does not exclude the existence of a Euclidean map.

The study area was located in the Soutpansberg mountain range with many topological features, such as cliffs and mountain tops that may have aided baboons in navigation. In particular, the highest peak of the Soutpansberg mountain range was visible from many locations within the baboons' home range and such a prominent landmark was likely to aid in navigation. Furthermore, many man-made tracks and natural game trails were present throughout the study area and junctions in such tracks seemed to be used as navigational landmarks (Chapter 6 Section 6.3.6). This notion was confirmed by the highway network was constructed which showed that baboons make frequent use of the existing trail network at the study site and that intersections of the highway network overlap with the existing trail network. Furthermore, decision hotspots coincided with these intersections. Decision hotspots thus distinguished those topological features that delineate the tight network of routes characteristic of network maps (Byrne 2000; Di Fiore & Suarez 2007; Noser & Byrne 2007a; 2010). The many topological features present at the study site are likely to have aided baboons in navigation, allowing them to travel efficiently between travel goals. Taken together, the different analyses discussed above are considered to point more towards the existence of a topological map in wild chacma baboons.

CHAPTER 9

CONCLUSIONS AND DISCUSSION

'He who understands baboon would do more towards Metaphysics than Locke'

(Charles Darwin, 1838, Notebook M84e)

The primary objective of this research was to give insight into the spatial cognitive abilities of chacma baboons (*Papio ursinus*) and to address the question whether chacma baboons internally represent spatial information of large-scale space in the form of a topological-based or a Euclidean-based spatial representation. Navigating the environment using a topological map envisions that animals acquire, remember and integrate a set of interconnected pathways or route segments that are linked by frequently used landmarks or nodes, at which animals make travel decisions. In contrast, when animals navigate using a Euclidean map, they encode information in the form of true angles and distances in order to compute novel routes or shortcuts to reach out of view goals. In this chapter, first the main findings of Chapters 3 through 8 are summarised. Next, the broader implications of this thesis are discussed in the wider context of spatial cognition. A discussion on the evolution of Euclidean representation is presented and based on the present findings this dissertation concludes with suggestions for future research recommendations.

9.1 Summary of research findings

Baboons' ranging was investigated in Chapter 3. Two methods were employed to estimate the home range of the baboons and to delineate the baboons' core area of use: the kernel density estimator (KDE) (Worton 1989) and the Local Convex Hull (LoCoH) method (Getz & Wilmers 2004). The KDE method is currently one of the best known and most widely applied nonparametric statistical methods for estimating home range in animal ecology (Strickland & McDonald 2006), but the LoCoH, although relatively new, is being increasingly favoured over the KDE (*e.g.*, Ryan *et al.* 2006; Beest *et al.* 2011; Getz *et al.* 2007) for a variety of reasons. Foremost, the LoCoH method accommodates user knowledge of known physical barriers and is more adept than the KDE at excluding geographical features such as rivers, lakes, inhospitable terrain, and so on (*e.g.*, Ryan *et al.* 2006; Getz & Wilmers 2004). Second, for the LoCoH method the user-specified parameter that determines the shape of the home range estimate produced by a given dataset, is relatively robust against suboptimal choices of this parameter and against changes in sample size (Getz *et al.* 2007), whereas the home range estimates generated by KDE methods are heavily affected by the choice of the user-specified parameter, called the ‘smoothing parameter’ for the KDE. The two main differences between the home range estimates of the two methods were that at larger isopleths levels the KDE had a tendency to produce ‘islands’ at the border of the home range and that the KDE produced somewhat smoother boundaries than the LoCoH method. In general, the two methods produced similar home range estimations, due to the large number of location records analysed and due to the lack of physical barriers such as rivers, lakes, inhospitable terrain, in the study area. Nevertheless, the LoCoH was considered a better and more convenient method to estimate the baboons’ home range, because (1) the KDE produced unrealistic patchy home range estimates ‘islands’ that the LoCoH did not (2) the KDE requires selection of an optimal smoothing parameter value and there is no consensus on what is the best method to do so (3) the value *a* in the LoCoH is robust to sub-optimal choices compared to the smoothing parameter in the KDE method (4) the LoCoH has the potential to exclude physical barriers and (5) the LoCoH was relatively easy to use with a user-friendly web-interface, user instructions and readily available scripts to use in R software.

With the baboons’ home range and the core area of their range delineated, the next step was to investigate the baboons’ movement patterns in more detail. In studies on spatial cognition, linear travel paths to out-of-sight resources have 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 (*e.g.*, Janmaat *et al*. 2006; Janson & Di Bitetti 1997; Noser & Byrne 2007b; Valero & Byrne 2007). Nevertheless, such an approach does not account for the potential effects of non-visual sensory cues, such as olfactory or vocal cues, which may be picked up from further away and does not necessarily imply that animals had a travel goal in mind, unless the animals are seen to by-pass detectable, but inferior resources in the route (Asensio *et al.* 2011). As such, a major challenge faced by researchers is to objectively identify the travel goal (if any) for an animal, as well as the points at which they supposedly decided to move towards a goal (Byrne *et al.* 2009).

To circumvent the problem that researchers cannot know what the goal is in the mind of the subject whose ranging behaviour is being recorded, Byrne and colleagues (2009) developed a method, termed the change-point test (CPT), which identifies locations at which animals start orienting towards the next goal based on the statistical characteristics of a subject’s travel route. The CPT identifies such locations, so-called ‘change-points’, independent of the possible reasons for the change, such as the animal’s demeanour at the change-point, or any resources to which the travel led (Byrne *et al.* 2009). As a consequence, the test removes much of the subjectivity and circularity inherent in more traditional methods of determining when an animal began heading in a particular direction or oriented towards a particular goal. Using the CPT to systematically identify change-points has thus been suggested as a first step to understanding how animals navigate their environment, and ultimately, how they represent and store spatial information of their home range (Byrne *et al.* 2009).

In Chapter 4, an extensive sensitivity analysis was conducted to determine optimal parameter values that need to be selected by the user, which is considered crucial to the successful application of the CPT (Byrne *et al.* 2009). Due to the nature of CPT, the type of sampling protocol used to collect location data was expected to affect the output due to differences in step length variation (*i.e.*, distance between consecutive location records) associated with different sampling protocol types (for example data recorded using a sampling protocol based on regular time intervals produced highly uneven spaced location records compared to a sampling protocol based on a regular distance intervals). When travel routes were relatively straight, variation in step length did not necessarily influence the results of the CPT, but when seemingly important changes of direction occurred, a time-based sampling protocol frequently failed to identify these locations as change-points, due to the uneven spacing of the waypoints that represented the travel route. Furthermore when a distance interval sampling protocol was used, smaller sampling intervals allowed the CPT to detect changes of direction at a smaller scale than at larger sampling intervals. Accordingly, future studies aiming to incorporate the CPT are strongly recommended to collect data using a distance based sampling protocol or to manipulate the data post-hoc to obtain data points at a regularly spaced distance interval with the selection of sampling interval depending on the on the scale of interest.

The sensitivity analysis revealed a complex interplay between sampling interval and CPT parameter values and showed it is essential to determine the correct scale of interest and to select an appropriate sampling interval dependent on the study species and aim of the research. Considering the challenges in selecting the appropriate parameter values and sampling interval associated with the CPT and the tendency of the CPT to indicate significant directional changes one or two locations or two ahead of the ‘true’ change-points under certain parameter settings, an alternative method to determine change-point locations, termed the turn angle (TA) method, was proposed in Chapter 5. This alternative method, based on an approach of Normand & Boesch (*submitted*) to identify resource as ‘decision points’, identified locations as change-points if the turn angle at a location was superior to the daily mean turn angle ± 2 times the standard deviation, using appropriate circular statistics. However, it became evident from the small percentage of change-point location overlap that the two methods were in fact measuring different things. The CPT examines changes of direction on a larger scale than the TA method, which allowed it to successfully identify locations at which the baboons started orienting towards a new goal in the vast majority of the data, whereas the TA method identified locations at one given point in time at which turn angles were greater than the daily threshold turn angle. As such, the TA method did not identify change-points at locations where baboons started orienting in a new direction when this was done with a relative wide turn and it wrongly identified change-points at locations where sharp, back-and-forth changes of direction at small scale were made, even though the same overall orientation was maintained at a larger scale. For this reason the TA method was considered inappropriate to identify locations at which animals start orienting towards a next goal and therewith to determine locations where travel decisions are being made, whereas the utility of the CPT to do so was confirmed.

In Chapter 6, the utility of the CPT was extended with a novel application of hotspot analysis in *CrimeStat* software, to provide the first quantitative analysis of the spatial distribution of change-points by delineating clusters of change-points where animals repeatedly change direction on multiple travel days, termed ‘decision hotpots’. Subsequent hotspot categorisation classed each decision hotspot into a resource hotspot or a non-resource hotspot, based on the availability of food resources. Resource hotspots were associated with key food resources and baboons spent significantly more time at change-points that fell within resource hotspots than they did at change-points that fell outside resource hotspots. Under the principle of ‘time = value’, it was concluded that the hotspot analysis provides an assessment of resource value, independent of the animals’ behaviour and without the need for detailed behavioural or phenological observations, and that resource hotspots are likely to represent highly valuable travel goals. Though decision hotspots coincided with highly valuable resources, they were also located at navigational landmarks such as junctions in roads or trails, without the presence of any food or water resource. Therewith, the hotspot analysis method reveals an important utility to the study of decision-making by allowing a range of sites to be selected for detailed observations, which were previously limited to sleeping sites or ‘stop’ sites.

Hotspot analysis provides empirical descriptions of locations where decisions are concentrated and are likely to be an invaluable addition to the toolkit of techniques for studying animal spatial behaviour and decision-making. However, there are several statistical techniques available to identify decision hotspots and it should thus be recognised that there is no single solution. Different techniques may reveal different clusters and one must be aware of this variability and choose techniques that reflect sample size and complement other types of analysis. Nevertheless, it is imperative that the underlying causes that link the change-points together are discovered in some systematic way and the identification of decision hotspots should thus represent an important second step following the CPT in many studies of spatial cognition and decision-making.

So far, travel goals are those locations identified as change-points by the CPT while highly valuable travel goals are those locations identified as resource hotspots by hotspot analysis. In Chapter 7, baboons were shown to travel significantly faster towards highly valuable goals than towards other goals, and showed more goal-directed travel to highly valuable resources during summer than winter, when the next goal was likely to be out-of-sight in the majority of cases. Sensory cues did seem to increase travel speed, but only at very close proximity of the travel goal when goals came into sight. These findings are consistent with other studies that showed that baboons used the shortest linear route to travel from one location to another and that they speeded up as they approached out-of-sight water or food sources (*e.g.*, Pochron 2001, 2005; Noser 2004; Noser & Byrne 2007a, 2007b, 2010;

Sueur 2011). In summary, the data provided evidence of goal-directed travel of baboons at the research site and they suggested that baboons seemed to ‘know’ when they were nearing their goals and adapted their speed accordingly, indicating goal-directed and mental map processes.

Finally, Chapter 8 addressed the question whether chacma baboons internally represent spatial information of large-scale space in the form of a topological-based or a Euclidean-based spatial representation. Baboons were shown to use habitual travel routes to navigate through their home range and they range significantly more in the vicinity of this route networks than further away. Although several researchers have reported repeated use of the same pathways or network of pathways for a wide variety of taxonomic groups, there is no clear definition on the criterion used to consider a route as habitual. The size of the route network and the proportion of location records falling inside the vicinity of the route network varied according to the criterion (two, four or ten repetitions) used to consider a route as habitual. In contrast to the findings of Presotto & Izar (2010), a less restrictive criterion did not so much result in a larger network, but rather in a denser route network. Regardless of the criterion used to consider a route habitual, the route networks were denser in relative flat areas where prominent landmarks were visible. It is thus likely, that while the baboons had continued sight of landmarks, they were able to navigate and orient themselves very efficiently. Furthermore, intersections in the route network were confirmed decision points and decision hotspots identified in Chapter 6 coincided with these intersections. This confirmed the utility of the hotspots analysis to the study of decision-making to point out those locations at which travel decision are being made.

Using a limited number of habitual routes to navigate towards a travel goal offers an advantage because single landmarks provide their most precise spatial information when viewed from the same direction or orientation (Byrne 2000). When an animal approaches a travel goal from another direction, it may not be familiar with the correct distance, angle, or view between the landmark and the goal. This may partly explain why many primate species are reported to reuse travel routes during travel (Garber & Jelink 2005). Some primates, including baboons, are able to use highly linear, but alternative travel routes to reach the same resource (Milton 1980; Garber & Jelink 2005; de Raad this study). Although the use of multiple landmarks to encode spatial information may require an increased capacity to store and integrate a relatively large number of points in the environment (Garber & Jelink 2005), Kamil and Cheng (2001 pp:107) argue that the use of “multiple landmarks functions to increase dramatically the precision of searching in the face of errors in the estimation of distance or direction”. It is difficult to identify which landscape features exactly were used by baboons for navigation, but it appears that baboons maintained information of the locations of numerous intersecting routes of travel and landmarks within their home range. This is consistent with topological spatial representation.

The use of habitual routes does not, however, necessarily exclude Euclidean navigation all together (Presotto & Izar 2010). Therefore, three predictions resulting from the hypothesized use of Euclidean maps and topological maps were tested to provide support for one alternative. Baboons travelled as efficiently in the periphery as in the core area of their home range, which was suggested to be more consistent with Euclidean spatial awareness. However, comparatively low travel linearity throughout the home range suggested it is more likely that the baboons accumulated a similar knowledge of the periphery as of the core area, which allowed them to navigate with a similar efficiently through both areas. The mountainous terrain at the study site provided ample prominent landmarks to aid the baboons in navigation and allowed baboons to initiate navigation to a travel goal with the same direction as when they reached that goal. Baboons did not approach travel goals from all directions, but instead they approached their goals from the same direction(s). Overall, these results were more consistent with a topological spatial representation in large scale space, where landmarks aid baboons to navigate efficiently through large scale space than with a Euclidean spatial representation of space.

9.2 Spatial representation in a wider context

Baboons are one of many non-human primate species (*e.g.*, orang-utans: Mackinnon 1974; howler monkeys: Milton 2000, Hopkins 2011; spider monkeys and woolly monkeys: Di Fiore & Suarez 2007; lemurs: Erhart & Overdorff 2008; black capuchin monkeys: Presotto & Izar 2010, Urbani 2009; proboscis monkeys: Boonrata 2000) that use habitual routes (Sigg & Stolba 1981, Byrne 2000, Noser & Byrne 2007a, 2010; de Raad this study). In non-human primates these habitual routes often coincide with streams, ridges of hills and tracks located in their home range (MacKinnon 1974; Di Fiore & Suarez 2007; de Raad this study) and the use of such landmarks for navigation are evidence of topological spatial awareness. Similarly, Amazonian hunters use particular features in the forest, such as ridges, creeks and rivers, as landmarks or trails (Milton 2000) which suggest that humans also navigate, at least in part, using a topological map. In support of this notion, experimental evidence recently showed that humans rely heavily on landmarks for accurate navigation when they are available (Foo *et al.* 2005). However, the use of habitual routes and landmarks does not necessarily mean that there is a complete lack a Euclidean spatial representation. Evidence for Euclidean spatial awareness in humans was found in Australia, where Walbiri aborigines use precise notions of distance and bearing in order to navigate through an open environment such as the Simpson Desert (Lewis 1976; Widlok 1997). Based on 34 experiments in which their navigation skills were tested in large open space, aborigines showed an average of 13.7 km of error in reaching places located at distances of approximately 200-300 km (range: 10-670 km). Foo *et al.* (2005) argued however that shortcuts in the desert world are of roughly the correct direction and distance, but that the information about distances and angles travelled could be provided by path integration. Their findings suggest that humans do not integrate experience on specific routes into a Euclidean map for navigation but rely on rough survey knowledge from path integration and primarily depend on a landmark-based navigation strategy (*i.e.*, topological spatial representation), which can be supported by qualitative topological knowledge of the environment. In a comprehensive review, Wang & Spelke (2002 pp: 5) also conclude that although cartographic maps created by humans are long-lasting, geocentric, and allow for complete flexibility and computation of distances and angles, “the internal representations that guide human navigation have none of these properties”, but instead humans rely on path integration and landmarks for navigation. In the biological and cognitive sciences, it is thus questioned whether *Homo* indeed possesses both topological and Euclidean spatial awareness.

In anthropological sciences it has been suggested that Euclidean spatial abilities were selected for when anatomically modern humans (AMHs) adopted a more mobile lifestyle and had to maintain spatially extensive social networks (Maguire *et al*. 2003; Hartley *et al*. 2007). The spatial distribution of archaeological sites in the East European plain suggests that AMHs were the first to expand their range into the plains (Pavlov *et al.* 2004). Neanderthals on the other hand thrived on the edges of the plains in areas that were topographically more complex, which have been suggested to be better-suited to navigational mechanisms using landmarks (Burke 2006) and where they retained a more local pattern of social interactions (Burke 2012). The challenge of maintaining complex, spatially extensive social networks and explanatory travel of AMHs (Leonard & Robertson 2000; Abrose 2001; Potts 2004), might have required specific spatial cognitive skills related to wayfinding that could have eventually lead to changes in spatial cognition between AMHs and Neanderthals (Mitchen 2003; Boehm 2004; Burke 2012).

If range expansion of AMHs and their associated explanatory travel and resulting complex spatial social network were indeed driving factors in the selection for Euclidean spatial awareness, it might be expected that species that live under similar complex social conditions might also have developed some degree of Euclidean spatial awareness. Species living in a fission-fusion society where individuals forage in small, temporary parties or subgroups that change in size and composition frequently also face the challenge of maintaining complex social networks. Chimpanzees live in fission-fusion communities composed of 20-150 individuals (Boesch & Boesch 2000) but travel in an average party size of 10 individuals, but ranging from one to 47 (Mitani *et al*. 2002). These subgroups are variable and can be highly fluid, changing members quickly or lasting a few days before rejoining the community (Goodall 1986; Chapman *et al*. 1993; Boesch 1996). Based on the complex social networks they must maintain, it might thus be expected chimpanzees possess Euclidean spatial awareness. Chimpanzees travel in equally high linear fashion both in the periphery of their home range as in the core area of their home range, although the distance between food trees in the periphery is smaller than that in the core area (Normand & Boesch 2009). Furthermore, the initial direction adopted by chimpanzees when leaving a food tree, does not differ from the general direction to reach the next tree and chimpanzees revisit food trees from all possible directions (Normand & Boesch 2009). Based on these findings, Normand and Boesch (2009) recently concluded that chimpanzees navigate using a Euclidean map in large-scale space. It is however, impossible to say whether the periphery is really a lesser known area to the chimpanzees. Therefore, the high route linearity found in the peripheral area might simply suggest that chimpanzees have accumulated a similar knowledge of landmarks of the peripheral part of their home range as of the core area and may therefore not be evidence of Euclidean spatial awareness (as suggested for baboons in this study). Normand and Boesch (2009) instead argued that since the distance travelled between food trees in the periphery was smaller than that in the core area, chimpanzees might be limited by the distances they could precisely remember using a Euclidean map in such lesser-known areas. An alternative explanation of this finding, however, is that chimpanzees have less time available in the periphery or that there is higher potential danger from neighbouring groups in these areas (Normand & Boesch 2009). The lack of difference in route linearity between the periphery and core area of the home range by itself, does therefore not provide robust evidence for Euclidean spatial awareness. Moreover, Normand & Boesch (2009) did not use circular statistics to analyse the directional data on tree revisits and travel directions. Instead they used linear statistics to simulate the mean deviation angle for if chimpanzees revisited food trees using one, two or five different approach routes and to simulate the deviation angle for if chimpanzees returned to the food resource from any direction. Further use of linear statistics indicated that the mean observed deviation angle was significantly higher than the simulated deviation of revisiting a resource using a unique route, two different routes and five different routes, but not significantly different from the simulation of going back to a resource from any possible direction (Normand & Boesch 2009). Furthermore, they showed that the initial direction adopted by chimpanzees when leaving a food tree did not significantly differ from the general direction to reach the next tree according to the linear statistics employed (Normand & Boesch 2009). However, since directional data are substantially different from linear data, many of the usual linear statistical techniques and measures are often misleading, if not entirely meaningless and directional data thus calls for the use of specialised statistical tools and techniques (Mardia & Jupp 2000; Jammalamadaka & Sengupta 2001; de Raad this study). Although the results of Normand and Boesch (2009) point more towards the existence of a Euclidean map than a topological map in chimpanzees, the data should be re-analysed using the appropriate techniques before such conclusion can be drawn with confidence.

Another primate species living in fission-fusion communities are spider monkeys. Their communities typically comprise only 20-40 individuals (Di Fiore & Suarez 2007) and the social cognitive challenges they face may thus be smaller compared to those of chimpanzees. In a study of spatial abilities of spider monkeys, Di Fiore & Suarez (2007) did not find any evidence for Euclidean spatial awareness, but instead they concluded that spider monkeys travel using a topological map. Whether the social complexity faced by spider monkey may not have been great enough to have developed

Euclidean spatial awareness or whether social complexity is not a selective pressure for enhanced spatial skills is a question that remains to be answered.

Another factor that might select for Euclidean spatial awareness in animals is predation risk. When animals encounter predators, those animals that are quickly able to find their way to refuge and find their way back to their habitual travel routes after the threat has gone, are likely to have a selective advantage and possession of Euclidean spatial awareness will benefit in this. When presented with a sudden stimulus simulating an oncoming predator, Mongolian gerbils (*Meriones unguiculates*) can compute the optimal route to a safe refuge, taking into account the position of the predator, the location of a clearly visible refuge, as well as several other related variables (Ellard 2005). A recent study on spatial representation in Mongolian gerbils revealed that gerbils maintain representations of their locations with respect to prominent landmarks and refuges, even when such locations are not continuously visible (Ellard & Eller 2012) indicating topological spatial awareness. Another mammal under very high predation pressure are meerkats (*Suricata suricatta*) (Clutton-Brock *et al*. 1999; Manser 2001) they also seem to have an accurate knowledge of the distance and direction to the closest bolthole (*i.e.*, shelter) in relation to their own position in their territory at any time (Manser & Bell 2004). Although it was concluded that meerkats did not use path integration, the authors were unable to distinguish between other navigational mechanisms, including place recognition, reorientation and Euclidean map (Manser & Bell 2004). Nevertheless, considering that high predation risk is likely to have selected for the ability to remember a large number of shelter location (meerkats have more than 1000 boltholes in their home range) and for the detailed knowledge that meerkats possess of direction and distance of their specific locations (Manser & Bell 2004), predation risk might act as a selective pressure for more advanced spatial representations. Since solitary species are generally considered at even greater risk of predation than social foraging species (*i.e.*, an advantage of living in a group is reduced predation risk), it might be expected that they would evolve some degree of Euclidean spatial awareness, although to date there is no evidence for Euclidean representation in solitary species.

This leads to the question how topological spatial representation might progress to a Euclidean spatial representation. In theory, Euclidean spatial awareness is characterised by greater flexibility and efficiency of behaviour and is therefore considered as the more advanced navigation mechanism. Because a prominent feature of evolution is precisely the emergence of increased behavioural flexibility, it follows that Euclidean maps may play a crucial role in the onset of more complex behaviour displayed by higher vertebrates (Poucet 1993). It has already been discussed how complex sociality has been suggested to be a selective pressure for Euclidean maps in AMHs and arguably chimpanzees. Poucet (1993) hypothesized that when travelling in small scale space animals make use of Euclidian metrics, whist when travelling in large scale space a topological representation (landmark use) is likely to be used. The degree of Euclidean spatial awareness might therefore be measured by the spatial scale over which an animal is able to use a Euclidean map. In this fashion, Normand & Boesch (2009) hypothesized that chimpanzees might be limited by the distances they could precisely remember using a Euclidean map in less familiar areas. Poucet’s model has received some support from studies on spatial representations in tamarins (Garber 1989, 2000), howler monkeys (Garber & Jelink 2005) and capuchin monkeys (Urbani 2009), which showed the use of a topological map in large-scale space and suggested the use of a Euclidean map in small-scale space. Urbani (2009 pp:184-185) concluded that capuchin monkeys possess Euclidean spatial representation at small-scale space based on the fact that capuchins’ highly direct travel to feeding/resting trees in the final 30m and based on that capuchins visited feeding trees from multiple directions. It is however highly likely that at short distances from the food resource, sensory cues, particularly olfactory and visual cues, play a major part in navigation and that this might be an alternative explanation for the high travel linearity in the final 30m approaching resources. Moreover, linear instead of circular statistics were employed to analyse approach directions and in addition it seems that instead of analysing all individual approach directions that were recorded per feeding tree, directions were classed in 45° sections around an azimuth rosette and based on the number of 45° sections surrounding the rosette it was determined whether approach directions were distributed homogenous or non-homogenous around the circle (Urbani 2009 pp:138-139). In this way, Urbani (2009) concluded that capuchins approached resources from several directions, which either suggested that multiple landmarks were associated with each tree (*i.e.*, several approach routes and thus topological map use) or Euclidean spatial awareness to locate these trees. The former explanation seems to have been excluded from his conclusion. Visual inspection of the circular distributions of approach directions (Urbani 2009 pp: 138 Figure 5.3) highly suggests that capuchins use one or more routes to approach resources (i.e. approach directions seem clumped and not evenly distributed around the circle), however, appropriate circular statistical techniques would have to be employed to give conclusive evidence. In similar fashion, it was concluded that tamarins and howler monkeys (Garber [1989, 2000] and Garber & Jelink [2005] respectively) use Euclidean maps in small scale space based on their linear travel at shorter distances from targets and based on that the study animals approach trees from a variety of directions. Again, it is extremely difficult to know that sensory cues are not responsible for the high route linearity when animals come in close proximity to travel goals and none of these studies have used appropriate circular statistics to analyse the distribution of approach directions.

If there would indeed be different degrees of Euclidean spatial awareness based on spatial scale (at which an animal uses a Euclidean map), some species might have sufficient directional awareness to follow novel shortcuts between two points, as long as those points are located close together (but whilst landmarks associated with each location are still out of sight). In a study on spatial memory of the solitary living grey mouse lemur, Lührs *et al*. (2009) analysed directional information of movement segments using circular statistics. They found a significant angular concentration in the animals' movements, indicating a spatial restriction in movements that pointed towards a topological mental representation of spatial relations of the environment (Luhrs *et al*. 2009). However, they observed an ability of short-cutting that could not be explained by topological representations and they therefore cautiously conclude that mouse lemurs seem to have a mental representation of space that is more detailed than a topological map is generally assumed to (Lührs *et al*. 2009). In their study, the goal directed movements and novel path use observed in grey mouse lemurs can be explained by both path integration and Euclidean map (Lührs *et al*. 2009). Path integration has been found to be one of the primary forms of navigation in insects (*e.g*., Collet & Collet 2000; Muller & Wehner 1988, 1994), birds (*e.g*., Saint Paul 1982; Regolin *et al*. 1995) and mammals (*e.g*., Alyan & McNaughton 1999; Etienne *et al*. 1996) and allows for sophisticated navigation performance, at least on small scale (Wang & Spelke 2002). It therefore seems likely that also grey mouse lemurs use path integration in their navigation and that this mechanism explains their observed movement patterns. Nevertheless, further study to eliminate the possibility of Euclidean spatial awareness is necessary. Testing for novel shortcuts, especially at small scale is extremely challenging since simpler explanations for shortcut performance, such as visual landmarks that were visible from the displaced location, sun compass information, and familiarity of the shortcut must be ruled out (Bennet 1996), before shortcut behaviour can be taken as evidence of a Euclidean map.

In conclusion, evidence for the existence of Euclidean spatial representation seems extremely limited at best in both animals and humans. Studies on spatial representation should exercise caution when citing "existing evidence" of Euclidean spatial awareness. To unambiguously demonstrate the existence of Euclidean spatial awareness, a high level of experimental control is likely to be necessary.

9.3 Future research recommendations

Methodologically, a strength of this thesis was the thorough testing of the CPT and the novel application of hotspot analysis. To date, studies involving animals' travel routes mainly employ time sampling when recording location data. However, it was shown in this thesis that studies that aim to use the CPT in the future should rather use distance interval sampling than time based sampling or alternatively to manipulate the data post-hoc to obtain regularly spaced data points, as to minimise variation in step length. In selecting the distance interval, it is essential to determine the appropriate scale for the species and research question under investigation, since this was shown to affect both the maximum number of change-points that will be identified and the q value under which the maximum number of change-points will be identified. The 'q-rule' recommended by Byrne and his colleagues (2009) [to select that value of q which identifies the highest number of change-points] was shown to only be appropriate if the researcher selected the "right" granularity (*i.e.*, scale). This introduces some degree of arbitrariness to the CPT and also the need to run multiple pilot tests to decide the appropriate scale. To facilitate this process, an automated version of the CPT that allows researchers to run the CPT on multiple routes using multiple values of q at once, has been developed for this thesis and is provided in Appendix II.

This thesis presented the first spatial analysis of change-points identified by the CPT. Using hotspot analysis (Levine 2009) to identify clusters of change-points will increase the ability to study decision-making processes by allowing a range of sites to be selected for detailed observations that would not otherwise have been identified (King & Sueur 2011). Especially, in group-living animals there is often no clear indication of when decisions about how and where to go are made (*i.e.*, no clear start and stop locations) and decision-making behaviours have therefore seldom been studied. Identification of change-points and the subsequent identification of decision hotspot locations might require a substantial data set of travel routes. New advances in global positioning system (GPS) technology (*e.g.*, GPS satellite collars) may alleviate the amount of labour involved in the data collection of animals' travel routes. Highly precise data loggers that record both positional and orientation data are becoming more common and economic (*e.g.*, Nagy *et al.* 2010; Tsoar *et al.* 2011). When it will become feasible to employ such devices to multiple individuals in a group or even to entire groups, measures of individuals' position to one another can be obtained, which will take research on how groups solve coordination problems and make collective decisions to an exciting new level.

The use of such precise data loggers will also allow researchers to investigate differences in navigational abilities between the sexes. In humans, men and women are believed to have evolved different navigational abilities as a result of a gendered division of labour in hunting and gathering societies and therewith gendered differences of ranging and mobility (Eals & Silverman 1994; Silverman *et al*. 2000, 2007). The "hunter-gatherer theory of spatial sex differences" (HGT) (Gaulin & Fitzgerald 1986) suggests that hunters (*i.e.*, men) develop a preference for an allocentric strategy (using Euclidean metrics), since this works best in large-scale space (Burgess 2006), while gatherers (*i.e.*, women) develop a preference for an egocentric strategy (using landmarks) for foraging activities at small-scale space. Experimental psychologists designed tests in order to measure spatial abilities that could reflect different preferences for navigational mechanisms between the sexes. Men were found to generally perform better than women in tests of spatial perception and mental rotation (Voyer *et al.* 1995; Montello *et al*. 1999), while women out-performed men in memorising spatial configurations (Tottenham *et al*. 2003; Levy *et al.* 2005). If men indeed developed a preference for an allocentric navigational strategy, this would give them an advantage in the spatial perception and mental rotation tests, while women's preference for an egocentric strategy would explain their better performance in memorising spatial configurations (Burke 2012). It is unclear whether sex-based differences in humans are a result of training (Feng *et al.* 2007) or intrinsic spatial cognitive differences (Burke 2012). To date, no studies have investigated sex differences in navigational abilities in animals, although there are differences between the sexes in feeding behaviour. For example, female chimpanzees participate less often than males in hunting activities, which may require spatial coordination skills (Normand 2009). To better understand sex-based differences in navigational abilities found in humans, it would be interesting to investigate whether similar differences are found in animals and how these might relate to feeding behaviour.

Another important area for continued research involves animals' ability to plan the most efficient travel routes. According to the 'mental time travel hypothesis' (Suddendorf & Corballis 1997) animals do not have the ability to use their memory of specific past events (episodic memory [Tulving 1972]) to anticipate future needs (future planning [Suddendorf & Corballis 1997]) and it has been argued that these are uniquely human abilities (Roberts 2002; Suddendorf & Corballis 1997, 2007; Tulving 1983, 2002). Based on the spatial distribution of archaeological sites and the organisation of their settlement systems, Binford (1989) suggested that anatomically modern humans were able to plan ahead, but that Neanderthals lacked this ability, moving from site to site as required, pursuing an opportunistic foraging strategy. This has been contested by faunal evidence, however, which suggests that Neanderthals were capable of targeting group-living prey, anticipating their movements and making efficient use of the landscape to hunt them and more recently it has been concluded that this sort of foraging strategy requires tactical and complicated planning (Gaudzinski 1996; Gaudzinski & Roebroeks 2000; Burke 2000) and that there thus seems to be little reason to suggest that Neanderthals lacked the cognitive inability to plan ahead (Burke 2012).

In animals, what constitutes of evidence for episodic memory and future planning is much debated. Clayton and colleagues (2003a) give a comprehensive account of the criteria of mental time travel and they conclude that "most studies of animal memory to date have not tested episodic recall in a way that meets the three criteria" (Clayton *et al*. 2003a pp.687). The three criteria they refer to are those of 1) content: recollecting what happened, where and when on the basis of a specific past experience; 2) structure: forming an integrated 'what-where-when' representation; and 3) flexibility: episodic memory is set within a declarative framework and so involves the flexible deployment of information. Recent experiments on memory of western scrub jays (Clayton & Dickenson 1998, 1999; Clayton *et al*. 2001, 2003b), however, have challenged the mental time travel hypothesis by showing that these food caching birds "acquire and update generic knowledge about the rates at which the different food types perish and integrate this information with their bound memory for a specific caching episode to flexibly control their search preferences at recovery" (Clayton *et al*. 2003a pp.689) and thus meet all three of the criteria of mental time travel.

Like episodic memory, planning the future has also been argued to be unique to humans. Anticipating future needs and actions has to be independent of present needs and over longer time scales than the short timescales sufficient for instrumental responding such as lever pressing to obtain immediate food reward (Clayton *et al.* 2003a). More recent research suggests that scrub jays have the ability to make provision for future needs (Raby *et al*. 2007; Correia *et al*. 2007). There is some evidence that chimpanzees save and collect tools for future needs (Boesch & Boesch 1984), which might indicate that they possess the ability to plan for the future (Byrne 1995). However, this ability may be limited since the behaviour may reflect the chimpanzees' current hunger state and doesn't require an explicit reference to a future need state (Clayton *et al*. 2003a). Several studies have shown that primates indeed seem to possess planning abilities that they use to plan foraging routes (*e.g.*, Janson 2007; Noser & Byrne 2007b, 2010; Normand & Boesch *submitted*; Joly & Zimmermann 2011) although this ability might be limited. Support for the notion that planning abilities are limited comes from the work of Joly & Zimmermann (2011), who found that mouse lemurs plan their visit to a *first* keystone food resource, but found no evidence for planning further ahead. Similarly, captive vervet monkeys were able to memorise only 6 locations at a time, where food sites were presented in a relatively small arena (Cramer & Gallistel 1997) and also baboons were shown to have only limited planning abilities (Noser & Byrne 2010) due to their use of habitual routes and topological navigation mechanism (Noser & Byrne 2007a, 2010; de Raad this study). It would be very interesting to investigate more precisely *how far* animals are able to plan ahead and how this ability is affected by navigational mechanism, the number of food sources encountered and by the group size that an animal travels in. Chimpanzees efficiently plan their whole daily travel route ahead by selecting the shortest path through 3 to 11 major food resources, whereby the success of efficient navigation was positively affected by the party size (Nomand & Boesch *submitted*). This raises another interesting research question of whether individuals of the same species that travel in larger groups have the advantage of sharing information and are therefore able to plan travel routes more efficiently.

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APPENDIX I

```
rm(list = ls(all = TRUE))

source=4    # 1, PS desktop; 3, PS laptop; 4, LdR desktop
switch(source,
      setwd("C:/Documents/Statistics/LdR/RegularPoints"),
      setwd("C:/Phil"),
      setwd("/Users/PAStephens/Desktop/LdR"))
      setwd("C:/Users/LOUISE/Documents/HR")

memory.limit(size=4095)
memory.size(NA)

Interval<-300     # desired interval (in seconds)

# read in data
data<-read.csv("All points in UTM.csv")

tracks<-max(data[,3])

for (Tr in 1:tracks){
      dat<-data[data[,3]==Tr,]
      if (dim(dat)[1]>0 & max(dat[,10])>Interval){
            low.s<-min(dat[,10])
            high.s<-max(dat[,10])
            req.points<-seq(low.s+Interval,high.s,Interval)
            store<-matrix(nrow=(length(req.points)+1),ncol=8,0)
            store[,6]<-c(low.s,req.points)
            colnames(store)<-
c("Date","Year","Month","Day","Track","Time","LAT","LONG")
            store<-as.data.frame(store)
            store[1,1:4]<-dat[1,4:7]
            store[1,5]<-dat[1,3]
            store[1,7:8]<-as.numeric(data[1,1:2])

            count=1
            for (t in req.points){
                  count=count+1
                  low<-max(which(dat$Total.seconds<t))
                  high<-min(which(dat$Total.seconds>t))
                  if (high-low!=1) low=high-1        #  this  just  a  safe-
guard against exact matches
                  prop.gone<-(t-
dat$Total.seconds[low])/(dat$Total.seconds[high]-dat$Total.seconds[low])
                  LAT.moved<-(dat$LAT[high]-dat$LAT[low])*prop.gone
                  LONG.moved<-(dat$LONG[high]-dat$LONG[low])*prop.gone
                  store[count,1:4]<-dat[low,4:7]
                  store[count,5]<-dat[low,3]
                  store[count,7]<-dat$LAT[low]+LAT.moved
                  store[count,8]<-dat$LONG[low]+LONG.moved
                  }
            if      (Tr==1)      store.all<-store      else      store.all<-
rbind(store.all,store)
            }
      }

write.table(store.all,"300.csv",row.names=F,sep=",")
```

APPENDIX II

```
# R code for performing the "circular change point test" (CPT)
# as described in "How did they get here from there?
# Detecting changes of direction in terrestrial ranging."
# by R W Byrne, R G Noser, L A Bates & P E Jupp.
# Animal Behaviour 77, 619-631, 2009.

# P. E. Jupp 23 July 2008
# Code supplied without guarantee

# R code adjusted to include a “day loop” and a “q loop” so that
# multiple days and multiple q values can be tested at once.


source=2    # SELECT WORKSPACE
if (source==1) setwd("C:/YOUR WORKSPACE")
if (source==2) setwd("C:/ALTERNATIVE WORKSPACE")

# set up a data frame to store the change points
CP<-data.frame(filenm="a",q=0,k=0,t=0,x=0,y=0)
cp.mirror<-CP
cp.count=0

# read in the csv file that contains all the files (day tracks)
fnms<-read.csv("filenames.csv",header=F)

# start the day loop here
for (day in 1:20){

infile=as.character(fnms[day,1])

inp2<-scan(file=infile,what=list(x1=0,x2=0))
x1<-inp2[[1]]
x2<-inp2[[2]]

# Reverse the time-ordering,
# so that (bx1[1], bx2[1]) refers to putative goal

bx1 <- 0*x1
bx2 <- 0*x2

n <- length(x1)
for (j in 1:n){
bx1[j] <- x1[n-j+1]
bx2[j] <- x2[n-j+1]
}

# Calculate the steps (bxdiff1, bxdiff2)
bx1diff <- diff(bx1)
bx2diff <- diff(bx2)

# qq = maximum value of q
# qq =3 (Louise is only using q=3)
qq <- 7

# goal.t = "time" (backwards in time) of putative goal
# goal.t = 0 is a convenient default
goal.t <- 0
s = 0


stop=0

while (stop==0){
```

```
goal.t <- goal.t+s

# last.t = "time" (backwards in time) of last position of interest
# last.t = length(x1) - qq - 1 is a convenient default
# (and includes all the positions)
last.t <- length(x1) - qq -1

no.of.t <- last.t - goal.t + 1


# Set up matrix P in which to store P-values
P <- matrix(rep(exp(2),qq* no.of.t),nrow = no.of.t, ncol = qq)

# N = total number of permutations (1 observed and N-1 simulated)
# N = 1000 is a convenient number
N <- 1000

Rsumrand <- 0*c(1:N)

for (k in 1:no.of.t){ # start of k loop
for (q in 7:qq){ # start of q loop (Louise is only using q=3)
R1  <-  sqrt((bx1[goal.t+k+1]  -  bx1[goal.t+1])^2  +  (bx2[goal.t+k+1]  -
bx2[goal.t+1])^2)
R2 <- sqrt((bx1[goal.t+k+q+1] - bx1[goal.t+k+1])^2 + (bx2[goal.t+k+q+1] -
bx2[goal.t+k+1])^2)

Rsum <- R1 + R2

# Rsumrand[1] = observed value of statistic R1 + R2
Rsumrand[1] <- Rsum

# Now calculate statistic R1 + R2 for a further N-1 random permutations
# and store in Rsumrand
for (it in 2:N){ # start of it loop
u <- runif(k+q,0,1)
perm <- order(u)
bx1r <- bx1[goal.t+1]
bx2r <- bx2[goal.t+1]
for (j in 1:k){ # start of j loop
bx1r <- bx1r + bx1diff[goal.t+perm[j]]
bx2r <- bx2r + bx2diff[goal.t+perm[j]]
} # end of j loop


R1rand <- sqrt((bx1r - bx1[goal.t+1])^2 + (bx2r - bx2[goal.t+1])^2)
R2rand  <-  sqrt((bx1[goal.t+k+q+1]  -  bx1r)^2  +  (bx2[goal.t+k+q+1]  -
bx2r)^2)
Rsumrand[it] <- R1rand + R2rand
} # end of it loop


# calculate P-values
P[k,q] <- sum(Rsumrand >= Rsum)/N

} # end of q loop
} # end of k loop

# identify column of interest
Pq <- P[,q]
# find significant values
s=0
sig<-which(Pq<0.01)
if (length(sig)==0) stop=1
if (length(sig)==1) s=sig[1]
if (length(sig)>1) {
      s=min(sig)
      cease=0
      while (cease==0 && s<max(sig)){
            if (Pq[s+1]>=Pq[s]){
```

```
                  loc.min <- s
                  cease=1
                  }
            if (cease==0) s=s+1
            }
      }
if (stop==0) print(paste("Local minimum occurs at k =",s))

if (s>0) {
      cp.mirror$filenm<-infile
      cp.mirror$k<-s
      cp.mirror$q<-q
      cp.mirror$t<-s+goal.t
      cp.mirror$x<-bx1[s+goal.t]
      cp.mirror$y<-bx2[s+goal.t]
      cp.count=cp.count+1
      if (cp.count==1) CP<-cp.mirror else CP<-rbind(CP,cp.mirror)
      }

}     ## end of "while (stop == 0)" loop

} # end of day loop

date<-as.POSIXlt(Sys.time())
date<-unlist(unclass(date))
ofile<-paste("CP                  ",substr(as.character(Sys.time()),1,10),"
",date[3],"h",date[2],", q=",q,".csv",sep="")
write.table(CP,ofile,row.names=F,sep=",")


###################################################
## stop here unless you need a graph
###################################################
```

APPENDIX II

Tree species	Latin name	Flowers	Fruit production
Flame thorn	*Acacia ataxacantha*	Jun-Feb	Jun-Oct
Sweet thorn	*Acacia karroo*	Dec-Jan	Dec-Jan
Paperback thorn	*Acacia sieberiana*	Sept-Nov	Mar
Forest false-nettle	*Acalypha glabrata*	Oct	Dec-Jan
Small-leaved yellowwood	*Afrocarpus falcatus*		Sept-May
Black false-currant	*Allophylus africanus*	Nov-Mar	Dec-May
Forest silver-oak	*Brachylaena transvaalensis*	Jul-Nov	Aug
Common turkey-berry	*Canthium inerme*	Sept-Nov	Nov-Mar
Rock alder	*Canthium mundianum*	Sept-Nov	Nov-May
Forest num-num	*Carissa bispinosa*	Aug-Mar	Jan-Oct
Simple-spined num-num	*Carissa edulis*	Sept-Dec	Nov-Jan
Bushman's tea	*Catha edulis*	Jan-Nov	Jan-Nov
White stinkwood	*Celtis Africana*	Aug-Oct	Oct-Dec
Tinderwood	*Clerodendrum glabrum*	Most of the year	Feb-Jul
River bushwillow	*Combretum erythrophyllum*	Sept-Nov	Jan-Oct
Forest bushwillow	*Combretum kraussii*	Aug-Jan	Feb-Jun
Velvet bushwillow	*Combretum molle*	Sept-Nov	Jan
Forest fever-berry	*Croton sylvaticus*	Sept-Jan	Dec-May
Mountain wild-quince	*Cryptocarya transvaalensis*	Dec-Feb	Mar-May
Cabbage-tree	*Cussonia spicata*	Nov-May	Jun-Sept
Sickle bush	*Dichrostachys cinearea*	Oct-Jan	May-Sept
Karoo bluebush	*Diospyros lycoides*	Jan-May	Sept-Dec
Pink dombeya	*Dombeya burgessiae*	Apr-Aug	Jun-Oct
Wild pear	*Dombeya rotundifolia*	Jul-Nov	Oct-Dec
Wild apricot	*Dovyalis zeyheri*	Aug-Dec	Nov-May
Forest ironplum	*Drypetes gerrardii*	Sept-Nov	Sept-Oct
Cape ash	*Ekebergia capensis*	Sept-Nov	Dec-Apr
Transvaal milkplum	*Englerophytum magalismontanum*	Jun-Dec	Dec-Feb
Common coral tree	*Erythrina lysistemon*	Dec	Jul-Oct
Twin Red-berry	*Erythrococca trichogyne*	Oct-Dec	Jan-Feb
Blue guarri	*Euclea crispa*	Oct-Feb	Apr-Dec
Hairy guarri	*Euclea natalensis*	May-Jan	Oct-Jan
Common forest myrtle	*Eugenia natalitia*	Jun-Dec	Nov-Jan
Hairy myrtle	*Eugenia woodii*	Sept-Dec	Jan-Mar
Common wild fig	*Ficus burkei*		Most of the year
Forest fig	*Ficus craterostoma*		Aug-Dec
Red-leaved fig	*Ficus ingens*		Jun-Dec
Wonderboom fig	*Ficus salicifolia*		Aug-May
Broom cluster fig	*Ficus sur*		Sept-Mar
Cross-berry	*Grewia occidentalis*	Oct-Jan	Jan-May
Common spike-thorn	*Gymnosporia buxifolia*	Sept-Apr	Most of the year
Black-forest spike-thorn	*Gymnosporia harveyana*	Most of the year	Mar-Sept
Thorny gardenia	*Hyperacanthus amoenus*	Nov-Mar	Jan-Jul
Climbing turkey-berry	*Keetia quenzii*	Sept-Nov/ Apr-Jun	Oct-May
Common bush-cherry	*Maerua cafra*	Aug-Oct	Oct-Dec
Koko tree	*Maytenus undata*	Sept-May	Mar-Sept
Transvaal red milkwood	*Mimusops zeyheri*	Oct-Mar	Apr-Oct

Cork-bush	*Mundelea sericea*	Oct-Jan	Feb-Apr
Forest nuxia	*Nuxia floribunda*	May-Sept	Jun-Oct
Northern stinkwood	*Ocotea kenyensis*	Nov-Jan	Feb-Mar
Wild olive	*Olea europaea*	Aug-Oct	Mar-Aug
Forest crowned-medlar	*Pachystigma bowkeri*	Oct-Dec	Dec-Feb
African-wattle	*Peltophorum africanum*	Sept-Feb	Feb-Jun
Broad-leaved yellowwood	*Podocarpus latifolius*		Jul-Sept/Dec-Feb
Redwing	*Pterolobium stellatum*	Feb-May	Mar-Aug
Cape beech	*Rapanea melanophloeos*	May-Aug until Dec	Aug-Dec
Quinine tree	*Rauvolfia caffra*	Jul-Oct	Oct-Mar
Common forest grape	*Rhoicissus tomentosa*	Oct-Jan	Jan-Apr
Northern bushman's grape	*Rhoicissus tridentate*	Nov-Apr	Feb-Dec
Red currant	*Rhus chirindensis*	Aug-Mar	Nov-Mar
Crow berry	*Rhus pentheri*	Aug-Mar	Sept-May
Monkey pod	*Senna petersiana*	May-Aug	Jan-Jun
Healing leaf-tree	*Solanum giganteum*	Dec-Apr	Dec-Apr
Water berry tree	*Syzygium cordatum*	Aug-May	Oct-Jun
Wild-mulberry	*Trimeria grandifolia*	Nov-Feb	Feb-Apr
Forest mahogany	*Trychillia dregeana*	Oct-Nov	Jan-May
Velvet Wild-medlar	*Vangueria infausta*	Sept-Oct	Jan-Apr
White iron-wood	*Vepris lanceolata*	Dec-Mar	May-Jul
Lemon wood	*Xymalos monospora*	Jun-Oct	Nov-May
Buffalo thorn	*Ziziphus mucronata*	Nov-Feb	Mar-Aug