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Ecology, route choice and cognitive maps

in wild chacma baboons *(Papio ursinus)*

by

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for the degree of Doctor of Philosophy

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Acknowledgements

Abstract

Strong selection pressures must have shaped the way how animals perceive the world and find important places, and any capacity to learn and memorise the spatial properties of resources must have increased individual fitness. Early field researchers postulated the cognitive map to be the mental tool which guides primates towards resources. However, empirical studies and any attempts to refine this statement are still lacking, and our understanding of how primates represent out-of-sight locations has remained rudimentary. I examined the ranging patterns of a wild chacma baboon group *(Papio ursinus)* in a 16-month field study in order to address this issue.

The study group's travel speed and straightness of paths were highest when travelling towards water holes and fruit sources, suggesting goal-directed movement over long distances. Among several hypotheses of varying cognitive sophistication, extensive spatial memory remained the only explanation for the observed ranging. Also, I found evidence for planning abilities and anticipation of resource contents and availability.

However, a natural experiment revealed no evidence for map-like mental representations that encode Euclidean relations among locations. During evasive manoeuvres from other groups, the study group used familiar routes in the absence of familiar landmarks, suggesting that baboons find their ways with a 'network map'. This was supported by the finding that they used cues along their paths for reorientation.

I developed a novel statistical tool for analysing animal ranging patterns. The idea behind the 'Jupp test' was that change points in foraging paths may give interesting insight into the cognitive processes involved in orientation. This revealed that when foraging in a featureless area, the baboons held an approximate bearing towards their resources over large distances, and adjusted it shortly before arriving. This finding suggests that baboons may have some knowledge of the Euclidean properties of space.

Contents

Chapter 1 Introduction

The ability of animals to move efficiently between resources such as feeding sites, nests, or hiding places is directly linked to individual fitness. In the evolutionary past, a strong selection pressure is likely to have shaped the way how animals perceive the world, identify important locations in space, and find their ways towards them. In addition, any capacity to learn and memorise the spatial properties of important locations must have significantly contributed to survival and reproduction. For this reason the need of animals to solve spatial problems has been viewed as a potential trigger of cognitive evolution (Milton, 1981; 1988; 2000; Menzel, 1997; Chown, 1999a).

Although the relation between brain size and intelligence is still under debate (eg. discussed in Byrne, 1995; Barton, 2000; van Schaik & Deaner, 2003), there is evidence that spatial competence may be involved in the enlargement of the neocortex in primates (Byrne, 1995), and of the hippocampus in food-storing birds (Krebs et al., 1990; Sherry et al., 1989; Sherry & Duff, 1996). However, compared with a remarkable body of literature available on how birds (Balda & Kamil, 1998; Shettleworth & Hampton, 1998; Wiltschko & Wiltschko, 2003), rodents (Save et al, 1998) and arthropods (Collet & Zeil, 1998) solve spatial tasks, our knowledge of how primates find their resources is scarce. Many primatologists have felt that their study animals forage by means of complex mental processes such as cognitive maps, but to date any attempts to refine this statement have remained vague.

This thesis aims at shedding some light on the spatial tasks faced by a group of wild chacma baboons *(Papio ursinus)* and on the mental processes likely to be involved in their foraging in large-scale space. In this chapter I will briefly discuss the literature on cognitive maps and two important, powerful mechanisms for orientation in animals, landmark-matching and path integration. On the basis of this background, I then review the primate literature on cognitive mapping.

1.1 Cognitive maps

When Tolman (1948) introduced the term cognitive map to describe the way how rats appear to use mental spatial representations for finding their ways, he caused a huge outcry in the scientific world. At this time, animals were believed to only connect particular responses to particular stimuli. The idea that animals may represent parts of the environment which were well beyond the scope of their senses was entirely new. Tolman hypothesised that rats, and by analogy also humans, construct a map-like representation of their environment that is structured in the same way as a cartographic map, and thus encodes Euclidean properties.

Tolman's cognitive map concept was further elaborated by O'Keefe & Nadel (1978), who proposed that humans, rats and migratory birds posses a unitary neural system, located in the hippocampus, with which they represent the outside world as if viewing it from a bird's perspective. Based on their electrophysiological work, they claimed that the acquisition of cognitive maps contrasts

with the learning of routes, in that the neurons involved in the two tasks are located in different parts of the brain. Although many of their claims have been abandoned in the meantime, both the idea that animals place objects onto a cognitive map that is isomorphic to the three-dimensional world through experience, and the importance of the hippocampus in spatial tasks have remained influential.

The idea that animals represent space in a map-like way subsequently gained considerable appeal, and cognitive maps were claimed for many wild and captive species, including humans (Gallistel, 1990, Portugali, 1996; Laszlo et al., 1996; Kitchin & Blades, 2002), non-human primates (chimpanzees: Menzel, 1978; Boesch & Boesch, 1981; baboons: Altmann & Altmann, 1970; Stolba, 1979, Sigg & Stolba, 1981; Sigg, 1986; tamarins: Garber, 1988; 1989), dogs (Thinus-Blanc, 1988), foxes (Fabrigoule & Maurel, 1982), rodents (golden hamsters: Thinus-Blanc, 1988, rats: Tolman, 1948; O'Keefe & Nadel, 1978), birds (eg. Wiltschko & Wiltschko, 1998) and insects (bees: Gould, 1986).

However, researchers have not always meant the same when using this term (reviewed in Kitchin, 1994; Kitchin & Blades, 2002; Bennet, 1996; Shettleworth, 1998; Wehner & Wehner, 1990). According to Tolman's (1948) and O'Keefe & Nadel's (1978) early definition a cognitive map is a set of mental representations which encodes the metric properties of large-scale space, that is of distances and directions, which allow the planning of novel routes to unseen goals. Cognitive maps are constructed when walking on the ground,

through latent learning. Although they are individualised and may be incomplete and distorted, they encode per definition Euclidean relations (Sholl, 1996; Dyer, 1991). Thus, a cognitive map sensu Tolman and O'Keefe & Nadel enables animals to move efficiently from any location A to any location B, to take novel shortcuts and to optimise travel routes between out-of-sight goals, an assumption that implicitly underlies many models of optimal foraging theory (Charnov, 1976).

Based on the errors that humans made when estimating angles and distances in familiar urban environments, Byrne (1978; 2000) proposed that the human cognitive mapping capacities of large-scale space may be overestimated. He refined the concept and differentiated between the term 'vector maps', a synonym for cognitive maps sensu Tolman and O'Keefe & Nadel, and 'network maps'. He suggested that humans predominantly navigate by network maps, that is, on the basis of propositional instructions that are organised as a network of many strings of non-verbal commands which are interconnected at common nodes. In contrast to the representations of vector maps, the commands of network maps only contain minimal directional and distance information, but preserve topological relations among locations. For example, a string may include the commands 'from front door go right, at police station turn left, at supermarket go half right, at post office stop' (Byrne 1978; 2000). In con-trast to the vector map hypothesis, network maps result in routes that are not necessarily optimal and do not allow individuals to take novel shortcuts.

1.2. Do bees and rats have cognitive maps?

On the basis of his experiments with honey bees *(Apis mellifera)* Gould (1986) suggested that arthropods possess vector maps. In his experiments, he captured the bees when they were leaving their hive for a well known feeding site A, and released them at a new, unfamiliar site B. The bees flew directly from the new site B to the feeding site A. Gould concluded that this performance could only result from a vector map, which allowed the bees to compute the relative locations of the sites A and B, even though the path between these locations was entirely novel.

The implications of Gould's results were important, since he was the first to implicitly claim mental representations in insects. It is therefore not surprising that his findings were challenged by two research teams (Wehner & Menzel, 1990; Dyer, 1991) who replicated his experiments.

Dyer (1991) criticized that Gould had not considered simpler explanations for the bee movement patterns. Therefore, he prevented the test bees from directly seeing any familiar landmarks at releasing site B. In contrast to Gould's findings, his bees did not fly to the feeding site A after displacement. Instead, they either chose the compass direction they usually used when flying from the hive to feeding site A, or else flew back to their hive. Wehner & Menzel (1990) similarly failed to replicate Gould's findings, and confirmed the lack of vector maps in bees. Both research teams concluded independently from each other that bees use simpler mechanisms for orientation.

Benhamou's (1996) water maze experiment with rats was based on a similar paradigm. The maze consisted of a circular pool filled with opaque water so that a small escape platform below the water surface became invisible to the rats. The pool was surrounded by a cylinder, which was open on one side, so that the test animals could see about a quarter of the room environment in which the experiments took place. The cylinder could be shifted around its center so that the opening offered different views at different stages of the experiment.

During each of the training trials, the opening of the cylinder was shifted, so that the rats could learn to use a limited number of extra-maze landmarks for navigation towards the platform. They learned the landmarks of the surrounding room very quickly, and were successful in reaching the escape platform in an efficient way only after a few training trials. During the test trials, the cylinder was shifted to a novel position, offering a new set of landmarks to the rats, which they had not seen during the training trials. The rats were released into a narrow channel outside the cylinder, from where they could see the learned landmarks. However, as soon as they entered the central maze area, the landmarks disappeared behind the screen. If the learned panorama shared some landmarks with the panorama available to them during the test, they were still able to swim to the hidden goal efficiently. However, when only offered unfamiliar panoramas, the rats searched for the escape platform at random. Benhamou (1996) concluded that his rats had not constructed a vector map of the maze and proposed that mammals lack cognitive mapping capacities that accurately encode distances and directions.

1.3. Path integration and landmark-matching

Researchers on animal orientation agree that locations can only be described with respect to a reference system (eg. McNamara, 2003). Reference systems have been classified as either 'egocentric', that is, based on body coordinates and memory, or else 'geocentric', that is, based on external cues such as the direction of gravity, the sun azimuth or landmarks in the environment.

Path integration, or dead reckoning, has been recognised as a powerful egocentric mechanism of orientation. It was first discovered in desert ants *(Cataglyphis fortis*, Müller & Wehner, 1988), but has been demonstrated in other invertebrate (Collet & Zeil, 1998) and vertebrate species (Etienne et al., 1998), including humans (Loomis et al., 1999).

Desert ants are solitary, and live in underground nests. After leaving their nest, they wander around randomly over hundreds of meters in search for food. As soon as they find a prey item, they capture it with their mandibles and rush directly back to the starting point of their journey, their nest entrance.

In order to investigate this remarkable navigational task, Müller & Wehner (1988) provided the ants with a food item during their random walk away from the nest. Before the animals could start their homeward journey, they picked them up and displaced them to a new location. The ants then were allowed to return to their nest. They dashed away in a straight line, but failed to find the

nest entrance. Instead, they searched for the entrance at a distance, which corresponded to the distance over which they had been displaced.

Desert ants apparently return to their nests by path integration. That is, they continuously integrate information about the changes of distances and direct-ions when walking away from the nest, and in this manner keep track of their own location relative to the nest location at all times, as if tightly connected to it with an invisible thread (Wehner & Wehner, 1990). Müller & Wehner (1988) showed that a comparatively simple, arithmetic algorithm based on mean angles and travel distances is sufficient to model this task.

A common 'geocentric' mechanism for returning to a certain place is the use of landmarks that surround a nest, a food source or a sleeping site. Tinbergen & Kruy (1938) demonstrated that digger wasps *(Philanthus triangulum)* learn the characteristic points of the area around their nest entrance by means of an 'orienting flight' before they fly off to search for food supplies. In his classic experiment, Tinbergen (1932) marked the nest entrance with a circle of pine cones. After giving the wasps the opportunity to learn these landmarks, he removed the cones in the absence of the wasps, and placed them in the same arrangement further away, at a distance of approximately 30 cm from the nest entrance. When returning from their foraging trip, the wasps searched for the entrance in the centre of the circle, and consequently failed to find it.

During landmark matching, animals are believed to compare a memorised view of the world at the goal location with the current view from the world. As

long as the animals are away from the goal location, they perceive a discrepancy between the current view and the learned 'target' view. By moving towards the goal the discrepancy decreases, and it vanishes completely at the goal location (Cheng & Spetch, 1998). A wide variety of experiments in the lab with both vertebrate and invertebrate species have shown that the geometric shape of the environment as well as the configuration of several landmarks serve as important cues (reviewed in Cheng & Spetch, 1998; Collet & Zeil, 1998).

1.4. Do primates have cognitive maps?

In comparison with an extensive body of literature on arthropods and small mammals, there is only a handful of information available on primate navigation and spatial knowledge. However, many primate species have been proposed to need increased spatial competence. Their food sources are relatively poor in energy and yet they lack any gut specializations (Byrne, 1995), so that they must forage selectively and often walk over long distances to cover their nutritional needs.

The first primatologists who mentioned the ability of wild primates to travel directly to their resources over long distances were Altmann & Altmann (1970), who studied savannah baboons in Eastern Africa. In the chapter 'mental maps' of their monograph they stated that

'Direct movement of baboons over long distances to some of the larger, semi-permanent rain pools, even when the baboons could not see the rain pool

during their progression, convinced us that they were familiar with the locations of these water sources. We believe that they were orienting on the basis of memory, rather than the immediate sensory perception of water. [...] We feel certain that the baboons were familiar with the major topography of their home range, and could navigate within it on the basis of that familiarity.'

Sigg & Stolba (1981; see also Sigg, 1986; Kummer, 1992) performed the first systematic study on cognitive mapping in a group of hamadryas baboons *(Papio hamadryas)* who lived in the Ethiopian semi-desert. They tested three hypotheses, random wandering, following topological features, and goal-directed movement. Only goal-directed movement, they argued, would support the notion of cognitive maps. Based on the records of 71 foraging journeys, they identified repeatedly used 'street segments', each 150 m wide and 500 m long.

They viewed the fact that they were able to identify such segments as evidence against random wandering. Also, they abandoned the hypothesis that their animals were following topological features, several wadis, a road and a railway line, because these features were considerably larger than the observed street segments. Evidence for goal-directed movement and 'cognitive mapping' came from their finding that the street segments were interconnected in a 'flexible way' and that travel speed increased shortly before the water holes (Sigg & Stolba, 1981).

Unfortunately, this study does not provide any information on the visibility of the resources. However, this information is crucial, because an increase of

travel speed and of 'street segment' length could well result from direct visual stimuli of the resources or any associated landmarks.

Data on 'cognitive mapping' is also available from a mixed-species group of tamarins, *Saguinus mystax* and *Saguinus fuscicollis*, who travelled efficiently between 10 flowering *Symphonia* trees which provided nectar during the dry season in the Peruvian Amazon forest (Garber, 1988; 1989). The paths during the nectar season bore no relation to the normal, rather repetitive routes through the forest in other times of year. The data presented comprise the records of 12 full days. During that time, the group visited the nectar tree nearest or second-nearest to the previous feeding tree in 89% of the time, with an average distance between feeding sites of 107m. After leaving a *Symphonia* tree, the tamarins did not visit the next tree in 11% of the cases. Instead, they bypassed a nectar-poor tree in favour of a more rewarding one. Garber (1988) therefore suggested that the tamarins anticipated the food amount on each *Symphonia* tree in advance, remembered the locations of all available trees, and assessed their distances and directions from any location. Again, no data on visibility are given in this paper. This kind of information could have revealed how far the *Symphonia* trees were visible in the area and thus could convincingly show that the tamarins were navigating on the basis of memory.

Cognitive maps were also claimed for wild chimpanzees *(Pan troglodytes verus)*. During habituation of their study community in the Tai forest, Boesch & Boesch (1984) marked the stone and wooden club hammers which the chimp-

anzees used to crack the preferred Panda nuts. They did not observe the hammer transports directly, but recorded all shifts of hammers to new anvils, for example to emerging roots or outcropping rocks. Visibility in the forest was around 20 m. The authors knew 20 Panda trees in a selected area of the home range, which was approximately 400 x 500 m in size.

They hypothesised that the chimpanzees could either take any stones and transport them to any Panda trees, or else use a cognitive map of the locations of the stones relative to the trees. Under the assumption that chimpanzees use cognitive maps, they expected that transport distances were short, and that the animals typically transport heavier stones over shorter distances than lighter ones.

Of a total of 76 hammer transports, 52 (68%) met the above assumptions of a 'cognitive map' (Boesch & Boesch, 1984). However, their data also suggested that 46 hammer transports occurred with the hammers in view of the Panda trees. Thus, only 30 transports were probably made on the basis of spatial knowledge. But since the transports of the hammers were not observed directly, other possibilities such as random search remain entirely open to speculation. Thus, the claim that the Tai chimpanzees use cognitive maps for their hammer transports to crack the Panda nuts remains unconvincing.

Reviews of cognitive mapping abilities in animals usually cite Emil Menzel's (1978) experiments with captive chimpanzees (Laszlo et al., 1996; Shettle-worth, 1998). Menzel carried one of 6 young chimpanzees in his arms while

he hid 18 food items in a 1-acre field (30m x 122 m). The path along which the food was hidden as well as the hide locations changed from trial to trial. 5 control animals were locked in a release cage and could not observe the hiding process. Before each trial, the test animal was returned to the group, and all chimpanzees were subsequently released into the experimental area.

The test animals found 12.5 food items per trial on average, whereas the control animals only found 0.2 items. From the release point, the test animals moved in direct lines between the food hides, and the hides were visited in a new sequence which did not resemble the sequence experienced during the hiding process. Although the animals did not necessarily minimise their overall route, they kept their paths short. Menzel (1978) concluded that his chimpanzees found the food on the basis of memory, and felt that the term 'cognitive map' explained best their performance.

A similar conclusion was drawn by Gallistel & Cramer (1996) and Cramer & Gallistel (1997), who replicated Menzel's experiment with vervet monkeys *(Cercopithecus aethiops)*. These experiments impressively demonstrated that chimpanzees and vervet monkeys memorise the locations of hidden food sources in small-scale space and are likely to perform sophisticated computations to keep travel distances short. However, they can not demonstrate the presence of cognitive maps that encode Euclidean relations among out-of-sight locations (Tolman, 1948; O'Keefe & Nadel, 1978; Byrne, 1978; 2000).

1.5. Summary and research questions

Orientation in space is a basic task that has to be solved by all animals. It can be viewed as a trade-off between keeping the neural processes as simple as possible by reducing the information provided by the real world to a minimum and competently solving the spatial tasks needed to survive and reproduce successfully (Chown, 1999a, 1999b).

The term cognitive map has been used ambiguously in the past. Some authors viewed it as an umbrella term for many different ways of how humans and animals use and represent their environment (Gallistel, 1990; Laszlo, 1996; Thinus-Blanc; 1988; Kitchin & Blades, 2002). Although not explicitly stated, primatologists seem to follow this point of view (Altmann & Altmann, 1970; Menzel, 1978; Sigg & Stolba, 1981; Sigg, 1986; Garber, 1988; 1989). In contrast, other researchers followed a stricter definition of the term (Tolman, 1948; O'Keefe & Nadel, 1978; Bennet, 1996; Benhamou, 1996; Dyer, 1991), and developed testable hypotheses on animal cognitive processes that underlie orientation (Byrne, 1978; 2000).

Researchers have failed to find vector maps (Byrne 1978; 2000) in rats (Benhamou, 1996) and bees (Dyer, 1991; Wehner & Menzel, 1990), but despite the repeated claim of cognitive maps in primates, our knowledge on how primates find their ways in large-scale space is still vague. This is partly due to the fact that researchers have not convincingly excluded direct visual stimuli of the resources as possible means of orientation.

In this thesis I use observational data to address questions about the nature of the cognitive processes underlying the foraging journeys of a wild group of chacma baboons *(Papio ursinus)* in large-scale space. In particular, I aim at examining the effect of ecological and topological factors on ranging, and to test several hypothetical searching strategies against the notion that baboons represent out-of-sight locations. I investigate whether the animals approach their resources in a goal-directed way, and the extent of their planning abilities. Furthermore, I examine the flexibility of path choice in two natural experiments, in order to test two hypotheses on cognitive maps, the vector map and the network map hypothesis. In addition, I introduce a novel statistical approach to the analysis of foraging routes with the intention to bring forward the comparative study of animal ranging and the underlying cognitive mechanisms.

Chapter 2 Study site and general methods

2.1. Study site

2.1.1. Geography and history

The study site for this project was Blouberg Nature Reserve, which is located in the Limpopo Province of South Africa, approximately 120 km N of the provincial capital of Polokwane (Figure 2.1). Blouberg Nature Reserve is situated on the Eastern foothills of the Blouberg mountain massive and reaches into the vast flatlands of the Limpopo plateau. Altitudes within the reserve range between 850 and 1600 m above sea level, with the peak of the mountain massive lying outside its borders. The reserve is naturally divided into three sections, the Southern flatlands, the central hill, and the Northern flatlands (Figure 2.2). Both, the Southern and the Northern flatlands encompass several human-made structures such as dust roads, fire breaks and artificial ground water supplies. The main study area (that is, approximately the home range of the study group) included parts of both the central hill and the Northern flatlands.

The grounds of Blouberg Nature Reserve were privately owned and used for hunting, cattle and crop farming until 1983, when the unusual wealth of flora and fauna of the area was recognised. Thereafter, an area of 9530 ha was set apart and proclaimed as a provincial nature reserve. Game that had disappeared from the area was reintroduced. Today, Blouberg Nature Reserve is largely surrounded by more or less intensely used farmlands, as well as by

Figure 2.1. Location of Blouberg Nature Reserve (arrow) within Southern Africa.

settlements. Tourism to the area is modest, and flora and fauna within the

reserve borders are well protected.

Figure 2.2. Blouberg Nature Reserve with fence, roads (black lines) and 20m-contour lines (grey lines). Numbers indicate height above sea level.
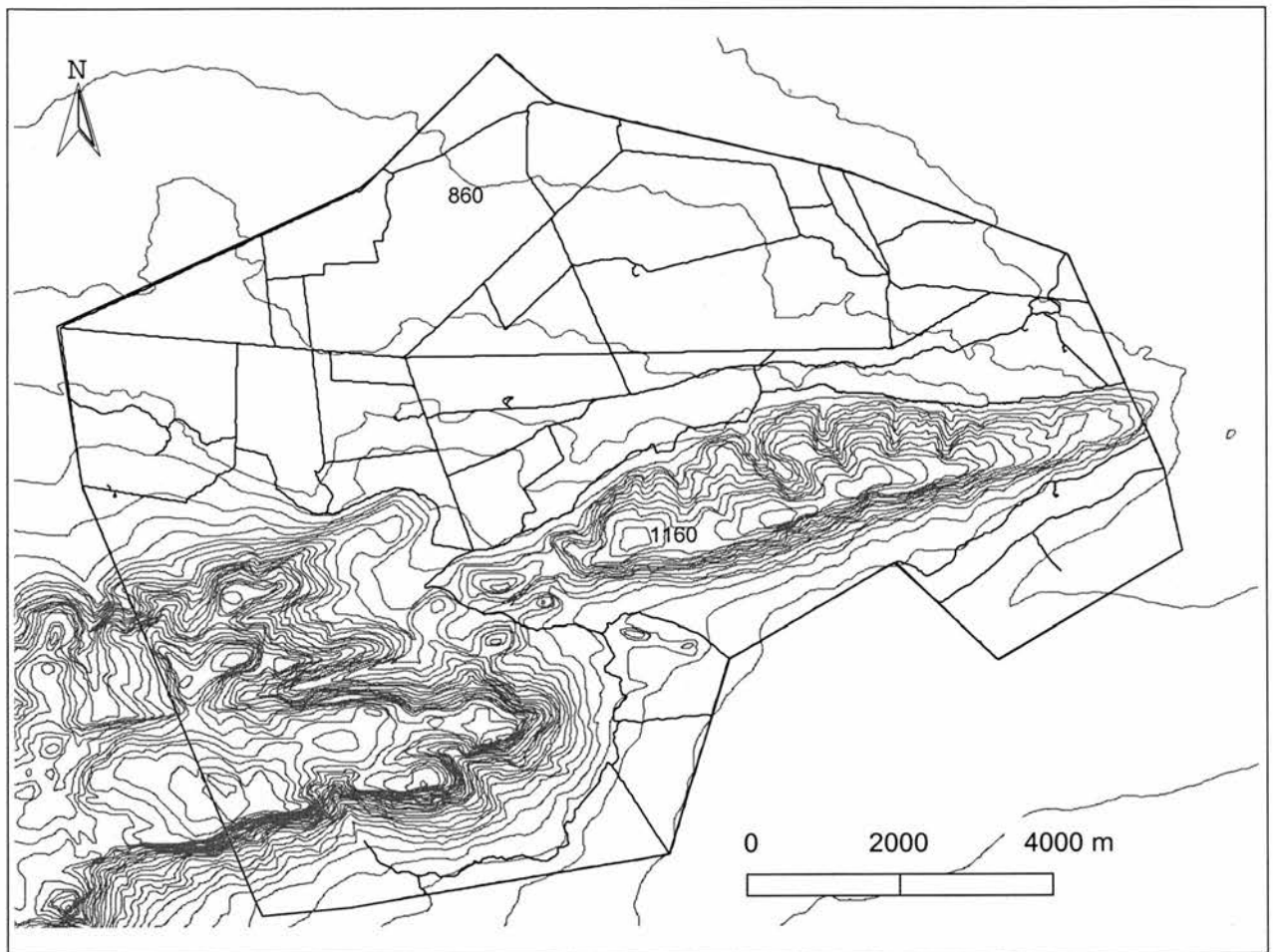
2.1.2. Climate and seasonality

Rainfall at Blouberg is confined to a single wet season between October and April approximately, that is, to the warm austral summer. The winter months are dry and mild. Research staff had collected rainfall data at several loca-

Figure 2.3. Temperatures and rainfall at Blouberg Nature Reserve. Mean monthly maximum and minimum temperatures (± SED) during the study period, and mean monthly rainfall between 1997 and 2002 (filled bars, ±SED). Open bars show the amount of rainfall per month during the study period.
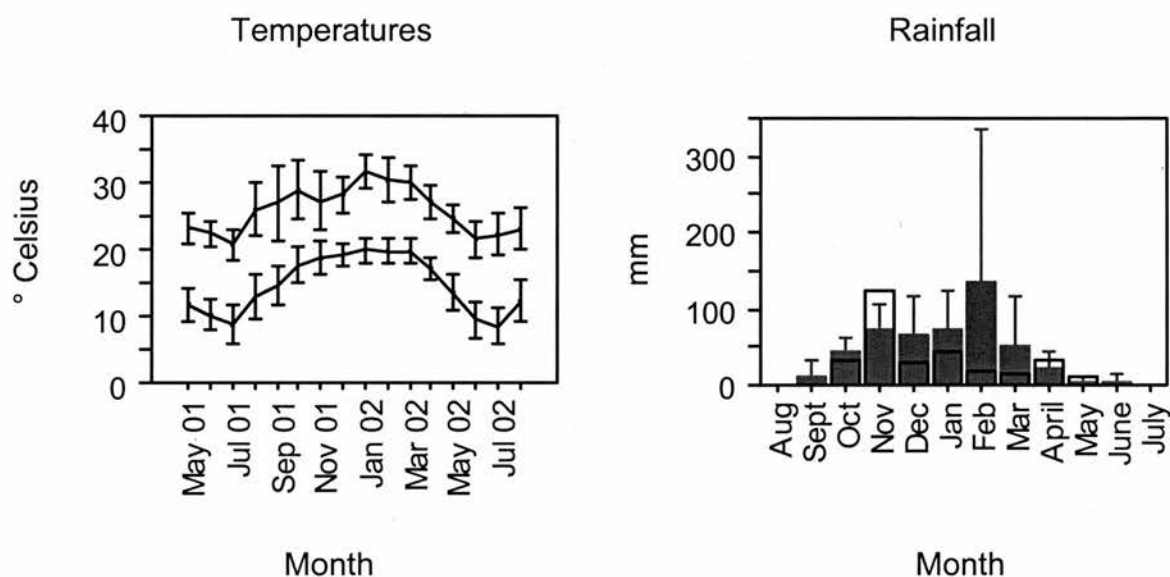
tions since 1997. Average annual rainfall during this time period was 482 mm (Figure 2.3.). This value includes a year of heavy floods with 1030 mm of precipitation. When excluding this unusual rainy season from the computations, an average yearly rainfall of 343 mm is obtained, a value that may be representative of the situation at Blouberg.

Each day I measured the minimum and maximum temperatures throughout the study period in the shade of the research camp, which was situated in the NE plain of the reserve. This revealed that average minimum and maximum temperatures were 15 ± 5 ° and 26 ± 5 ° Celsius, respectively, and absolute

temperatures ranged between 3° during the coldest winter nights and 38° on warm spring and summer days.

2.1.3. Vegetation and water

The vegetation at the study site falls into the category of 'woodland savannah', with a grassy ground layer and a relatively dense intermediate-sized upper layer of shrubs and trees which grow on shallow sandy and loamy soils. Due to the differences in altitude, the vegetation in the main study area exhibited characteristics of both the 'Arid Mountain' and 'Mixed Bushveld' biome (Low & Rebelo, 1996). Typical tree species on the hill are the white seringa *(Kirkia acuminata)*, the velvet sweetberry *(Bridelia mollis)* and the shakama plum *(Hexalobus monopetalus)*, whereas the tall marula *(Scelerocarya birrea)* and baobab trees *(Adansonia digitata)* as well as knobthorn acacias *(Acacia nigrescens)* and several grewia species *(Grewia spp)* are abundant in the dense woodland of the Northern flatland. A detailed list of the plant species which have been significantly exploited as foods by the study group is given in Appendix 1.

Five water holes were available to the study group. Two of them were artificial 'dams' in the Northern plain which offered fresh ground water at all times of the year. Three natural pools carrying rain water were situated in the rocky valleys of the central hill, of which only one was permanent, whereas the other two dried out in the course of winter.

2.1.4. Fauna

The fauna at Blouberg Nature Reserve consists of a wide variety of amphibians and reptiles, birds and mammals. As potential predators of young baboons, large snakes, ie the African rock python, and large raptors may have some impact on the Blouberg baboon population. From the large African felides, leopards, cheetahs, and brown and spotted hyenas are present in the area, all of which have been reported to prey on baboons (Cowlishaw, 1997b). I observed two instances of a leopard approaching the study group's sleeping site at nightfall, but neither of them resulted in an attack. The study group actively mobbed a brown hyena on one occasion, resulting in the withdrawal of the hyena. I never found any carcasses of baboons that had been taken by a predator.

Due to extensive hunting practices in the past, the large herbivores such as buffaloes, giraffes, zebras and several antelope species had disappeared from the area, but were reintroduced after the proclamation of the area as a nature reserve. A wide variety of smaller mammals have probably not suffered this fate, some of which may be important competitors for the Blouberg baboons, for example the warthog. Primate species other than baboons include the Southern lesser bushbaby *(Galago moholi)* and the vervet monkey *(Cercopithecus aethiops)*.

2.1.5. Blouberg baboons and study group

The Blouberg mountain has a large baboon population. During the study period, I was aware of eight social groups which all used several cliffs along the Northern foot of the hill as sleeping sites. An additional group regularly slept in a cluster of tall fig trees in the Northern plain. I knew of a single sleeping site situated on the Southern slope of the hill, but it was not evident whether it was used by an additional group.

Several baboon groups left Blouberg Nature Reserve in the mornings on a daily basis, and they re-entered it in the afternoons. This suggested that although they foraged in more distant areas, they needed to return to the sleeping cliffs around the Blouberg mountain. The animals are comparatively well protected within the reserve boundaries, but are hunted for food, as crop raiders and as predators of small cattle outside the fences.

I performed ad libitum censuses of baboon groups whenever possible. The largest two groups consisted of 107 and 97 animals, but group sizes of around 40 – 70 animals seemed to be more common. Also, I knew of two groups of around 25 members. One of these small groups, the Kloof group, became the study group, based on the ideal location of its sleeping cliff.

I counted the individuals of the Kloof group throughout the study period, whenever all members were visible. It consisted of 20 members at the be-ginning of data collection, among them 6 adult females, a central male and two peripheral males, one of which was adolescent (Table 2.1.). All females

Table 2.1. Demographic changes in the Kloof group between May 2001 and August 2002. Im: Immigration, Em: Emigration. Numbers in brackets represent two females who were subadult at the beginning of data collection, and became pregnant during the study period.

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	adult females	adult males	adolescent males	subadult females	subadult males	infants/ juveniles	Total
May 2001	6	2	1	2	3	6	20
Im/Births	(+2)	+1	0	0	0	+ 8	+ 9
Em/Deaths	0	-1	0	(-2)	0	- 3	- 4
Aug 2002	8	2	1	0	3	11	25

remained in the group throughout the study period, and each of them gave birth to an infant. I viewed two females as subadult at the beginning of data collection, based on the small size of their nipples. As soon as they became pregnant for the first time I counted them as adults (Table 2.1., numbers in brackets). Five of the eight infants born during data collection survived until August 2002. An infant died two days after birth, and two juveniles disappeared at the age of approximately 7 months. The adult peripheral male disappeared (probably emigrated) in September 2001, and an unknown adult male joined the study group in late June 2002. The number of group members had increased to 25 at the end of the field study (Table 2.1.). Interestingly, the main male held his dominant status throughout the two years I stayed at Blouberg, and he still did so in August 2003, a year after the completion of my field work.

2.2. General methods

2.2.1. Habituation

Since Blouberg is a new study site, I started to habituate the study group in August 2000. Together with a field assistant, I met the Kloof group every morning at the sleeping site, and we followed them on foot as long as possible. I habituated the animals to two observers for reasons of convenience and safety. The vegetation at Blouberg is considerably dense in many areas, and visibility is correspondingly low. When following the Kloof group, a short stop for handling the equipment was sometimes enough to lose the animals, and not to reencounter them until the following day. It was therefore essential that one of the observers kept a close eye on the animals at all times, whereas the other was free to handle the equipment. Also, loose boulders and rocks on the remote, steep slopes of the central hill made walking very demanding, and I felt that an additional person was essential in case any accidents should occur.

Flight distance at the beginning of the habituation process was approximately 50 m in the vicinity of the sleeping site, but increased to 200 m and more as soon as the animals foraged away from the cliff. In mid-May 2001, flight distance had decreased to around 30 - 40 m throughout the day which I viewed as sufficient for good quality data collection. It further decreased to 10 - 20 m in the course of the field study.

2.2.2. Study period

Data were collected between May 2001 and August 2002. During this time, we (that is myself and a field assistant) followed the Kloof group for a total of 1604 h on 224 days (Table 2.2). Follows lasted from dawn to dusk on 96 days, and from dawn to afternoon on 47days. 81 follows lasted less than half a day, mainly because steep slopes on the hill or the animals' high travel speed in the plain impaired continuous, good quality data collection through-out the day.

Three long-term field workers assisted in collecting the data. Furthermore, a team of three field assistants continued to collect data during my absence from Blouberg in February. Although they were familiar with ethological methodology from their own educational background, I carefully introduced them to their tasks for three months prior to my departure, so that they were well experienced with the sampling techniques and familiar with the study group.

2.2.3. GPS data sampling techniques

When following the Kloof group we walked at the rear of the group. The assistant carried a Trimble Geoexplorer 3 GPS receiver and determined their position at 5 min intervals throughout the days. Intervals were indicated by a beeper. Since the animals allowed observations only from a distance, the locations of the GPS receiver and the study group were not identical at a given time. However, when given the distance, the difference in altitude and

Table 2.2. Days and hours of data collection throughout the study period (May 2001 – August 2002). Numbers of whole-day and half-day follows per month, number of days with fragmented data collection, total days and total hours of data collection.

Month	Year	Whole days	Half days	Fragments	Total hours
May	2001	2	5	19	110
Jun		2	6	6	69
Jul		4	5	11	98
Aug		11	4	4	136
Sep		4	6	5	111
Oct		3	5	4	55
Nov		6	4	8	118
Dec		7	2	7	109
Jan	2002	6	4	5	112
Feb		5	2	7	87
Mar		8	3	2	136
Apr		8	0	2	82
May		9	1	1	133
Jun		12	0	0	140
Jul		8	0	0	97
Aug		1	0	0	11
Total days		**96**	**47**	**90**	**224 d**
					1604 h

the bearing to the animals, the receiver automatically computed the animals' position instead of its own. I used these 'offset' positions throughout the study. The distances and differences in altitude were estimated by eye, whereas the bearings were measured with a compass which offered a resolution of 1°.

I trained the field assistants on a regular basis to estimate distances in space. This training consisted in walking through the bush in the absence of the study group, and in estimating the distance from a present location A to another

location B (eg. a tall tree or a burnt log). We then measured this distance with the GPS receiver and compared estimates and measurement. Subsequently, we estimated and measured the distance from location B to a new location C, and so on. Since the GPS readings had turned out to be accurate to approximately 15 m, we repeated this procedure until the estimates deviated from the GPS measurements for a maximum of 20 m.

During the follows, it was not possible to assess the centre of the group, which would have been the best estimate of the group's position, because the group as a whole was only visible on rare occasions. Therefore, I took the location of the animal walking at the rear of the group to represent the whole group's position.

Since the number of animals in view varied, I categorised the GPS readings as either 'position', 'single animal' or as 'not visible'. When several animals were in view at the beep, I took the corresponding GPS reading as a good estimate of the group's actual position and named it 'position'. Readings were classified as 'single animal' when only a single member of the group was in view at the beep, and the location of the remainder of the group was uncertain. I used the category 'not visible' when none of the animals were in view on the beep. On these occasions, the position of the receiver was measured, and an offset reading was performed between two beeps, as soon as the animals came into sight.

Other baboon groups seemed to affect the ranging patterns of the Kloof group. Based on their vocalisations, I therefore took a GPS reading of their position relative to the study group *ad libitum*. I classified their calls as coming from either very close by (from a distance of approximately 100 m), close by (300 m) or far away (500 m), and determined the corresponding bearings by means of the compass.

The locations at which the movement of the study group came to a halt were determined twice. The first reading was the offset location of the animals, esti-mated from a distance. An additional GPS reading was performed in immedi-ate vicinity of that resource, after the animals had left. This technique allowed me to retrospectively examine how accurate distance estimates were, and facilitated the assessment of the visibility of the resources in space.

2.2.4. Behavioural data sampling techniques

The rapid travel speed of the study group and the low visibility in some areas of their home range did not allow for a time consuming means of data collec-tion. I therefore chose a handheld tape recorder for collecting behavioural data. I performed scan samplings at 5 min intervals, which corresponded to the intervals of the GPS readings. I classified the behaviours of all animals in view at the beep as either 'move', 'feed', 'sit', 'lie', 'stand still', 'groom', 'being carried' or 'play', and whether they took place on the ground or in a tree (Table 2.3.).

Table 2.3. Behaviours of scan samplings.

Behaviour	Definition
move	locomotion on ground or in trees
feed	processing and ingesting food items while standing still or sitting
sit	sit on ground or in tree without engaging in feeding or in social behaviours
lie	lie on ground without engaging in feeding or social behaviours
stand still	stand on four legs without engaging in feeding or social behaviours
groom	groom social partner or be groomed by social partner
being carried	ride on back or cling on mother's or other group member's belly
play	social play

As soon as a minimum of three animals started feeding on the same resource, I viewed this resource as potentially important. In order to examine resource size, I determined the arrival and leaving time of each animal accurate to 1 min, in addition to the identity of the plant and the parts eaten. This 'focal tree sampling' stopped as soon as the last animal left the resource. Samples and digital photographs of unknown plants were collected for later identification (Grant & Val, 2000; van Wyk & van Wyk, 1997).

Similarly, a water hole became the focus of observations as soon as the first animal started drinking. I viewed water holes as vital resources to the baboons irrespective of the time spent for drinking, and determined only the time of day and the number of animals that visited it, but not resource size.

Table 2.4. Names and descriptions of recorded loud calls.

Call type	Description
wahoo	double-phase loud call, first phase higher pitched than second phase. Given only by males.
bark	dog-like, single-phase loud call of females, adolescents and juveniles.
scream	single-phase high-pitched call, given by all group members except by dominant male.
copulation call	staccato series of bark-like calls with decreasing pitch and increasing frequency towards the end, sometimes followed by a series of grunts. Given only by females shortly after copulation, on rare occasions without preceding copulation.
roargrunt	humming grunt, given through inflated cheeks, followed by a pause of 2-3 seconds and then by a series of 3-6 loud roars with decreasing pitch. Given only by dominant male.

In addition, I recorded all loud calls of the study group and of other baboon groups *ad libitum* by means of a tape recorder, and classified them as 'wahoo', 'bark', 'scream', 'copulation call', and 'roargrunt' (Table 2.4). Also, I recorded all occurrences of 'herding' in the study group (Buskirk et al., 1974). A herding bout was characterised by the Alpha male aggressively chasing one or several females, which was typically accompanied by many 'wahoo' calls of the male and by extended screaming by the females.

Chapter 3 Ranging and Ecology

3.1 Introduction

Baboons *(Papio spp)* are among the best studied primate taxa. Their use of
large-scale space has mainly been investigated from an ecological and socio-
ecological point of view (reviewed in Barton, 1989; Hill, 1999; Henzi & Barrett,
2003). It is not the aim of this thesis to investigate baboon socio-ecology, but
to shed some light on the cognitive mechanisms underlying orientation in
large-scale space. However, the spatial decisions and ranging patterns of my
study group are likely to be influenced by a wide variety of environmental
factors, some of which potentially obscure a direct insight into the cognitive
processes involved in ranging. I therefore view it as essential to start this
thesis with a chapter on the ecology of the baboons at Blouberg.

Baboons populate most unforested regions of the African continent between
Sahara and Cape of Good Hope. They possess an amazing capacity to adapt
to a wide variety of habitats, from semi-deserts (Hamilton et al., 1976; Sigg &
Stolba, 1981; Cowlishaw, 1997) to the edge of tropical forests (Ransom,
1981; Rowell, 1979) and subalpine regions (Whiten et al., 1987; Byrne et al.,
1990). Also, their social organisation is highly flexible. At some research sites,
groups are usually large and many females live and mate with many males
(Altmann & Altmann, 1970; Smuts, 1985; Barton, 1989; Henzi et al., 1997). In
some populations several foraging parties aggregate to large bands up to 700
individuals at the sleeping sites (Hamadryas baboons: Kummer, 1968, Sigg &
Stolba, 1981; Guinea baboons: Byrne, 1981). In contrast, groups at other

sites are smaller, with some not exceeding a single adult male, a few adult females and their offspring (Drakensberg chacma baboons: Byrne et al 1987; Henzi et al., 1997). In most populations, the males are reported to emigrate from their natal groups (Altmann & Altmann, 1970; Chacma baboons: Hamilton & Bulger, 1993), but female dispersal has been observed in others (Hamadryas baboons: Sigg et al. 1982; Chacma baboons: Anderson, 1982; reviewed in Pusey & Packer, 1987).

This variety of baboon social behaviour in different ecological contexts has attracted the interest of researchers who aim at understanding the socio-ecology of primate groups (Hall, 1963; Altmann & Altmann, 1970; Altmann, 1974; Whiten et al., 1987; Barton, 1989; Henzi et al., 1997; Hill, 1999). For example, baboon groups have been studied to identify the ecological factors which are likely to determine primate group size (eg. Hill, 1999; Chapman & Chapman, 2000) and social organisation (eg. Byrne et al., 1987; Barton et al., 1996).

It is well known that both home range size and day journey lengths in prima-tes are positively correlated with group size (Clutton-Brock & Harvey, 1977; Melnik & Pearl, 1987). This correlation persists across baboon populations (Barton, 1989; Barton et al., 1992). Thus, larger groups are thought to need to travel for longer distances to sustain all members than smaller groups, be-cause larger groups deplete resources quicker than smaller ones (Melnik & Pearl, 1987). Consequently, their home ranges are larger. However, several additional factors have been proposed to influence home range size and daily

ranging, such as resource density (Barton, 1989; Barton et al., 1992), food composition (Milton, 1981; Oates, 1987), climate (Hill, 1999), the degree of predation risk (Stacey, 1986; Cowlishaw, 1997a, b, c; Hill, 1999) and the availability of adequate sleeping sites (Anderson, 1984, 1998, 2000).

In this chapter I take advantage of a comparatively large amount of information available on baboon ranging and ecology across Africa with the aim to pinpoint some of the main ecological factors that affect the ranging patterns of the Kloof group. At the same time, I intend to contribute towards a comprehensive baboon socio-ecology with the relevant data from a new study site, and to lay the foundation stone for further studies on the behavioural ecology of the Blouberg baboons.

3.2. Methods

I applied two different methods for examining home range size. The first method is facilitated by GPS and GIS. I used the Trimble Pathfinder Office 2.51 software to connect the GPS readings of the Kloof group's locations throughout the days with a line, in chronological order. This resulted in a line representing the path recorded each day of data collection (n=224 days). By means of the ArcView GIS 3.2 software, I then combined all paths over the entire study period on a single map, and viewed the outmost paths as the border of the home range. ArcView then allowed me to calculate the enclosed area.

Traditionally, home range size in baboons has been calculated by dividing the ranging area into quadrats (usually of 250x250 m or 500x500 m in size), and by counting the total number of quadrats that was entered by the study subjects in the course of data collection (Altmann & Altmann, 1970; Sigg & Stolba, 1981; Whiten et al., 1987; Barton, 1989, Hill, 1999).

Although this latter method leads to an overestimation of home range size depending on the number of the partially used quadrats, it facilitates quantitative analysis of home range use. Usually, authors have viewed each quadrat as an independent data point. They then have correlated ecological variables with this measure of use intensity. This method neglects the fact that adjacent quadrats are likely to share spatial and temporal properties. Although I am aware of this methodological problem, I follow the tradition of the quadrate method for the sake of comparability of the data.

I determined day journey lengths two- and three-dimensionally. For this purpose, I exported the Northing and Easting (and for the 3D calculations also the Altitude) readings of each position of a given whole-day journey into the Excel software, calculated the vector lengths between subsequent readings, and built the sum of all vector lengths. A total of 96 whole day records entered the analysis of both, home range use and day journey length.

In order to roughly estimate food composition, feeding bouts and time spent feeding on different diet types, I used the observational data collected at the resources. Recall that I did not collect focal animal samples on feeding beha-

viour, but viewed food sources as potentially important if they were simultaneously used by three or more animals for at least 2 min. For the present analysis, I defined all such events as feeding bouts. Bout duration was calculated as the number of animals x time spent feeding. This approach tends to bias the results towards clumped food, and neglects evenly distributed food sources occurring in small patches, as well as all small food sources consumed during travel-feeding. However, it allowed to identify the most important food sources of the Kloof group.

3.3. Results

3.3.1. Sleeping site

The Kloof group used a single sleeping site during the entire habituation and study period. It was situated in a vertical cliff at the entrance of the Kloof canyon at the Northern foot of the central hill. The Blouberg baboons generally seemed to prefer cliffs over trees, with only one out of nine known groups regularly sleeping in a few emerging trees, the Fig tree group.

Several groups seemed to be based at a single sleeping site. For example, I regularly met the Fig tree group and two other groups in the area of their sleeping site at dusk and dawn, on my way to and from the Kloof canyon. Also, an unknown baboon group appeared at the Kloof cliff towards the end of the study period, and used it during all subsequent nights. This led to aggressive interactions between the two groups at dawn and at dusk. In the evenings, the two groups settled at the opposite edges of the main cliff, leaving

the most inaccessible sleeping sites unoccupied. A year later, during a short visit at Blouberg, both groups were still present at the cliff and seemed to be familiar to each other. The Kloof group reused their old sites in the main cliff, aggressive interactions between the two groups did no longer occur, and the juveniles and subadults intermingled with each other.

3.3.2. Water supplies

Most baboon groups drink on a daily basis. Therefore, their ranging is tied to the neighbourhoods of water supplies (Barton, 1992). At Blouberg water is abundant during the rainy season, but surface water is naturally scarce during the dry season. Five different water holes were available to the Kloof group . Three rain pools occurred naturally on the central hill, which I named 'kudu', 'kloof' and 'frog' holes. Only the Kloof hole persisted the dry months, but it became covered with a thick layer of green leaves towards the end. Also, it was heavily used by swarms of bees, suggesting that the resource quality decreased in the course of the dry season. In addition to the natural water pools, two artificial dams were situated in the plain, the 'buffalo' and the 'baobab hole', which provided fresh ground water at all times of year. Thus, although water supply was not limited at Blouberg, only a few sources were available at all times.

3.3.3. Home range size, home range use and day journey length

The traditional quadrat method resulted in a home range size of 13.5 km^2, with a total of 213 quadrats entered by the end of the study period. All quadrats within the home range area were entered at least once. For comparison, the home range area obtained with the GIS method was only 10.3 km^2. Thus, the difference between the traditional quadrat method and the more accurate GIS method is relatively large (23.7 %) for the small home range size of the Kloof group.

Under the assumption that the study group used their home range evenly across time, I expected the cumulative number of quadrats entered over time to approximate an asymptotic curve. Figure 3.1. reveals that this was not the case. Instead, the curve increased asymptotically from day 1 to day 103 to an area of approximately 7 km^2. It then increased dramatically over the next few days of observation. The final home range size of 13.5 km^2 was reached only in the last few days of observation. This alone suggested that the Kloof group did not forage at random, because random wandering would not produce such a sudden range expansion.

It is interesting to note that this dramatic range expansion occurred during the wet season. Prior to this day, the Kloof group foraged mainly on fresh marula fruit *(Sclerocarya birrea)* in the immediate vicinity of their sleeping site for several days. On day 103, they travelled North for over 3 km before they started feeding on the same food type, and did so for the next few days.

Figure 3.1. Cumulative area occupied by the Kloof group in the course of the 16-month study period.
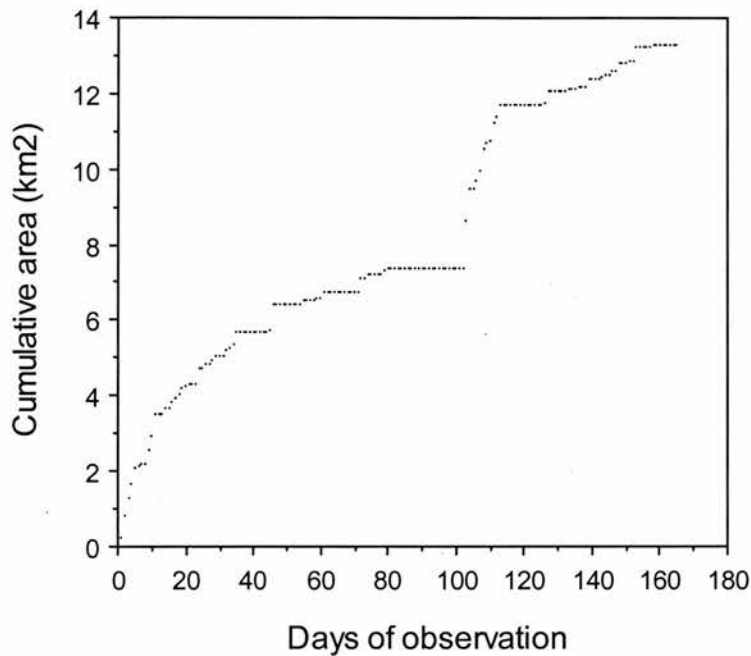
Apparently, the marula fruit in the vicinity of the sleeping site had been depleted, and could only be found in more distant regions.

This distant marula field was not an unknown location to me. I had observed the Kloof group foraging in this region 12 months earlier, during the habitu-ation process. In the year between these two observations, I had never followed the animals to this place. I do not have a complete record of all their ranging for that year, and therefore I cannot exclude that they had visited this area in my absence. But I view it as likely that they did not visit the marula region until the next fruiting season, but kept memorised this feeding site over many months. In this context it is also noteworthy that they visited the baobab

water hole in my presence for the first time after 14 months of data collection, suggesting that they had memorised this location over more than a year.

Three-dimensional analysis resulted in a average day journey length of 7.7 ± 2.1 km per day (n=96 days), with a maximum of 11.8 km and a minimum of 4.4 km. Both of these extremes occurred during the dry season 2002. The two-dimensional analysis gave only slightly shorter day ranges, with 7.6 ± 2.1 km travelled per day. Statistically, season had no effect on distance travelled per day (dry season: n=43, pooled sample from the first and the second dry season, wet season: n= 53, t-test, t=-0.392, p>0.1). However, when testing the data from the two dry seasons separately, season had a significant effect on day journey length (ANOVA, df=2, F=9.544, p<0.001). The journeys of the dry season 2001 were significantly shorter than both those of the rainy season and those of the dry season 2002 (Tukey-Kramer post-hoc, p<0.05).

Ranging patterns as well as food composition differed markedly between the two dry seasons (Figure 3.2.). During the first dry season in 2001, the Kloof group mainly foraged on the hill S and SW of their sleeping cliff (Figure 3.2.A). Their main food source during that time were kooboo berries *(Mystroxylon aethiopicum)* which were confined to a narrow belt of bushes on the S- and SW-facing slopes of the hill. At the end of the dry season 2001 the Kloof group had entered a total of 104 quadrats, which corresponded to an area of 6.5 km². In contrast, they entered a total of 127 quadrats during the dry sea-son in the following year, and used an area of 7.9 km². Their ranging in the two dry seasons overlapped in an area of only 2.9 km² (46 quadrats). The

Figure 3.2. Whole day's ranging during the two dry seasons 2001 (A; May - September) and 2002 (B; May - August).
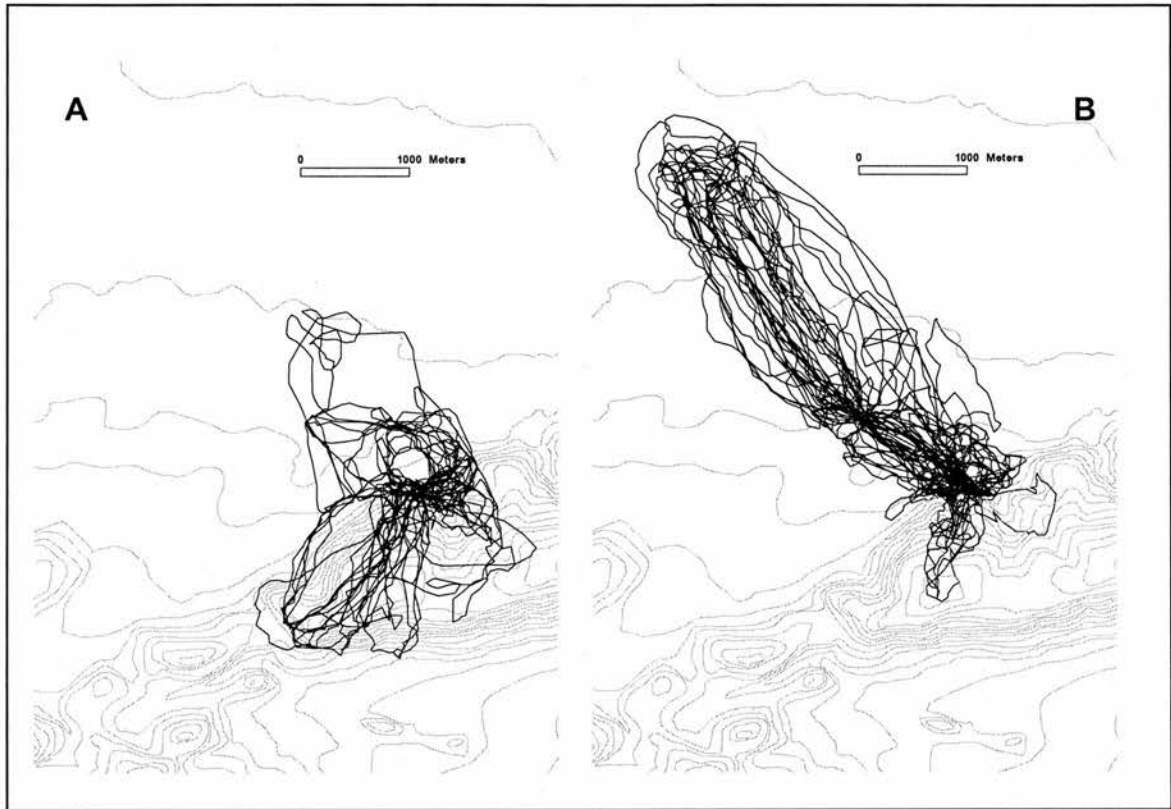
main food source in the second dry season was the abundant grewia berries *(Grewia spp)* which occurred in the flat area N of the sleeping cliff (Figure 3.2.B).

In order to examine why they did not revisit the kooboo berry bushes during the second dry season, I performed an excursion to this area in 2002. This revealed that none of the bushes carried any fruit that year. Thus, the fruiting

Figure 3.3. Day journey length and home range size in relation to baboon group size across populations. Open circles: East African baboons, solid circles: Chacma baboons, Triangle: Kloof group. Data from Hill (1999; data of forest habitats excluded, data of less than 11 months recording period excluded) and own study.

Day journey length

Home range size

Group size   Group size
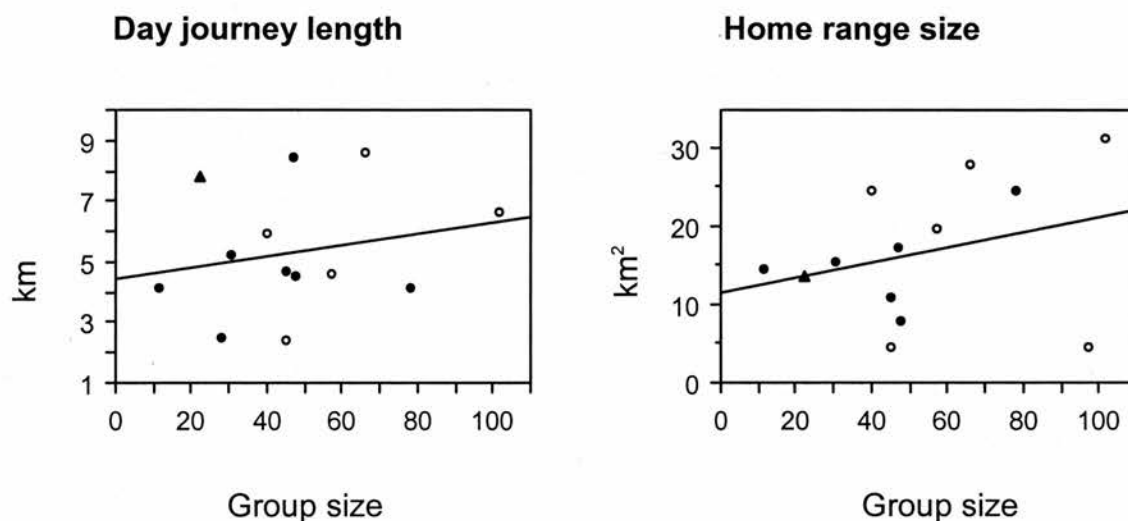
cycle of kooboo berries did not follow an annual cycle, and the ranging patterns of the Kloof group during the two dry seasons seemed to be closely related to this phenomenon.

Both day journey length and home range size are positively related to group size across baboon populations (Barton, 1989, Barton, 1992; Hill, 1999). I therefore compared the Kloof group's day journey length and home range size with the existing data of other baboon populations (data from Hill, 1999). Figure 3.3. reveals that the home range of the Kloof group was approximately as large as expected from observations at other study sites. However, their day journeys were long in comparison with other baboon groups of similar

size, suggesting that they visited a comparatively large area of their home range every day.

The intensity of habitat utilisation relative to the distance from refuges such as hills and cliffs has often been viewed as an indicator of predator avoidance behaviour (Stacey, 1986; Cowlishaw, 1997; Hill, 1999; reviewed in Hill & Cowlishaw, 2002). I do not wish to impute any anti-predator strategies to the ranging patterns of the Kloof group. Instead I expect them to simply stay in the vicinity of the sleeping site whenever food availability allowed them to do so, in order to save travel costs. In contrast, a tendency to stay in the center of the home range may be explained by a strategy to reduce the risk of encountering groups of conspecifics in habitats with a high population density.

I performed a multiple regression with the number of quadrat entries as dependent, and both distance from the sleeping site and distance from the home range border as independent variables. Following Zar (1999), I used the square root transformation for dependent and independent variables. This regression model explained 58.4 % of the variability of the dependent variable (df=2, F=115.3, p<0.0001). Distance from sleeping site was negatively correlated with quadrat use intensity (regression coefficient: -0.041), and positively correlated with distance from border (regression coefficient: 0.155). This suggested that the Kloof group used their home range most intensely in its center, close to the sleeping site and away from the border.

Figure 3.4. Number of entries recorded per quadrat of 250 x 250 m during 96 days
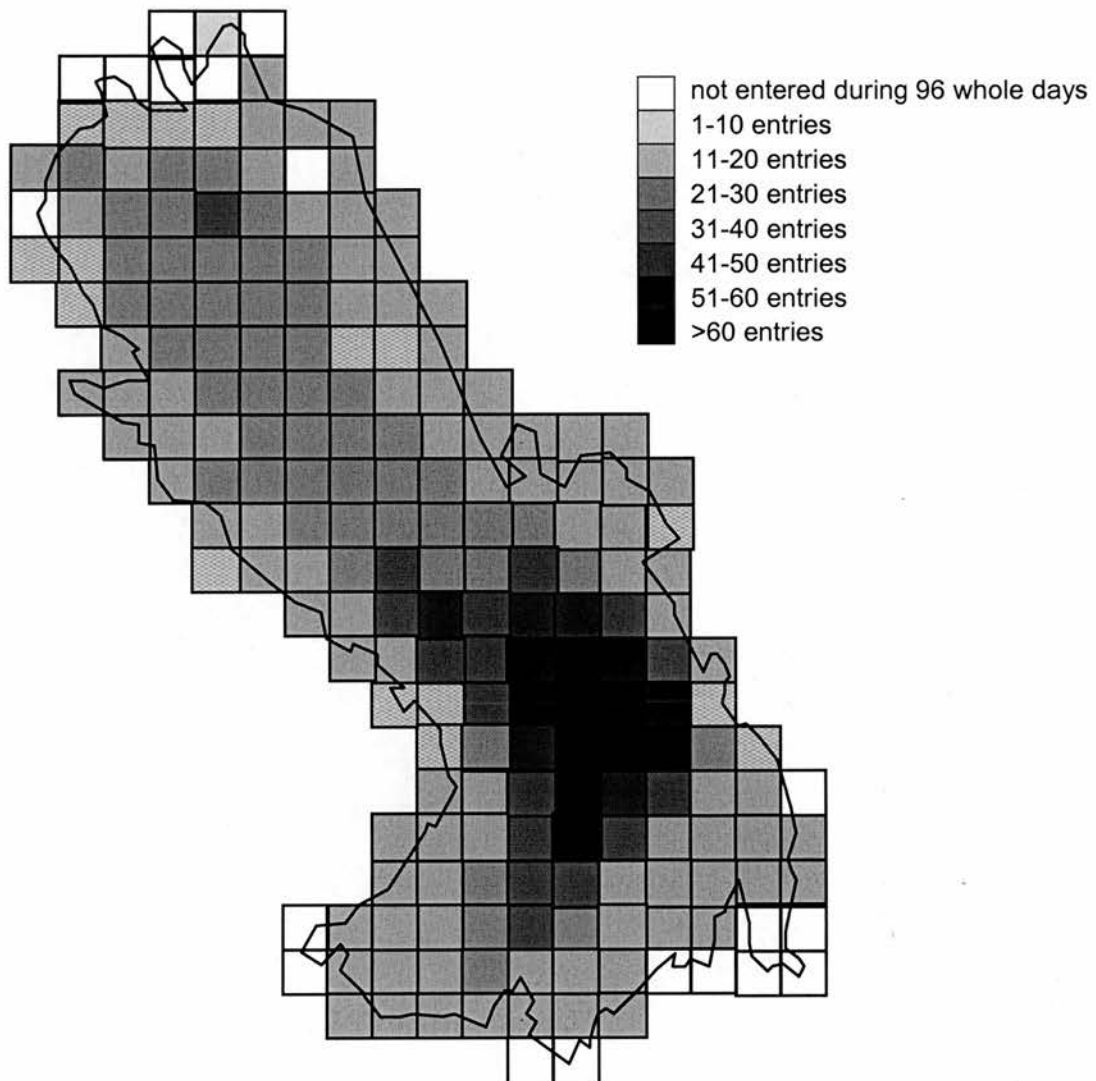
Figure 3.4. illustrates this finding in more detail by qualitatively indicating the number of quadrat entries recorded during 96 whole day records of the Kloof group's ranging. Unsurprisingly, it shows that the Kloof group used the area around the sleeping cliff most often. Bearing in mind that the animals returned to the same sleeping site every day, I expected that the number of entries would decrease quadratically with increasing distance from the sleeping site if the animals used their home range evenly. This was not the case. Instead,

they used also distant areas of their home range relatively intensely and evenly.

3.3.4. Food sources

The Kloof group mainly fed on plant matter. I observed them to feed on termites and insect eggs occasionally during the wet season. Amphibians and reptiles did not seem to form part of their diet. Despite many reports from local farmers and hunters, I never observed them to attempt hunting for any mammals, ie small or young antelope.

They fed on a total of 63 different food types, stemming from 54 different species (Appendix 1). This list is likely be incomplete, due to the comparatively large distance from which I observed the animals. Figure 3.5. illustrates the monthly food composition of all sources that contributed to the total time spent feeding with at least 1% in the course of the study period.

The abundant marula trees *(Sclerocarya birrea caffra)* were the most important food source of the Kloof group. Marula trees contributed 42.5 % to the total time spent feeding, including flowers (2.7%), fruit (11.6%), seeds (26.0%), sap (0.1 %) and the stems of an unidentified plant that parasites their outer branches (2.1%). Marula products were eaten throughout the year with exception of the month of December. This was the main season of one of three fig species occurring in the ranging area of the study group, the mountain fig *(Ficus glumosa).* Figs contributed with 9.5 % to the total time

Figure 3.5. Food composition throughout the study period. Only food sources contributing to the total time spent feeding for more than 1% are included. See Appendix 1 for scientific names and a complete record of food species.

Stems	Marula parasite	
	Knobthorn parasite	
Seeds	Shakama plum	
	Red Acacia	
	Marula	
	Knobthorn	
	Corkwood	
Roots	Grass spp	
Panicles	Grass spp	
Leaves	Torchwood	
Fruit	Shepard's tree	
	Shakama plum	
	Mupulu	
	Marula	
	Kudu berry	
	Kooboo berry	
	Guarri	
	Grewia spp	
	Fig spp	
	Buffalothorn	
Flowers	Shepard's tree	
	Shakama plum	
	Marula	
	Knobthorn	

M J J A S O N D J F M A M J J A
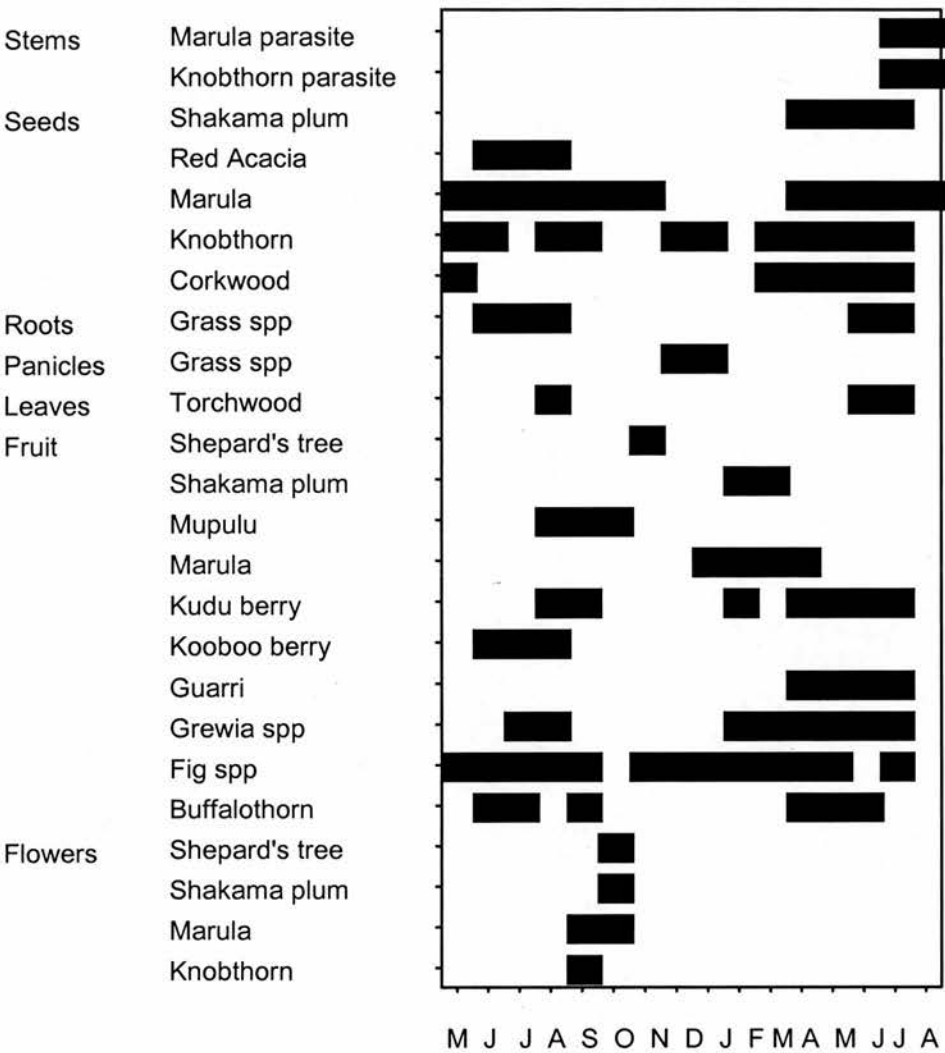
spent feeding, and thus were also highly preferred. Figure 3.6. shows the percentage of both, time spent feeding and number of feeding bouts on fruit, seeds, flowers, leaves and miscellaneous food items in the course of the study period. The vast majority of the study group's food items consisted of

fruit and seeds, whereas the percentage of leaves, other plant parts and insects was comparatively small.

Figure 3.6. Percentages of total time spent feeding (A; n=620.7 h) and total feeding bouts (B; n=874) on fruit (FR), seeds (SE), flowers (FL), leaves (LE) and miscellaneous food items (MI; insects, stems, grass roots and panicles) throughout the study period. Only clumped food sources were considered (see methods and text for explanation).
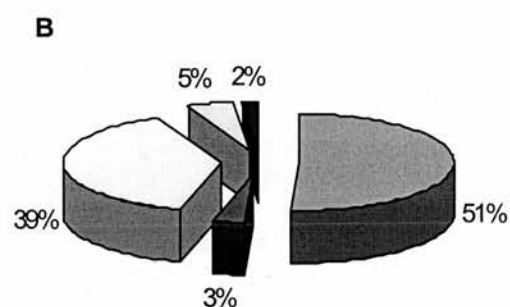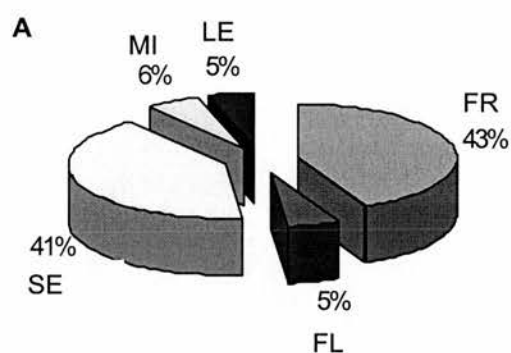
3.4. Discussion

In this chapter, I have pinpointed some ecological characteristics likely to play an important role for the Blouberg baboon population in general, and for the ranging patterns of the study group in particular. I investigated home range size, home range use, day journey length and resource availability, and compared my results with existing data from other baboon populations.

The woodland biome at Blouberg Nature Reserve produced a wealth of energy-rich food sources throughout the year, with a wide variety of fruit and seeds. Water was plentiful at all times, although seasonally limited to a few sites. It is therefore not surprising that Blouberg sustains a large baboon population.

However, safe sleeping sites were restricted to a few cliffs on the Blouberg scarp, and these seemed to be a limited resource for baboons groups, causing sleeping site fidelity. There are few reports of primate groups using only one or two sleeping sites over a prolonged time period, including hamadryas baboons at Erer-Gota (Stolba, 1979; Sigg & Stolba, 1981), olive baboons at Gombe (Ransom, 1981), and a group of chacmas at Okavango (Hamilton, 1982). The vast majority of primate social groups use several trees, cliffs or nests for night time resting (reviewed in Anderson, 1984). Multiple potential sites are generally viewed as more advantageous in that they reduce predictability for predators (eg. Bert, 1973), reduce the energy costs of long journeys between sleeping sites and food (Rasmussen, 1979) or water sources (Gow, 1973, cited in Anderson, 1984), and reduce the chances of parasite infections (Hausfater & Meade, 1982).

Day journey length and home range use could best be understood in the light of resource availability. In particular, resource depletion caused by both the large baboon population and the sleeping site distribution along the North-facing scarps of the hill was an important factor that affected the ranging patterns of the study group, and probably of the Blouberg baboons in general.

With 7.7 km, day journey length of the study group was large in comparison with baboon groups of similar size in populations elsewhere in Africa. It is likely that not only the study group, but all groups at Blouberg intensely used the areas next to their sleeping sites for foraging, which caused important food sources in these areas to become rapidly depleted. This, coupled with the need to return to a single location every night, forced the Kloof group to travel over long distances every day.

Day journeys recorded during the dry months were as long as those recorded during the rainy season, despite the pronounced seasonality of rainfall and biomass production at the study site. This was partly due to the fact that the Kloof group used two different parts of their home range as their main feeding areas in the two dry seasons. In 2001, they visited kooboo berry bushes and acacia trees on the South- and Southwest-facing slopes of the hill, which were situated at comparatively short distances from the sleeping site. Kooboo bu-shes did not fruit in the dry season 2002, and the Kloof group mainly foraged for distant grewia berries in the Northern plain during that time.

However, due to the fact that both the shortest and the longest day journeys were recorded in the dry season 2002, resource availability does not entirely explain the observed ranging patterns. I found that the study group tended to stay in the center of their home range. Since the sleeping cliff was situated in this area, this must be partly viewed as a result of foraging close to the sleep-ing site in times of food abundance. However, intensity of home range use was not a simple function of the distance to the sleeping site. Instead, the

Kloof group used the quadrats that were distant from their home range border more often than the more peripheral ones. Therefore, group avoidance seems to be an important component of the Kloof group's every-day ranging.

This suspicion was corroborated by the observation that when following the Kloof group, I often met other baboon groups ranging in the same area, suggesting that the home ranges of many groups overlap. However, from the vocalisations of other groups I often had the impression that groups were travelling parallel to the Kloof group, especially during the journeys away from the sleeping site in the mornings. Therefore it is likely that the Kloof group tried to avoid encounters with other groups by using only a small corridor leading from the sleeping site towards the North. It will be interesting to investigate the effect of group avoidance on ranging patterns in more detail in the next chapter.

Home range size was 13.5 km^2, and thus as large as expected from groups of similar size at other study sites. However, it reached its final size only in the last few days of data collection, and a dramatic increase within only a few days occurred in the middle of the rainy season, when food was available in large quantities. An expansion of the ranging area within a few days has also been observed in a group of yellow baboons (Altmann & Altmann, 1970), in hamadryas baboons (Sigg & Stolba, 1981) and in two groups of chacma baboons, one living in the semi-desert of Namibia (Cowlishaw, 1997) and the other in the Drakensberg mountains (Whiten et al., 1987).

This phenomenon has been viewed as an adaptation to arid habitats. It has been argued that during the rainy season, the baboons are no longer tied to permanent water pools, and thus are free to exploit new areas, whereas during the dry months they must forage in the vicinity of water resources in order to prevent dehydration (Altmann & Altmann, 1970; Hill, 1999).That explanation does clearly not apply to the Kloof group, because water did not seem to be a limiting factor to their ranging. Two artificial dams and a per-anent natural water pool, all in the vicinity of the sleeping cliff, enabled them to visit the most distant areas not only during the wet season, but also during the dry season. Therefore it rather seems that the expansion in their ranging patterns was a response to the depletion of their preferred food source at that time, the fresh marula fruit, in the vicinity of the sleeping cliff.

From a cognitive point of view, the differential home range use in the dry seasons of two subsequent years is a first piece of evidence that baboons do move towards some of their resources in a goal-directed fashion. Kooboo berries occurred only in discrete patches in a remote area of the home range. In order to reach them, they needed to walk over the hill. It is safe to assume that the Kloof group was not in a position to perceive them directly by vision or olfaction at their sleeping site, and for a long time along their path towards them.

Also, it is interesting to note that kooboo and grewia berries were situated at opposite borders of the home range, with the sleeping cliff in between. I view it as highly unlikely that a simple behavioural rule, such as 'always follow a

density gradient' (Garber & Hannon, 1993; Janson, 1998; 2000) could have produced this differential home range use coupled with differential food availability in subsequent years. Therefore, I suspect that the Kloof group visited them on the basis of spatial memory. It will be interesting to examine the nature of their paths to these distant resources in chapter 4 and 5.

In the case of the animals foraging in the Northern plain, the question of how they oriented themselves becomes particularly interesting. Orientation seems to be difficult in these featureless, comparatively dense woodlands, unless the animals possess intimate knowledge of the area and recognise individual trees or bushes.

In summary, this chapter revealed that permanent water and a wide variety of energy-rich food sources was available to a large baboon population at Blouberg Nature Reserve. However, sleeping sites were restricted to a few cliffs, and seemed to be a highly limited resource. This was likely to explain why sleeping site fidelity seemed to be the rule rather than the exception among the baboon groups at Blouberg.

Sleeping sites were distributed along the scarps of the hill. The study group, and probably all baboon groups, used the adjacent areas intensely, causing food sources in these areas to deplete rapidly. Resource depletion was likely to explain both the comparatively large day journeys, and a sudden expansion of the ranging area of the study group. Group avoidance seemed to be an important factor affecting ranging patterns. Also, resource availability partly

explained differential home range use and day journey lengths in two subsequent dry seasons.

From a cognitive point of view, differential home range use per se is evidence against simple searching strategies that have been proposed for primates in the past (Janson, 1998; Garber & Hannon, 1993), such as random wandering or applying inflexible behavioural rules. My data supported the notion of spatial memory not only on a day-to-day basis, but over extended time periods of a year or more.

Chapter 4 Path characteristics

4.1. Introduction

Animals have a limited amount of time and energy available for foraging and other fitness-related activities (Pianka, 1988). In the evolutionary past, natural selection should have favoured those individuals which maximise their benefits from foraging relative to the costs. The obvious benefits of foraging are the resources obtained which cover the animals' energetic and nutritional requirements. On the other hand, costs have been proposed to include energy spent while moving, time taken away from other activities, predation risk (Bell, 1991) or factors intrinsic to the food sources themselves, such as secondary compounds, thorns or hard and siliceous material that wear down an animal's teeth (Altmann, 1998).

Empirical studies on the cost-benefit balance of foraging in primates such as baboons have focused on the use of space in the light of predation risk (Cowlishaw, 1997; Hill, 1999); on time spent in different activities throughout the day (Post, 1981; Hill, 1999) or on the impact of contest competition on individuals (Barton, 1989). These measures have been discussed in terms of primate socio-ecology, particularly in relation to group size. Also, food composition (Barton, 1989; Whiten et al., 1991; Altmann, 1998), or the energetic costs of travelling (Steudel, 2000) have been carefully examined in search of the 'currency' for cost-benefit considerations.

In the light of the crucial role of foraging efficiency, it is surprising how little we know about the nature of the routes primates use to reach their resources. There is good evidence that some captive primates do travel efficiently in small-scale space (Menzel, 1978; MacDonald & Wilkie, 1990; Gallistel & Cramer, 1996). However, experimental spatial tasks in the lab have little in common with the problems faced by wild animals. In natural environments, some resources may be distant and out of sight of each other, whereas others are nearby. Resource availability may change in the course of a day, a year, or even over longer time spans (Chapter 3). Predators or other dangers may sometimes force individuals or groups to choose detour routes, and competitors have to be dealt with on a daily basis.

For example, Kinnaird & O'Brien (2000) investigated the environmental factors which shaped the movement patterns of two primate species, the African Tana River crested mangabey *(Cercocebus galeritus)* and the Sulawesi crested black macaque *(Macaca nigra)*. Based on the number of instances the study groups crossed their own paths and the mean turning angles per day, they found that the presence of neighbouring groups significantly influenced ranging. The large number of path crossings and the large turning angles in the presence of other groups suggested that the study animals tended to avoid each other (Kinnaird & O'Brien, 2000).

This hints at one of the problems researchers face when examining path efficiency in primate groups. Although movement patterns may deviate from least-effort routes, they may still be efficient given the ecological constraints.

An additional problem emerges from the possibility that primates may find some resources by chance and others intentionally. Traditionally, high travel speed and directedness of movements have been viewed as indicators for goal-directed movements (Altmann, 1970; Sigg & Stolba, 1981; Kummer, 1992; Garber, 1988; 1989). However, it has also been pointed out that linearity of routes can result from simple searching strategies, rather than from intention (Garber & Hannon, 1993; Janson, 1998).

Pochron (2001) examined path linearity and concurrent travel speed in order to differentiate between random and intentional encounters with food in savannah baboons in Eastern Africa. He found that baobab trees and combretum shrubs as well as impala were approached in a linear and fast way, whereas encounters with water holes and other resources seemed to be random (Pochron, 2001). Given that water is a crucial resource for baboons, the reliability of path linearity and concurrent travel speed as an indicator for goal-directedness needs to be questioned.

I therefore start the analysis of the Kloof group's foraging journeys with an investigative chapter on path characteristics. In particular, I ask to what extent their movements were characterised by linearity and high travel speed, and investigate the reliability of these two variables as indicators for goal-directed movement. Also, I address the questions of how environmental factors such as food abundance, topography, time of day, groups of conspecifics and different resource types are associated with deviations from least-effort routes. By doing so, I aim at isolating those movements which provide the

best insight into the mental mechanisms involved in orientation, and thus will serve as a good data basis for the following chapters.

4.2. Methods

In order to examine the directional variability of the baboon paths, I exported the GPS data points into Excel, so that each location was described by its Easting, Northing and Altitude coordinates. Because GPS readings were accurate to approximately 15 m, I calculated the distances between any two successive data points, and discarded the second of two readings when the locations were less than 15 m apart from each other.

Subsequently, I cut the foraging journeys into path segments leading from one important resource to the next. For example, a segment may represent the route between the sleeping site and the first feeding source visited that morning, or the path between a water hole and the location where the animals subsequently spent some time for resting and grooming. The criteria for defining a location as a starting or an end point are described in Table 4.1. I chose a minimum criterion for a food resource to become a starting or an end point when at least 3 animals were feeding at the same resource for 2 min. With such a low criterion I intended to find as many locations as possible which were of potential importance to the baboons.

I discarded all path segments which exhibited 3 or more subsequent 'not visible' GPS recordings, that is, when I did not know the exact position of the Kloof group for longer than 15 min during the follows. Also, I neglected very

Table 4.1. Definition of important resources.

Resource type	Criteria
Food sources	a minimum of 3 animals spend at least 2 min feeding on the same resource
Water sources	majority of group members drink
Sleeping site	majority of group members sit, lie, play, or groom each other at the sleeping site
Unknown resources	movement comes to a halt for unknown reasons for more than 6 min.

short path segments consisting of only a few vectors, that is, when the resources were located in close vicinity to each other. Based on statistical considerations, my decision rule was to only include segments that consisted of 4 or more vectors.

In order to calculate the dispersion of the path segments, I transformed the vectors of each segment into unit vectors. For each of the segments, I calculated an r-value, a measure of concentration about the mean direction (Batschelet, 1965). In the extreme case of all vectors exhibiting identical bearings, the total mass is concentrated in one point, and $r = 1$. On the other hand, $r = 0$ occurs when the dispersion of circular data reaches such a high degree that no mean direction exists any more. In other words, the closer r approaches the value 1, the smaller the angular deviation of the vectors, and

thus the more linear the movement of the animals. I used this measure of angular deviation as an indicator of path linearity.

I calculated travel speed by dividing the distance travelled in a path segment by the time needed to cover it. Time readings were accurate to 1 min. I calculated the distances in three dimensions, because this allowed comparison between the segments on the hill and on the plain.

Also, I included a topological variable with the two classes 'hill' and 'plain' into the analysis, because energy expenditures when walking uphill were likely to be increased compared to the movements in the plain. I therefore determined whether each of the path segments were situated on the hill or on the plain and expected that travel speed during the journeys on the hill was reduced in comparison with those on the plain.

Seasonal changes in temperature and rainfall are considerable at Blouberg (Figure 2.3.). Food is more abundant and less clumped during rains in summer compared to the dry winter months. I therefore suspect that the Kloof group needed to forage in a goal-directed way during the dry season, but foraged more at random during the rains. I determined season based on the rainfall during the study period, and viewed the data collected before the first day of rainfall in October 2001, and after the last day of rainfall in May 2002 as belonging to the dry season, and the remaining data as belonging to the wet season.

The animals' motivation for finding food, water and a safe sleeping site is likely to change throughout the day, depending on the amount eaten or the time of day. Based on this consideration I included a temporal variable into my analysis by examining whether the segments led away from the sleeping site (outward movements) or towards it (inward movements).

I performed a factorial Anova with each of the dependent variables linearity (as indicated by the r-values), travel speed and distance travelled. I checked each category of the dependent variables for similar variance by calculating the ratio of the largest to the smallest group. The commonly used rule of thumb that this value should not exceed 3.0 (Zar, 1999) was met for all categories. Since I do not apply Anova to an experimental design here, sample sizes in the categories vary. I therefore used a post-hoc test which is recommended for unequal sample sizes, the Tukey-Kramer test (Zar, 1999).

4.3. Results

I obtained a total of 1026 path segments leading from one resource to the next. The histograms in Figure 4.1 illustrate the distributions of the r-values, travel speed and segment lengths. Median r-value was 0.879, with a maximum of 0.999 and a minimum of 0.023. The r-values of around 450 segments (44%) reached a value between 0.9 and 1, suggesting that many segments were highly directed. Median travel speed was 17.4 m/min, with 53.7 m/min reached maximally, and 4.1 m/min minimally. Median distance

between resources was 438 m and reached a maximum of 4540 m and a minimum of 75 m.

The distributions of all three variables were skewed to a varying degree (Figure 4.1.). Therefore, I applied log-transformation to the travel speed and segment length data, and logit-transformation to the r-values (Stahel, 2002). The logit-data transformation is based on considerations of the logistic regression, and the corresponding transformation is $x_i \to \log(x_i/1-x_i)$.

After data transformation, I investigated the z-scores of each variable by calculating the percentage of data points larger than $|3|$ and larger than $|2|$. Results are shown in Table 4.1. Since less than 1% of the z-scores were larger than 3 and -3, and less than 5% larger than 2 and -2, I concluded that my data were now approximately normally distributed and in appropriate form to apply multivariate test procedures.

By means of a correlation matrix, I investigated how the dependent variables were related to each other. All three variables were significantly correlated (Table 4.3). The Pearson correlation coefficient for linearity and travel speed was positive, but very small. Because the sample size is large (n=1026), I concluded that this correlation was only weak, despite the low p-value. In contrast, directedness and distance travelled between resources were negatively correlated. Again, the comparatively small correlation coefficient suggested that this relationship was only weak. However, the large correlation coefficient between travel speed and distance travelled is trustworthy, and I

Figure 4.1. Histograms of path linearity, travel speed and distance travelled before data transformation, and z-score histograms after Logit and Log transformation.

Raw data

Transformed data
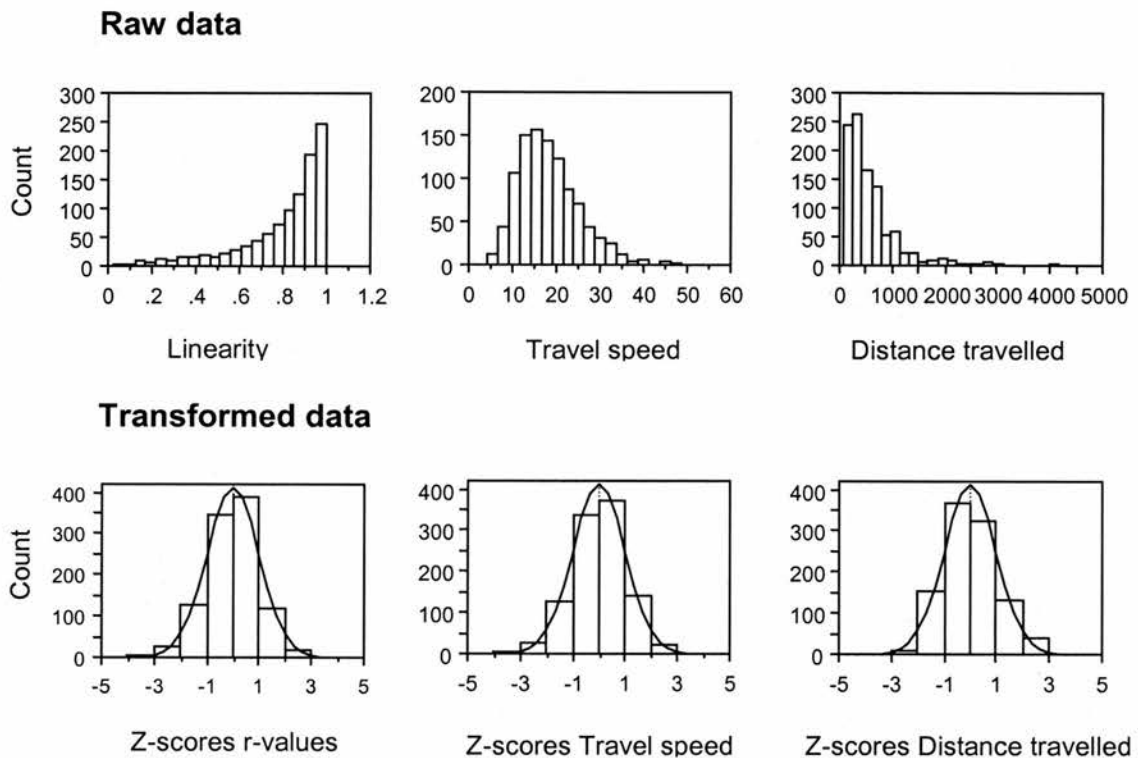
concluded that travel speed and distance travelled were significantly positively associated. In other words, the study group covered larger distances between two resources at higher speed, and shorter distances more slowly. I view this result as a first piece of evidence for goal- directed movement, because it suggests that the study group adjusted their travel speed with respect to the distance they needed to travel. It is noteworthy that both variables contain a related measure, namely m and m/min. However, this alone cannot explain the positive correlation, because a reverse relation between the two variables would also have been possible, that is, low travel speed when distances between the resources were large.

Table 4.2. Percentage of z-scores larger than +3 and –3, and larger than +2 and –2.

Variable	> |3|	|3| > |2|
R-values	0.6	4.7
Travel speed	0.4	4.5
Distance travelled	0.1	4.5

Table 4.3. Pearson correlations between the dependent variables.

Pair of dependents	Coefficient	p
Linearity and travel speed	0.211	<0.0001
Linearity and distance	-0.125	<0.0001
Travel speed and distance	0.606	<0.0001

4.3.1. Seasonality, direction of movement and topological factors

In order to investigate the effects of environmental factors on the path

characteristics, I performed three factorial Anovas, one for path linearity, one

for travel speed and one for segment length. The factors included were

season, the direction of movement away or towards the sleeping site (inward

and outward), and the area in which the segments were situated, on the hill or

in the plain of the home range area.

All three independent variables, season, direction of movement, and area had

significant effects on path characteristics (Table 4.4.). Season had the

strongest effect on linearity. Path segments covered during the dry season

Table 4.4. Anova tables for effects of season, direction of movement and home range area on path linearity, travel speed and distance travelled between resources. MS= Mean square. All main effects but only significant interactions are shown.

Dependents	Independents	MS	F	p	Power
linearity	season	11.8	28.47	<0.0001	1
	direction	10.384	25.054	<0.0001	1
	area	1.397	3.37	0.0667	0.433
travel speed	season	0.281	11.162	0.0009	0.935
	direction	3.121	124.169	<0.0001	1
	area	0.712	28.32	<0.0001	1
	season * area	0.179	7.135	0.0077	0.77
	season * direction * area	0.131	5.224	0.0225	0.622
distance travelled	season	0.631	6.534	0.0107	0.729
	direction	4.318	44.703	<0.0001	1
	area	0.813	8.414	0.0038	0.842
	season * area	0.525	5.438	0.0199	0.641

were significantly more directed than those covered during the wet months (Figure 4.2.).

Also, outbound journeys were more directed than movements towards the sleeping site. I found a nearly significant difference between the paths covered on the hill and in the plain (p=0.07), but I take this result with some reservation, because the power of this test is only 0.43, suggesting that the probability of committing a type II error is high.

Season, direction of movement and area also had significant effects on travel speed (Table 4.4). The Kloof group travelled faster during the dry season,

Figure 4.2. Effect of season (dry and rain), direction of movement (inward and outward) and home range area (hill and plain) on path characteristics. Bars indicate ± 1 SED.
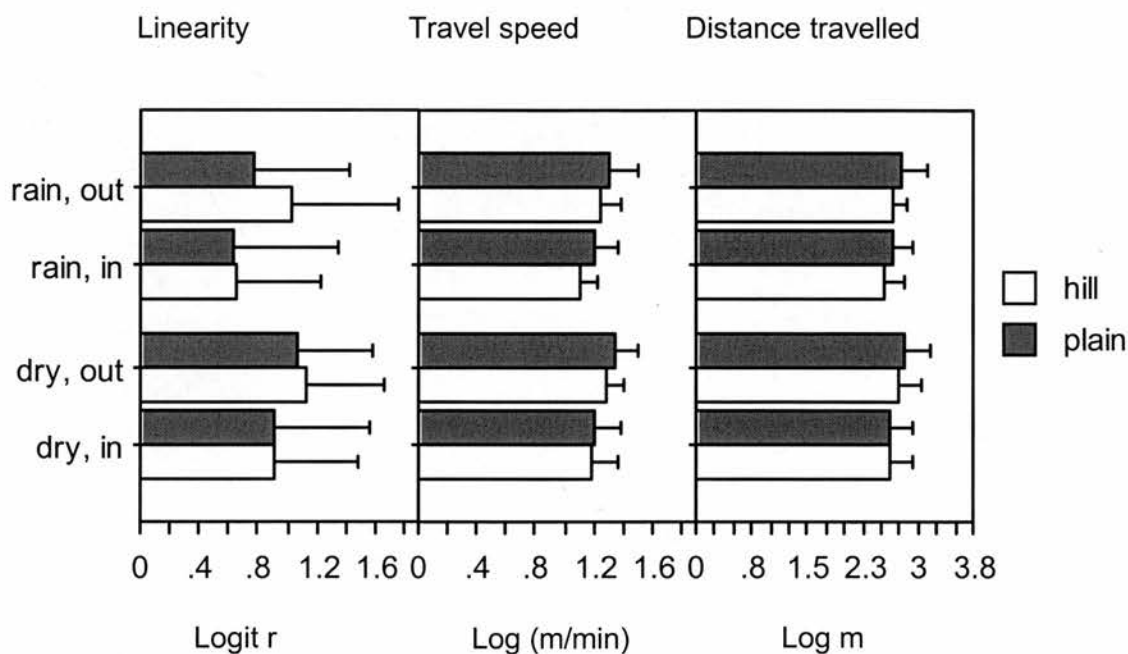
compared to the rainy season. Outward movements were faster than inward movements, and, as expected, travel speed was higher in the plain than on the hill (Figure 4.2). I found two significant interactions in this analysis, one between season and area, and the second between season, direction and area.

Figure 4.2. reveals that although travel speed was significantly higher during the dry season than during the rains (main effect), this result was mainly due to the 'rain, hill' condition. During the dry season, travel speed on the hill and in the plain did not differ (Tukey-Kramer, $p>0.05$). But during the wet months, travel speed was significantly lower on the hill than in the plain ($p<0.05$). The interaction between season, direction and area sheds some more light on the

Table 4.5. Results of the Tukey-Kramer post hoc tests for path linearity (r-values), travel speed (TS) and distance travelled (DT). Conditions in the first row are compared with all other conditions. Columns 2-7 show significant differences to condition in first row at a significance level of 5% (regular font style) and 1% (bold).

Condition	r-values dry	rain	TS dry	rain	DT dry	rain
rain out plain	out plain out hill	-	in hill in plain	in hill **in plain**	in plain	**in plain** **in hill**
rain out hill	-	**in hill** **in plain**	out plain	**in hill**	out plain	-
rain in plain	out plain out hill in plain in hill	out hill	out plain out hill	out plain in hill	out plain	out plain in hill
rain in hill	out plain out hill in plain	out hill	out plain out hill in plain in hill	out plain out hill **in plain**	out plain out hill	out plain in plain
dry out plain	-	out plain **in hill** **in plain**	**in hill** in plain	**out hill** **in hill** **in plain**	**in plain** **in hill**	out hill **in plain** **in hill**
dry out hill	-	**out plain** **in hill** **in plain**	in hill in plain	in hill in plain	**in plain**	in hill
dry in plain	-	in hill **in plain**	out plain out hill	**out plain** **in hill**	out plain out hill	**out plain**
dry in hill	-	in plain	out plain out hill	**out plain** **in hill**	out plain	-

'rain, hill' condition (Table 4.5). The Kloof group travelled slowly during the inward movements only, but the outward movements were fast. Thus, travel speed was generally fast during the dry season, but it was also fast during the wet season on the hill, when the Kloof group moved away from the sleeping site. Curiously, the inward movements on the hill in the same season were the slowest ever recorded. This pronounced difference suggests that the hill must have been of special significance to the Kloof group in the rainy season.

When looking at travel speed on the hill only, it becomes apparent that the Kloof group travelled significantly faster during the dry season compared to the wet season (p<0.05). But in the plain, there was no difference in travel speed between the seasons.

Season, direction, and area all had significant effects on the distance travelled between two resources (Table 4.4). The Kloof group travelled significantly larger distances during the dry season than during the wet season, suggesting that food was scarce in the dry months and more abundant during the rains. Also, distances were larger when moving away from the sleeping site compared to the inward journeys.

Distances travelled in the plain were larger than on the hill. However, there was a significant interaction between season and area (Figure 4.2). It revealed that this was only true in the rainy season, when short distances were covered on the hill. In the dry season, there was no difference between the distances covered on the hill and in the plain (p>0.05).

In summary, I recorded the most linear movements in the dry season, both when the Kloof group travelled away from the sleeping site on the hill and in the plain. During those movements, travel speed was comparatively high, but higher on the plain than on the hill. In addition, distance travelled between resources was large. Movements on the hill were also highly linear in the rainy season. During those movements, travel speed was comparatively fast, but distance travelled between resources was low.

In contrast, movements in the plain were fast but less linear during the rainy season. Interestingly, the longest distances between resources were covered during that time, despite the increased resource availability. This suggested that factors other than resource distribution must have been involved. The next section will shed more light on this issue.

4.3.2. Other groups

Chapter 2 has revealed that the Kloof group preferred to forage in areas which were far from the home range border. I viewed this as evidence that they needed to avoid encounters with neighbouring groups. In this section, I examine this issue more closely, because such a strategy is likely to affect path characteristics.

I asked how the distance from other groups affected the paths covered by the Kloof group. Because I collected data on distance to other goups in an ordinal form, I performed a factorial Anova for path linearity, travel speed and distance travelled, each as dependent variables, and used distance to other groups as independent variable. The independent variable divided the data into four groups, namely 'other groups absent', 'other groups far away' (that is, at a distance of approximately 500 m), 'other groups close by' (300 m) and 'other groups very close by' (100 m).

Figure 4.3. Path linearity, travel speed and distance travelled when other groups are absent, far away (at 500m distance), close by (300m) and very close by (100m).
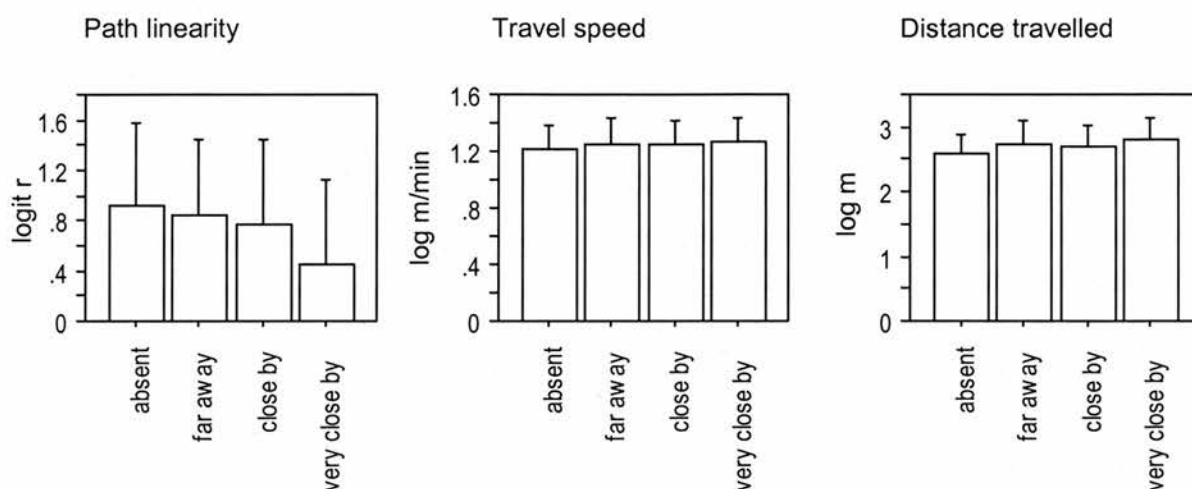
The overall Anova model for linearity was significant (df=3, F=13.499, $p<0.0001$, power = 1). Path linearity was highest when other groups were absent, and subsequently decreased the closer other groups came. Statistically, path linearity was larger when other groups were absent and far away than when other groups were close by and very close by (Tukey-Kramer post-hoc tests, both $p<0.05$). Although linearity was highest when other groups were absent, there was no difference between 'absent' and 'far away' ($p>0.05$). The path segments were least linear in the 'very close by' condition, and differed significantly from all other conditions (Tukey-Kramer post hoc test, $p<0.05$, Figure 4.3.).

The Kloof group travelled fastest when other groups were very close by (20.0 ± 6.8 m/min on average), and slowest when groups of conspecifics were absent (17.7 ± 6.9 m/min). Average travel speed was 18.9 ± 7.8 m/min in the 'close by' condition, and 19.5 ± 8.0 m/min in the 'far away' condition. Distance

from other groups had a significant effect on travel speed (Anova, df=3, F=4.719, p=0.0028, Power = 0.909). However, there was only one pair of conditions with a significant difference. The Kloof group travelled significantly faster when other groups were very close by than when other groups were absent (p<0.05).

Distance to other groups had a significant effect on distance travelled between resources (Anova, df=3, F=20.474, p<0.0001, power = 1). The post-hoc tests detected significant differences between the 'absent' condition and each of the 'present' conditions (all p<0.05), but there was no difference among neither to any of the 'present' pairs (all p>0.05).

In the first result section of this chapter it became evident that path linearity generally decreased during the rainy season (with exception of the outward movements on the hill). However, the distances travelled between resources were large during that time. This suggested that food abundance was not the only factor affecting resource choice, because food was abundant during the rainy season. The present analysis has shown that distances travelled between resources increase in the close presence of other groups.

Because the preferred marula fruit, the main food source available during the rainy season, was much more abundant in the N plain on the reserve than elsewhere, it is possible that food distribution correlated with baboon group distribution. If this was true, then the decreased path linearity during the rainy

Figure 4.4. Number of loud vocalisations (wahoos, barks, roar-grunts) from other groups per 100 m travelled by the study group in relation to season and home range area. Arrows indicate significant differences to the condition at the starting point of the arrow.
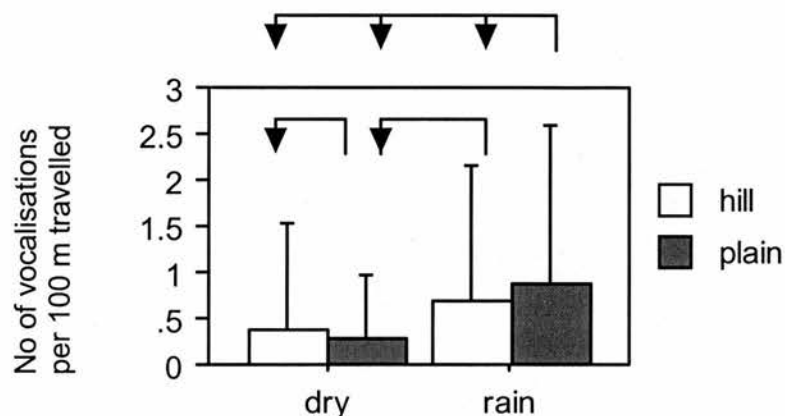
season could be explained by an increased need of the Kloof group to avoid other groups than at other times of year.

I therefore calculated the number of loud vocalisations given by other groups relative to the time the study group needed to travel 100 m and investigated whether there was a difference in the frequency of vocalisations between the seasons and the home range areas.

The number of vocalisations of other groups differed significantly across the four groups (Kruskall-Wallis, df=3, H=48.64, p<0.0001). Dunn's post-hoc tests for unequal numbers of data in the groups (Zar, 1999) revealed that significantly more vocalisations were given during the rainy season in the plain, than both during the rainy season on the hill, and during the dry season (Figure 4.4.). In contrast, significantly less vocalisations were given in the plain during the dry season, compared to all other conditions. This suggested that the

comparatively low directedness in the plain during the rainy season was at least partly a result of a group avoidance strategy, in addition to resource distribution.

4.3.3. Resource types

The above analyses have shown that part of the variability in path linearity, travel speed and distance travelled between resources can be explained by season, direction of movement away or towards the sleeping site, foraging area and the presence of other groups. In this section, I address the question of whether there were differences in how the Kloof group approached different resources.

I grouped the path segments according to the nature of their end point as either leading to food sources (n=603), to water holes (n=108), to the sleeping site (n=63), or to a location where the movement had stopped for other reasons, eg. when my goal definition was not fulfilled and the animals fed widely dispersed (n=252). Again, I performed an Anova in order to search for differences in the data.

Resource type had a significant effect on path linearity (Anova, df=3, F=7.586, p<0.0001, power = 0.993). Statistically, movements towards water holes were significantly more directed than those towards all other resources (Tukey-Kramer post-hoc test, all p<0.05). There was no difference between linearity of segments towards food sources, locations of unknown content and the sleeping site (all p>0.05, Figure 4.5.).

Figure 4.5. Effect of resource type at the end of the path segments on linearity, travel speed and distance travelled. S = Sleeping site, U = locations of unknown significance, F = food sources, W = Water holes.
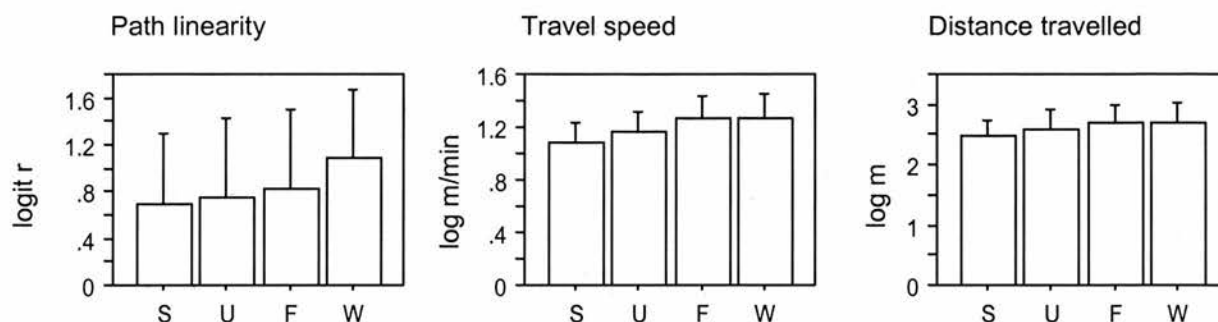
Resource type also had a significant effect on travel speed (Anova, df=3, F=37,621, p<0.0001, power = 1). Travel speed was highest for segments leading towards water holes, followed by segments towards food sources. In contrast, travel speed was lowest for segments leading towards the sleeping site. Post-hoc tests revealed that all pairs of groups differed significantly from each other (all p<0.05, Tukey-Kramer), except the 'food', 'water' pair. Thus, travel speed towards food and water sources was statistically not different, but it was higher towards food and water than towards unknown resources and the sleeping site.

Finally, distance travelled between resources was also affected by resource type (Anova, df=3, F=8.657, p<0.0001, power = 0.998). The distances tra-velled to food and water sources did not differ from each other (p>0.05, Tukey-Kramer), neither did the distances to unknown resources and to the sleeping site. However, distances travelled were significantly larger to food

and water sources than to unknown resources and to the sleeping site (all p<0.05).

In order to examine whether there was a difference in the content of the visited food sources during the outbound and the inward journeys, I split the path segments leading to known food sources into three classes, fruit, seeds and miscellaneous food, with the latter class including grass roots and panicles, stems, leaves etc. Under the assumption that the Kloof group foraged randomly and did favour particular food sources over others, I expected that they ate whatever they recognised as a potential food source during their journeys. For this reason, the amount of fruit, seeds and miscellaneous foods eaten should be equal during the outward and the inward journeys.

I performed a Chi-square test for dry (n=242) and rainy season (n=361) separately. Figure 4.6. illustrates the results. During the rainy season, when fruit was abundant, the frequency of visits to resources providing fruit, seeds and miscellaneous food was independent of the direction of movements (Chi-square test, df=2, $\chi2$=6.408, p>0.05). However, I could reject the null hypothesis for the dry season (df=2, $\chi2$=27.98, p<0.001). The Kloof group visited more fruit sources than expected during the outward journeys, and more seed sources during the inward journeys, whereas miscellaneous food sources were visited independently of the direction of movement.

I then tested whether this was a result from the differing distances of fruit, seed and miscellaneous resources from the sleeping site. There was indeed a

Figure 4.6. Mosaic display of the observed frequencies of path segments leading to fruit (FR), seed (SE) and miscellaneous (MI) food sources during outward and inward journeys. Dark grey tiles indicate observed frequencies above expected frequencies, light grey tiles indicate observed frequencies below expected frequencies. White tiles: Observed and expected frequencies do not differ. The height of the tiles indicates the percentage of outward and inward path segments. The width of the tiles indicates the percentage of fruit, seeds, and miscellaneous food for inward and outward journeys.
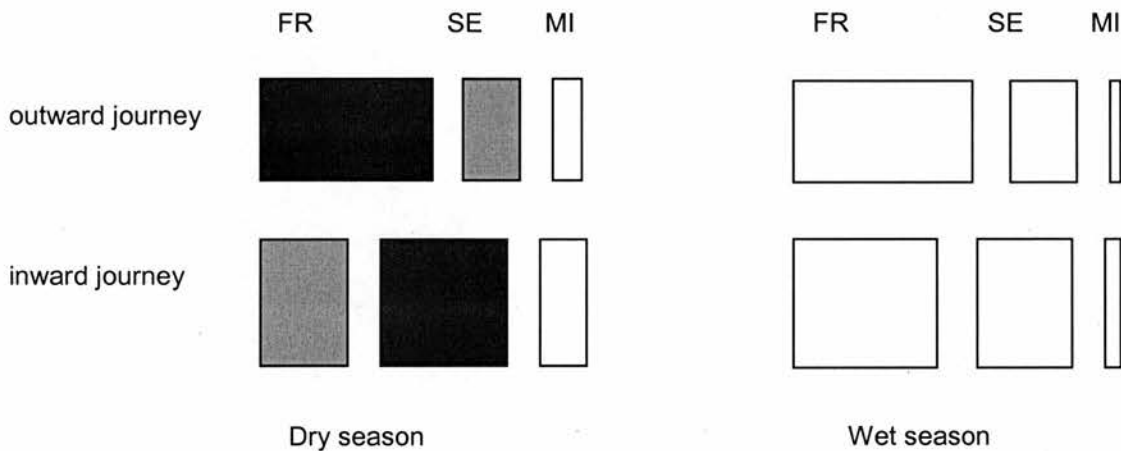
significant difference between the distances of fruit, seed and miscellaneous resources from the sleeping site (log-transformed data, Anova, df=2, F=11.97, p<0.0001, power=0.998). Seed sources were situated significantly closer to the sleeping site than both fruit and miscellaneous food sources (Tukey-Kramer, both p<0.05), whereas the distances of fruit and miscellaneous food sources from the sleeping site were statistically not different (p>0.05). This finding suggests that the Kloof group actively decided to first feed on fruit when this food source was scarce, and to leave the abundant seeds for later in the day.

4.4. Discussion

In this chapter, I have investigated the some ecological factors that influenced the movement patterns of the study group. Also, I examined whether their movements were goal-directed, and whether concurrent path linearity and travel speed can be viewed as an appropriate indicator for goal-directed movement.

I have found that the study group approached some of their resources in a goal-directed way. During the dry season, they did not visit fruit and seed resources randomly, but fed on fruit more often than expected in the mornings, when moving away from their sleeping site in a directed and fast manner. On the other hand, they fed on seeds more often during their comparatively undirected and slow home-bound journeys.

Variation in the diet in the course of the day has also been reported for gelada baboons (Theropithecus gelada), who mainly fed on grass leaves in the early mornings and afternoons, and on grass roots around midday. However, this could be explained by the distribution of fresh grass, which mainly occurred in the vicinity of the sleeping cliffs (Dunbar, 1977).

I could not find such a simple explanation for my results, because the seed sources were situated closer to the sleeping site than the fruiting trees. This suggests that the Kloof group bypassed the seed sources during their outward journeys, and visited them later, when travelling back to the sleeping site. By-passing a potential type of food in favour of a distant alternative is not consistent with the notion of merely responding to salient stimuli, but suggests

that baboons represent and categorise alternative food types, and approach them in a goal-directed way.

There are two reasons suggesting that the Kloof group, by favouring fruit over seeds in the early mornings, optimised their benefit-cost balance of foraging. First, fruit was scarce during the dry season at Blouberg. The travel costs associated with them were relatively high, but the costs of processing and ingesting them were low, ie baboons pluck and ingested them at intervals of 1-2 seconds.

Second, the main seed source came from the abundant marula trees (*Sclerocarya birrea*), which occur in large quantities in the Northern plain. Their nut-like kernels are embedded in an extraordinarily hard shell and are hard to open for humans, even by means of a robust hammer. Adult baboons are able to crack them between their molars, but I never saw infants or younger juveniles feeding on them, probably because their jaws are too weak. Thus, the most important seed source at Blouberg is low in travel costs, that is, situated close to the sleeping cliff. But seeds are costly in that they can only be consumed by some group members, and probably have a large impact on tooth structure. I therefore propose that the Kloof group optimised their foraging success by first visiting the more favourable, but probably depletable fruit sources in the mornings, and supplemented their diet with less advantageous seeds in the afternoons.

Thus, there are two reasons to suspect that the movements towards fruit sources in the dry season were goal-directed: the Kloof group favoured fruit sources over seed sources, and the corresponding movements showed clear characteristics of goal-directedness, that is, they were highly directed and fast. These movements clearly warrant further investigation of the study group's spatial abilities (chapter 8).

Also, water holes were approached directly, fast, and over long distances. Water holes were restricted to only five locations, and it is highly unlikely that the study group encountered them by chance. I therefore view movements leading to water holes as goal-directed, and will further analyse them in chapter 8.

Interestingly, the least directed and slowest movements led the Kloof group to the sleeping site, a highly limited and crucial resource at Blouberg. The observation that they returned to a single cliff every day alone implies goal-directed movement. This finding suggests that path linearity and concurrent high travel speed are on some occasions unreliable predictors of goal-directedness.

This finding can be understood in the light of time budget constraints. The animals always arrived in the vicinity of their sleeping site well before nightfall, and spent the remaining hours in daytime activities, such as foraging or socialising in its surroundings. Since there was no need to arrive early in the cliffs, they spent the rest of their time with activities that were subject to time con-

straints. I therefore propose that the sleeping site was approached in a goal-directed way, but that the food sources visited in the afternoons in the vicinity of the sleeping site were used as 'fall-back' foods in the remaining time until nightfall.

One of the most important factors that affected path characteristics was season. Movements were more directed, faster and longer during the dry season compared to the wet months, when food and water at Blouberg were abundant and more evenly distributed in space. In contrast, the animals were forced to walk over long distances at comparatively high speed during the periods of drought.

However, food distribution was not the only factor responsible for comparatively slow and undirected movements during the rainy season. Also, the frequency of baboon loud-calls at Blouberg was significantly increased during that time, suggesting that the Kloof group needed to avoid other groups more often than during the dry season. When other groups approached them to 300 m or less, the directedness of movement decreased, while travel speed increased. Interestingly, distance to other groups had also a significant effect on distance travelled between resources, indicating that during these evasive manoeuvres, the Kloof group bypassed resources that they would have visited in the absence of conspecifics.

Baboon loud-calls have been functionally divided into within-group contact calls (Cheney et al., 1996; Rendall et al., 1999), alarm calls in response to

predators (Fischer et al., 2001b) and between-group contact calls (Byrne, 1981). During the rainy season at Blouberg, at least some baboon loud-calls seem to fall into the latter category. I propose that the increased frequency of loud-calls correlates with the fruiting cycle of marula trees *(Sclerocarya birrea)*. Marula trees are largely confined to the Northern plain of Blouberg Nature Reserve. On the basis of the increased frequency of group encounters during that time, it became evident that baboon groups who foraged else-where during the rest of the year assembled in the Northern plain in order to forage on this highly preferred fruit. Thus, the loud-calls seemed to function as 'beacon' which signalled other groups their own presence. This contrasts with the findings from other chacma baboon study sites, where loud-calls have been viewed as intra-group signals (Fischer, 2001; Kitchen et al., 2003).

During the rainy season, movements were comparatively slow and undi-rected. Interestingly, there was a single condition when direct, fast, but comparatively short movements also occurred during the rainy season: the outward movements on the hill. It is puzzling that the corresponding inward movements, in contrast, were the slowest and least directed in the whole data set. The Kloof group foraged for mountain figs *(Ficus glumosa)* during that time period. Mountain figs are prominent trees which grow singly on the hill, that is, their fruit is distributed in discrete patches and they occur only in limited numbers. In addition, their fruiting period is highly synchronised. Since these are excellent prerequisites for investigating spatial knowledge, I view the fruiting period of mountain figs as a natural experiment, and present my findings in a separate chapter (chapter 6).

In summary, I have investigated the path characteristics of the Kloof group's journeys in order to examine goal-directedness, and to identify those movements which provide the best data for a thorough examination of the baboons' spatial abilities in the following chapters. For this purpose, I have viewed path linearity, travel speed and distance travelled between resources as indicators for goal-directed movement. The results suggest that the movements in the dry season to water holes, and to fruit sources in the early mornings exhibit characteristics of goal-directedness, and therefore warrant closer examination in the next chapters.

However, path linearity and travel speed were not always reliable predictors of goal-directedness. Approaches to the sleeping site, a highly limited resource at Blouberg, were typically undirected and slow. However, the fact that the study group approached this location every night alone suggested goal-directed movement. I explained this phenomenon in the light of time constraints for daytime activities.

The paths during the fruiting period of the mountain figs were highly directed and fast, and thus untypical for the rainy season. In addition, I found that baboon groups at Blouberg sometimes approached each other to 100 m or less during foraging. The distance to other groups significantly affected path characteristics in a way that suggested that the Kloof group avoided groups of conspecifics. These encounters were likely to be unintentional, and unpredictable for the Kloof group. I therefore view group encounters during which

the study group was forced to alter their paths and to reorient themselves as a natural experiment, which can further illuminate the mental representations of space in the study group (chapter 7).

Chapter 5 Locating distant resources

5.1. Introduction

In the previous chapter, I have analysed how the Kloof group moved from one resource place to the next. I have investigated path linearity, travel speed, distance travelled and some ecological factors involved in their variability. However, I have not attempted to draw any conclusions as to the cognitive processes that underlie such movements. In this and the three following chapters I will now draw the focus of investigation onto the cognitive aspects of the Kloof group's ranging. The main question addressed in the present chapter is how they located distant resources. For this purpose, I compare the predictions of several hypothetical searching strategies that have been pro- posed for foraging animals in the past with the observed movement patterns.

When animals move without any information about the locations of resources, they must attempt to optimise their chances of random encounters with food (Bell, 1991). Three possible searching strategies have been proposed for animals unable to predict the locations of distant resources. Such strategies include random walk (Bell, 1991; Garber & Hannon, 1993; Janson, 1998), systematic search, such as walking in straight lines or in loops or spirals from a central starting point, and search based on sensory information that becomes available in the course of the journey, for example through olfaction or vision (Bell, 1991; Garber & Hannon, 1993).

On the other hand, it is well known that a wide variety of animals visit particular food locations on the basis of spatial memory. For example, intensive research on food storing birds such as black-capped chickadees *(Parus atricapillus*, Shettleworth, 2002) and Clarks's nutcrackers *(Nucifraga columbiana*, Balda & Kamil, 1998, 2002) has revealed that they are highly specialised in remembering large numbers of seed caches, and retrieve them with high accuracy for up to 9 months in the lab.

Memory-based retrieval of hidden food items in small-scale space has also been documented in captive chimpanzees (Menzel, 1978) and vervet monkeys (Gallistel & Cramer, 1996; Cramer & Gallistel, 1997). More recently, Menzel et al. (2002) tested whether the bonobo Kanzi was able to find out-of-sight rewards in a 20-hectare outdoor enclosure on the basis of information given by a road sign which was presented at an arbitrary starting location. In all 12 trials, Kanzi led a naive test person to the designated location on an efficient route, suggesting that he used the information on the sign to find it.

There is evidence that wild monkeys memorise the locations of food sources over an extended time period. Menzel (1991) showed that after finding an experimentally introduced akebi fruit native to their natural environment, Japanese monkeys *(Macaca fuscata)* stared upwards to and manipulated nearby akebi vines more often than conspecifics who found pieces of chocolate or banana that did not naturally occur in their habitat. This suggests that once they had consumed the highly preferred, experimentally provided food item, the macaques extrapolated their search to locations where this fruit

naturally occurred, and remembered the physical appearance of the plant providing akebi fruit. Interestingly, they did so even in times when akebi fruit were out of season, suggesting that they were able to retrieve this memory over long time periods.

However, since akebi vines occurred in the proximity of the experimental test area, it remains unclear whether the macaques also remembered where additional out-of-sight specimens were situated. Menzel (1991) reports that after their find, two animals travelled quickly and directly to the nearest akebi vines, located 23 and 65 m away. He felt that these vines were not visible from the previous location, but on this basis evidence for remembering out-of-sight locations remains weak.

Another experiment on spatial knowledge in primates has been performed with a group of wild capuchin monkeys *(Cebus apella)* in Argentina (Janson, 1998). They were provisioned with tangerines which were presented on 17 feeding platforms, each at least 180 m apart from the next one. Janson tested two null models of movements assuming no spatial memory, and compared them with the observed movements. The first model assumed that the group moved from a starting location in a random direction for a fixed distance, and then headed into a new direction which deviated from the previous one for 90° maximally. The second model assumed that the group moved in straight lines until detecting a food source. On the basis of the distances between the platforms and several hypothetical angles within which the group could detect a food source, he calculated the probabilities with which each of the platforms

would be approached from any other site if the monkeys moved without spatial memory.

Neither of the two models explained the observed movement patterns in a satisfactory way. The capuchins did not move at random, and the observed frequency of visits to platforms would have required detection fields that were considerably larger than the estimated average visibility in the animals' home range. Janson (1998) concluded that the movements of the capuchins between the feeding platforms were best explained by spatial memory.

Although this study provides the best evidence for large-scale spatial knowledge in monkeys so far, it leaves some important questions open. Janson was not able to bait the feeding platforms prior to each experimental trial, because other animals in the forest had learned how to use them as well. So he was forced to race to the platforms and to fill them during the trials before the capuchins arrived. He did so as soon as he felt that the animals had made a clear choice, at distances of maximally 50 m from the platforms. It remains open as to what degree this procedure influenced the animals' movements. Also, the distance from which the animals could spot the platforms was examined only five years after the experiment was performed. Janson & Di Bitetti (1997) then experimentally tested from what distance capuchins at the same study site could see feeding platforms that were similar to those used in the above study. From a distance of 41 m, the animals dashed to the platforms in 50% of the trials. It remains open whether at least some of the platforms had been inter-visible in the experiment 5 years before. In his computer models,

Janson (1998) indeed showed that a hypothetical detection distance of more than 90 m, but less than 250 m was sufficient to explain the movement patterns of the capuchins.

The olfactory bulb of old world monkeys is reduced in comparison to the respective brain areas of their prosimian relatives (eg. Fleagle, 1988), suggesting that olfaction is less important for finding food in monkeys and apes. However, little is known about the role of olfaction in the foraging decisions of primates. Garber & Hannon (1993) addressed this question with a series of computer-simulated experiments, with the aim to establish how effectively simulated 'animals' find a resource by means of olfaction as opposed to random walking and strategic search. They found that simulated monkeys which were equipped with a sense of smell dramatically increased the probabilities of encountering the target location in comparison to their artificial relatives who lacked olfaction. However, the routes taken by the olfaction simulations were not efficient. In order to find the steepest ascent of the odour gradient (and thus to constantly move towards the target), they needed to walk in zigzag lines, also referred to as 'tacking', which enabled them to compare the intensity of the smells at three nearby locations. Tacking explained fairly well the movement patterns of nocturnal sea birds and hyenas (Hutchinson & Wenzel, 1980; Mills, 1989, cited in Garber & Hannon, 1993; Bell, 1991), but has not been reported from any primate species so far.

The movement patterns of the Kloof group did not exhibit any signs of tacking, and it is unlikely that they perceived smells over the large distances between

their resources (up to 4500m, Chapter 4). In addition, if the movements of baboons would be primarily guided by olfaction, I would expect the strong Southern winds which occur at Blouberg in regular time periods in winter to alter the study group's movement patterns. This was clearly not the case, and the directions chosen did not depend on wind conditions. Based on these considerations, I decided to neglect olfaction as a possible means of locating distant resources, and viewed vision as the most important sensory input during their foraging journeys.

In this chapter, I examine to what degree the Kloof group moved at random, used simple searching strategies or foraged at sight, and under what conditions spatial memory remains the only explanation for the observed movement patterns. I investigate their journeys with respect to resource availability and visibility.

5.2. Methods

5.2.1. Random walking

Chapter 4 has already revealed that the Kloof group did not walk at random for most part of their journeys. The mean vector lengths (linearity) of the path segments leading from one resource to the next were typically high, suggesting directed movement. In order to examine to what extent the path segments were directed, I applied the Rayleigh test for randomness (Batschelet, 1981) to each of the segments.

Since path segments consisting of only 4 or less vectors cannot be tested formally, I viewed 5 as the critical sample size to which this statistic test can be applied with confidence (see also Table H in Batschelet, 1981, which offers critical values of the Rayleigh test for a minimum of 5 vectors).

I am aware that by statistically testing a large number of samples, I will probably falsely reject the null hypothesis in p% of the cases. However, I performed this analysis to test the null hypothesis of random wandering as the *only* strategy by which the Kloof group found their resources, and did not aim to assert directedness for particular path segments. I therefore view this analysis as means to roughly estimate to what degree the movement of the Kloof group was directed, and interpret the results with respect to the errors committed with multiple testing. I used p-values of 2% for these tests.

5.2.2. Strategic search

Under the assumption that the Kloof group strategically searched for food, I hypothesise that the locations of the resources encountered in this way should be randomly distributed in space. Thus, the bearings of the path segments leading from one resource to the next should be uniformly distributed over the unit circle.

Since searching strategies are likely to depend on food availability and distribution, I divided the data into 7 different time periods, based on the main food types eaten by the Kloof group, and pooled the corresponding path segments. Again, I tested this data set by means of the Rayleigh test for randomness.

The Kloof group returned to the same sleeping site every night. Because this implies that they needed to reverse their movement at least once per day, the bearings of the path segments over entire days must be bi-directional to some extent. I did not test my data for bi-directionality, as proposed by Batschelet (1981), because Chapter 4 has revealed that the movements leading towards the sleeping site were less directed than the ones leading away from it. This suggests the study group may have used different strategies for locating their resources at different times of day. Therefore, I divided the segments into inward and outward movements, and tested them separately.

The fidelity to a single sleeping site also implies that the first and the last segment of a given day were covered relative to a single location. Because repeatedly covered path segments potentially bias the results of the Rayleigh test, I run each test twice, once including and once excluding the sleeping site-related segments.

5.2.3. Foraging at sight

I established the maximum distance from which the study group could visually perceive their resources on the hill and in the plain separately, because visibility conditions in these two areas differed. On the hill, vegetation was comparatively thin. Visibility of resources was restricted by topography, mainly by the slopes, and remained constant throughout the year. In contrast, direct views to distant locations in the plain were mainly hindered by dense vege-tation, and thus fluctuated in the course of the year.

I established visibility of all important resources on the hill individually. To-gether with a field assistant, I revisited the resources that had been used by the Kloof group previously, on days when we did not follow the animals. One person was standing next to the resource, for example to a fig tree, and waived a white plastic bag which was fixed to a large stick at approximately the height of the tree crown.

By means of GPS, the other person tracked back the route along which the baboons had approached this tree previously. As soon as the moving flag disappeared from view, for example behind a large rock, a GPS reading was taken. Two more readings to the left and to the right of the first reading were made, so that the three visibility readings built a line approximately perpen-dicular to the baboon path and was at least 300 m long. Since the study group maximally spread over 150 m when foraging, this procedure made sure that none of the animals could have seen the resource before crossing this visibility line.

In the plain, I examined visibility on the ground once a month between Octo-ber 2001 and the end of data collection in August 2002 at 16 randomly chosen locations. At each of these locations, one person stood on the spot and waived the white plastic bag about $1/2$ m above her head. By means of a compass, the other person walked towards N and took a GPS reading as soon as the moving bag disappeared behind the dense vegetation, at the height of a baboon that walks on the ground. Three more readings were taken

to the W, S and E of the bag. This procedure resulted in a total of 16 x 4 = 64 visibility readings per month for the flat area of the home range.

The Kloof group mainly foraged on the ground. But some food items such as the flowers (but not the fruit) of marula trees and the flowers and pods of knobthorn acacias were only available in the tree crowns. Food sources that are located in the tree crowns are visible from larger distances than food sources on the ground in the woodland savannah. I therefore roughly estimated from what distance tree crowns were visible from the ground at Blouberg.

For this purpose, I climbed the north facing slopes of the hill, and determined the minimal altitude at three locations from which I could still see one of the water holes in the plain by means of a telescope (Kowa TSN-2) through the tree crowns. I did so in August 2002, when all deciduous trees had lost their leaves. Since I knew the distance to the water hole and the difference in altitude between the water hole and the three positions, I was able to calculate the angle that is on average necessary in the plain to see an elevated location at a given distance (Figure 5.1).

Figure 5.1. Estimating visibility of distant tree crowns from the ground
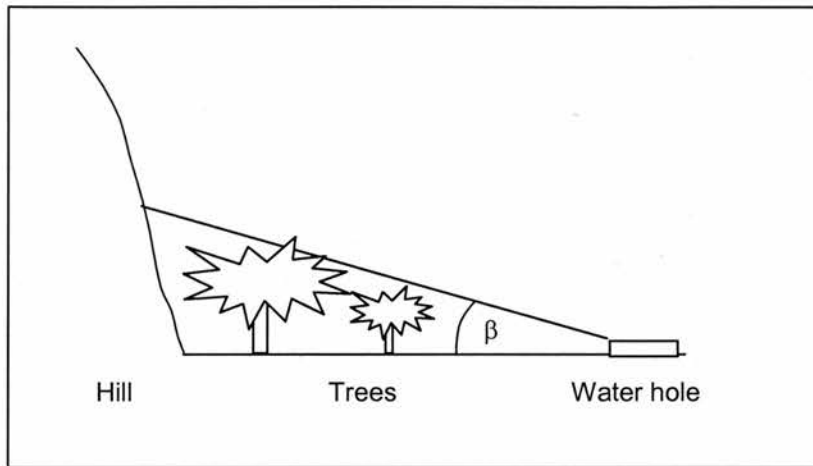
5.3. Results

5.3.1. Random walking

A total of 611 path segments (Chapter 4) consisted of 5 or more vectors, and were therefore long enough for statistical testing. 133 segments stemmed from the first dry season in 2001. For this time period, I could reject the null hypothesis of random wandering at an α-level of 2% for 109 segments (82 %, Rayleigh test), and only 24 segments were undirected. Since I performed a total of 133 tests at $p \leq 0.02$ for this time span, it is probable that I falsely rejected H0 in 3 cases.

Out of 339 path segments of the rainy season, I could reject the null hypothesis of random wandering for 204 tests This suggests that the Kloof group walked in a directed fashion towards the next resource in 60% of the cases.

Again, given the fact that I used p≤0.02 for these tests, 8 significancies are likely to result from chance, and the percentage of directed movements during the rainy season is probably even smaller. And finally, 117 (84 %) of out of 139 segments covered during the second dry season were significantly directed (p≤0.02), whereas 22 were covered at random (Rayleigh test).

These results are not consistent with the notion that baboons always move between resources at random, but suggests that they often walk in a directed manner. This becomes especially evident during the dry season, when food is scarce. However, the above results do not exclude other simple strategies for finding food.

5.3.2. Strategic search

Under the assumption that the Kloof group foraged by searching their environment systematically without any spatial knowledge, I expect that the bearings of departure from the sleeping site are chosen at random every day, and that the departing angles from food resources randomly deviate from the arriving angle.

In the first dry season, this did not apply to the time when the Kloof group was mainly foraging for kooboo berries (May - August 2001, Figure 5.2 A). I could reject the null hypothesis of randomness for both the outward and the inward movements, when including and when excluding the sleeping site-related segments (see Figure 5.2 A for corresponding r and p-values).

However, the Kloof group moved in a different way when foraging for the flowers of the marula tree and the knobthorn acacia later in the first dry season, shortly before the rainfalls started (September - October). None of the tests was significant below p=0.05, suggesting that the directional variability of the path segments was large and the resources were visited at random (Figure 5.2 B).

Figure 5.2. Mean bearings of the path segments recorded during the first dry season 2001 (A) when kooboo berries were the main foods and (B) when the Kloof group foraged for the flowers of marula trees and knobthorn acacias. Left panels: Outward movements; right panels: Inward movements. Black circles: Segments from and to the sleeping site. Bare circles: Segments covered when distant from the sleeping site. R- and p-values in brackets are results of tests performed without the sleeping site-related segments.

A

r=0.745
p<0.001

(r=0.666
p<0.001)

r=0.415
p<0.001

(r=0.554
p<0.001)

B

r=0.215
p>0.05

(r=0.201
p>0.05)

r=0.087
p>0.05

(r=0.155
p>0.05)
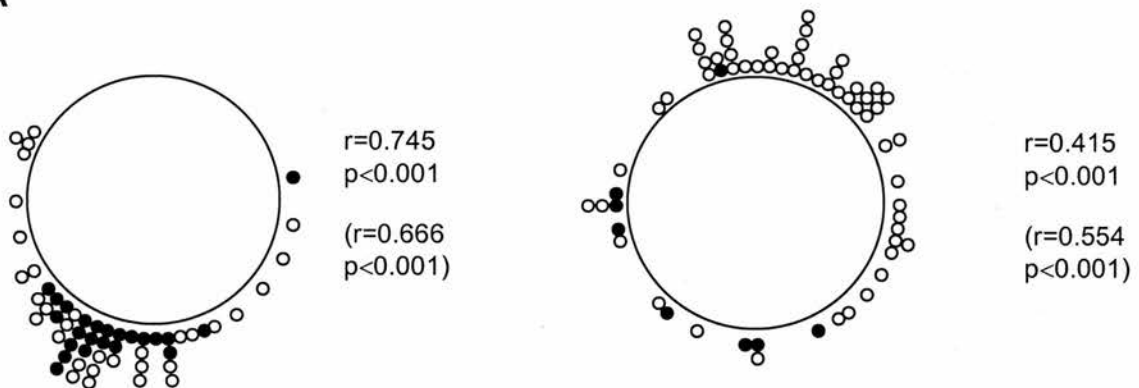
Figure 5.3. Mean bearings of the path segments recorded during the wet season when the Kloof group foraged for a wide variety of different food types (A), for Mountain figs (B) and for Marula fruit (C). Left panels: Outward movements; right panels: Inward movements. Black circles: Segments from and to the sleeping site. Bare circles: Segments covered when distant from the sleeping site. R- and p-values in brackets are results of tests performed without the segments from and to the sleeping site.
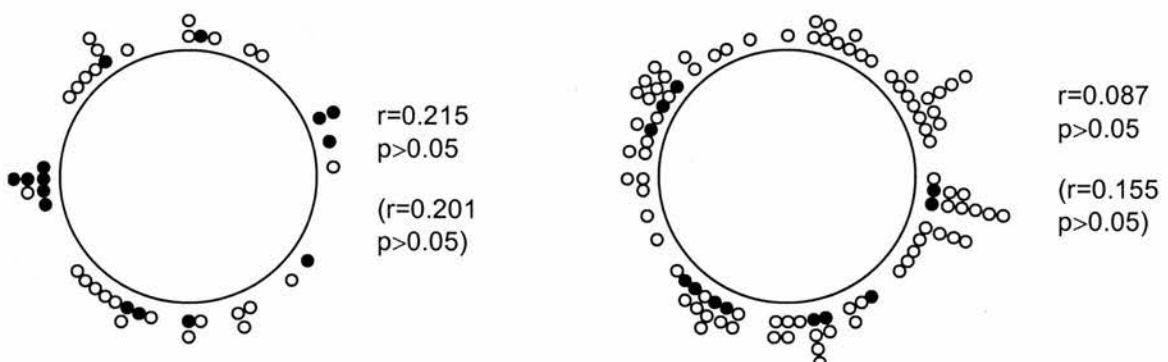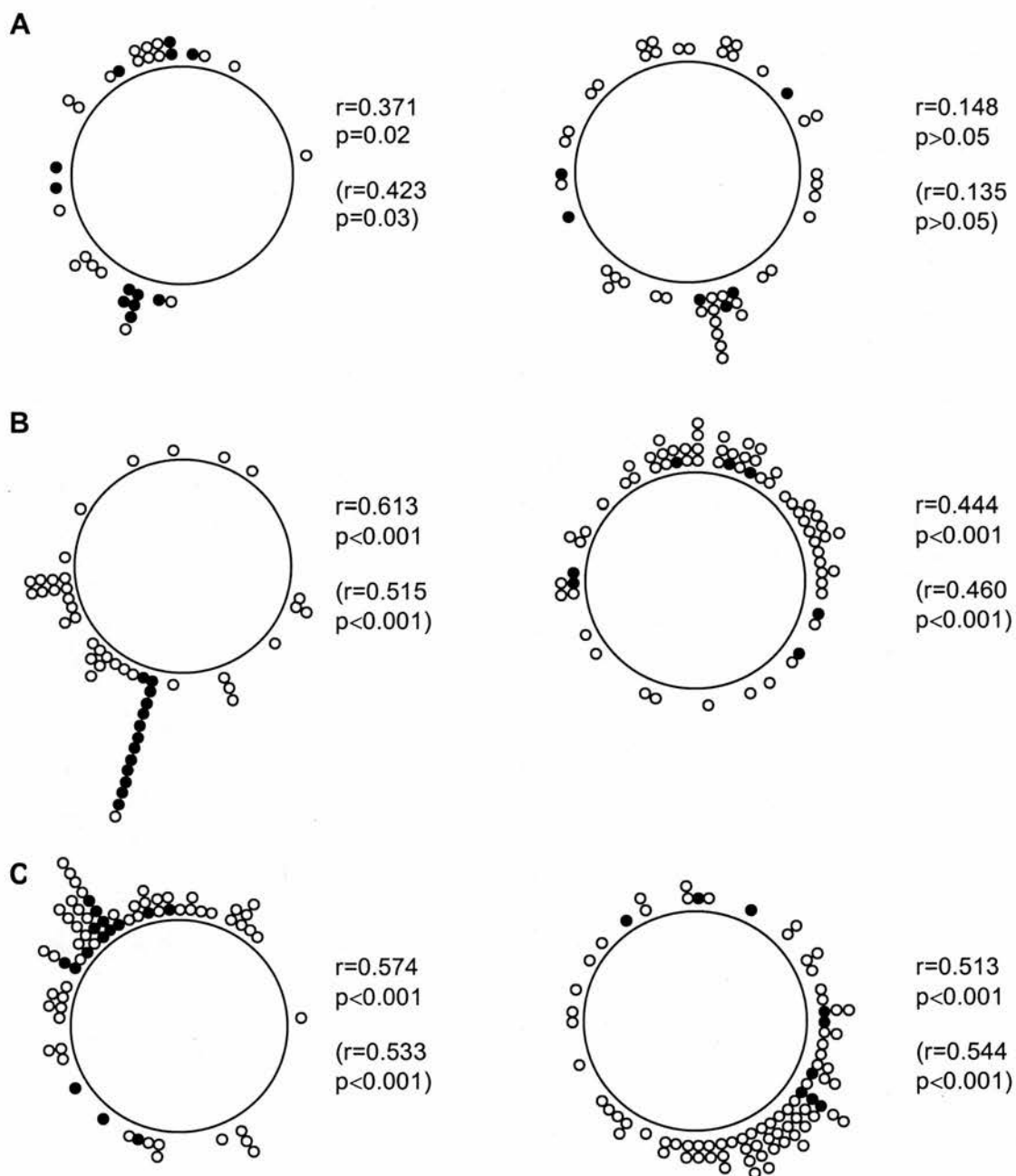
A

r=0.371
p=0.02

(r=0.423
p=0.03)

r=0.148
p>0.05

(r=0.135
p>0.05)

B

r=0.613
p<0.001

(r=0.515
p<0.001)

r=0.444
p<0.001

(r=0.460
p<0.001)

C

r=0.574
p<0.001

(r=0.533
p<0.001)

r=0.513
p<0.001

(r=0.544
p<0.001)

By the end of October, the Kloof group foraged for a wide variety of different food types that became available during the wet season, such as flowers, fruit, berries and pods. During that time, the bearings of the outward movements were not uniformly distributed (Figure 5.3 A), but those of the inward movements were. This result held when the segments from and to the sleeping site were excluded from analysis.

During a short time period between late December and early January, the Kloof group mainly fed on mountain figs *(Ficus glumosa,* Figure 5.3 B). During that time, the variability of the segment bearings leading away from the sleeping site dramatically decreased. I could reject the null hypothesis of randomness both for the outward and inward movements, and this result remained when I excluded the first and last segments per day. Again, this suggests that the Kloof group did not forage at random.

Figure 5.3 C shows the directional variability of the path segments when the Kloof group was foraging for the preferred marula fruit (January - March). Again, the Rayleigh test was significant for outward and inward segments, with and without including the first and last segments of a given day into the analysis.

Also, I could reject the null hypothesis of uniform distribution of the segment bearings for the last few weeks of the rainy season (March - May) when corkwood seeds *(Commiphora mollis)* were the main food source as well as

for the second dry season (May - August 2002), when the Kloof group foraged for grewia berries (Figure 5.4).

Figure 5.4. Mean bearings of the path segments recorded during the last months of the wet season when the Kloof group mainly foraged for corkwood kernels (A), and then shifted to grewia berries during the subsequent dry season (B). Left panels: Outward movements; right panels: Inward movements. Black circles: Segments from and to the sleeping site. Bare circles: Segments covered when distant from the sleeping site. R- and p-values in brackets are results of tests performed without the segments from and to the sleeping site.

A

r=0.509
p<0.001

(r=0.418
p<0.001)

r=0.362
p<0.001

(r=0.363
p<0.001)

B

r=0.763
p<0.001

(r=0.787
p<0.001)

r=0.719
p<0.001

(r=0.755
p<0.001)
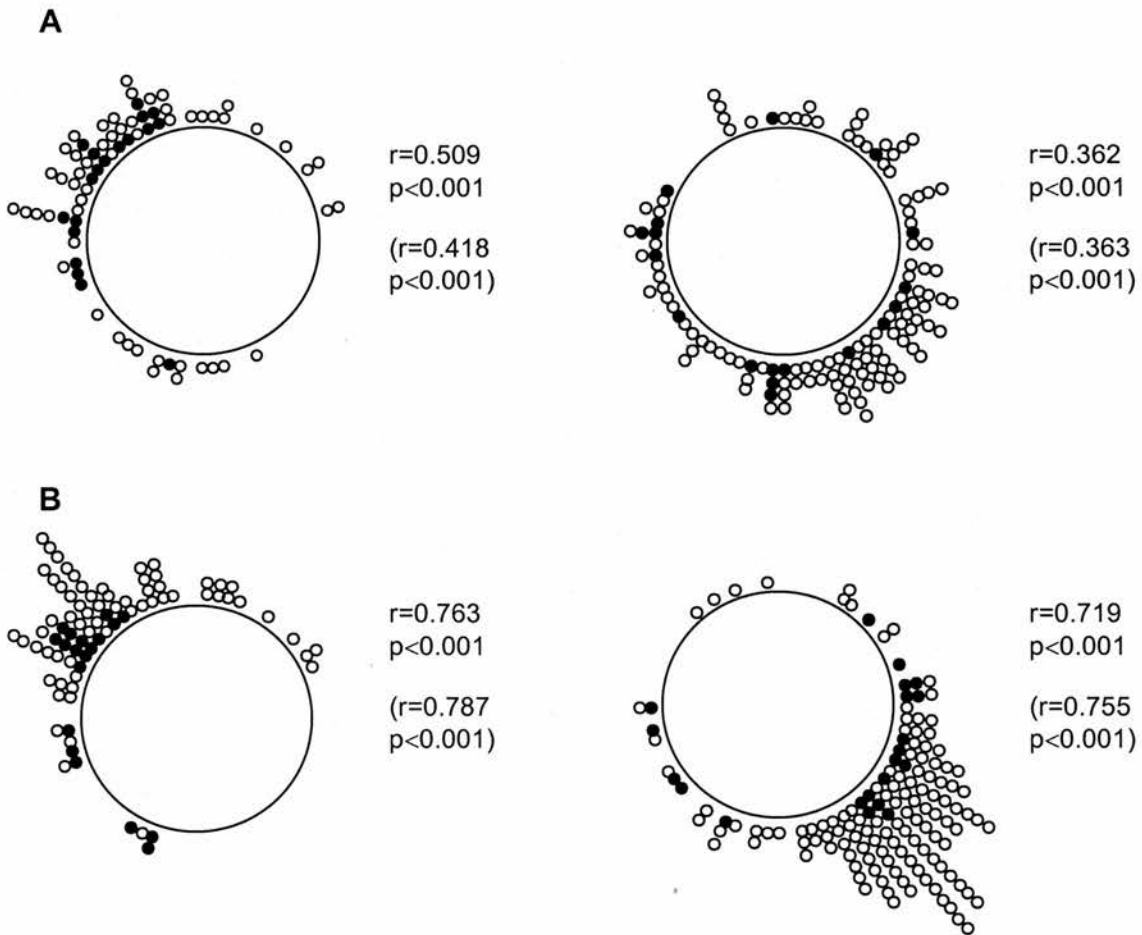
5.3.3. Foraging at sight

a) Visibility in the plain

Average distance from which a moving object could be spotted on the ground throughout the study period was 83 m. It was largest during the dry season in July, with an average of 104 m. This was also the month when I recorded a maximum visibility of 219 m at one of the locations. For comparison, the months with the lowest visibility were December and January, with an average of 65 m each.

In order to test whether the path lengths from one resource to the next covaried with varying visibility throughout the months, I regressed the average path length per month against the average visibility (log transformed data). The relation between distance travelled and the distance from which resources were visible was weakly positive, but the regression was not significant (df=9, R^2=0.033, a=1.348, p>>0.05). This suggests that distances travelled between resources did not depend on visibility on the ground.

In order to roughly estimate visibility from the ground to the tree crowns in the plain, I examined how high I had to climb the N-slopes on the hill in order to see a distant waterhole in the plain. From the three points on the N-slope that I used for this estimation, the distance to the water hole was 952 m, 978 m and 1100 m, and the difference in height to the water hole was 52 m, 54 m and 56 m. From these measurements, I obtained the critical angles of 3.13°, 3.16° and 2.92°. I therefore viewed the maximum angle of 3.2° as critical

under which resources of given heights can be seen at given distances when walking on the ground.

Marula trees are among the tallest trees at Blouberg, with a maximum height of 17 m (Grant & Val, 2000). Only two tree species are higher, the baobab *(Adansonia digitata)* and the nyala tree *(Xanthocercis zambesiaca)*, with maximum heights of 25 m. Single baobab and nyala specimens were confined to the immediate vicinity of water holes in the home range of the Kloof group, but did not occur elsewhere.

In order to estimate from what distance the Kloof group could spot a distant marula tree as well as a baobab or nyala tree from the ground, I divided the tree heights by the tangents of the critical angle of 3.2°. By this means I found that from the ground marula trees can be spotted from a distance of 333 m, and the tall baobab and nyala trees from a distance of 447 m.

In order to test whether the Kloof group foraged on the basis of visibility on the ground I performed a one-sample t-test with the log-transformed distance travelled between food sources each month. For the hypothesised mean, I took the maximum visibility on the ground to of 220 m, the visibility on the ground to the crowns of Marula trees of 340 m.

Figure 5.5. and Table 5.1. summarise the results. In August 2001, the path segments between resources were shorter than both visibility on the ground and visibility from the ground to the tree crowns. This was the time when the

Figure 5.5. Distance travelled between food sources in the plain (n=592) per month relative to the maximum distance from which they were visible. Maximum visibility on the ground is indicated by the lower of the two arrows, visibility from the ground to the tree crowns by the upper arrow.
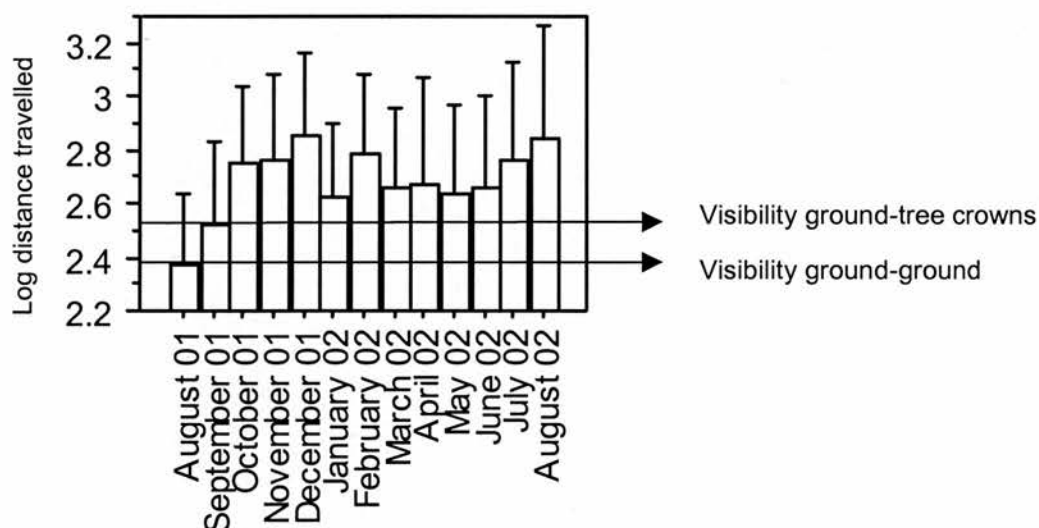
Kloof only stayed in the plain near the sleeping site to forage on marula kernels in the afternoons. The hypothesis that they foraged on the basis of visibility cannot be rejected for this time period. This was also true for the months of September and October, when the marula trees and knobthorn acacias were flowering. During that time, the distances travelled between resources were significantly larger than visibility on the ground, but they were not larger than visibility from the ground to the tree crowns, where these flowers were situated. Thus, it is likely that the Kloof group foraged at sight, and from each tree simply chose the next visible one.

Table 5. 1. Main food types eaten per month, abundance, height above ground and results of the one-sample t-test relating visibility on the ground and visibility from the ground to the tree crowns to the distances travelled between food sources each month. * p<0.05, ** p<0.001.

Month	Main food type	Abundance	Height (m)	df	t ground	t crowns
August 01	Marula kernels	abundant	0	29	-.676	-3.837 *
September	Marula/knobthorn flowers	abundant	17	45	2.746 *	-0.752
October	Marula/knobthorn flowers	abundant	17	5	3.054 *	1.710
November	Flowers, fresh pods, fruit	abundant	0 - 10	25	5.546 **	3.125 *
December	Flowers, fresh pods, fruit	abundant	0 - 10	23	7.008 **	4.578 **
January 02	Marula fruit	abundant	0	39	5.135 **	1.573
February	Marula fruit	scarce	0	56	9.793 **	5.805 **
March	Corkwood seeds	abundant	5	98	8.413 **	3.265 *
April	Corkwood seeds	abundant	5	36	4.237 *	1.826
May	Corkwood seeds/grewia	scarce	5	72	6.235 **	2.182 *
June	Grewia berries	scarce	5	88	6.762 **	2.587 *
July	Grewia berries	scarce	5	59	7.488 **	4.248 **

In November and December, the Kloof group foraged for a wide variety of food types in the plain, such as ground-dwelling flowers, flowers of trees, fresh pods and different types of fruit. The distances covered between resources were significantly larger than the distance from which these resources were visible. However, since food was available in large amounts, the study group often foraged widely dispersed, and my criterion for a place to become the focus of observation (a minimum of 3 animals feeding at a patch) may not have been fine enough to capture the locations of feeding sites. I therefore take this result with caution.

Table 5.1 reveals that in January, the Kloof group was likely to have found the preferred marula fruit at sight. The distances between the marula trees used

were larger than visibility on the ground, but not larger than the distances from which the crowns of the marula tree were visible. In February and March, in contrast, distances travelled between resources became significantly larger than visibility.

I recorded a total of 192 visits to 154 different marula trees during their fruiting season. 123 trees (79.8%) were visited on a single occasion, 24 trees (15.6%) were visited twice, and 7 trees (4.6%) were visited on three occasions.

I hypothesised that if multiple visits to the same tree were due to chance, then the number of visits to a tree should be an exponential function of the distance to the sleeping site. In contrast, if the Kloof group revisited some trees purposefully, and thus had remembered their locations, the number of visits to a particular tree should be independent of its distance to the sleeping site. Furthermore, the reward of multiply revisited trees should be larger than the reward of trees that were only visited a single time.

Figure 5.6 A shows that the number of visits to a specimen did not depend on its distance from the sleeping site, and distant trees were visited as often as closer ones. Also, the reward gained from multiply visited specimens (n=33) was larger than the reward from singly visited ones (n=110). However, this difference is significant at a level of $p=0.09$ only (square root transformed data, unpaired t-test, df=141, t=-1.715).

Figure 5.6. A Frequency of visits to each of 154 fruiting marula trees as a function of their distance to the sleeping site. The line is a lowess-smoother (tension = 30). B. Reward (number of animals x time spent feeding) of singly and multiply visited specimens.
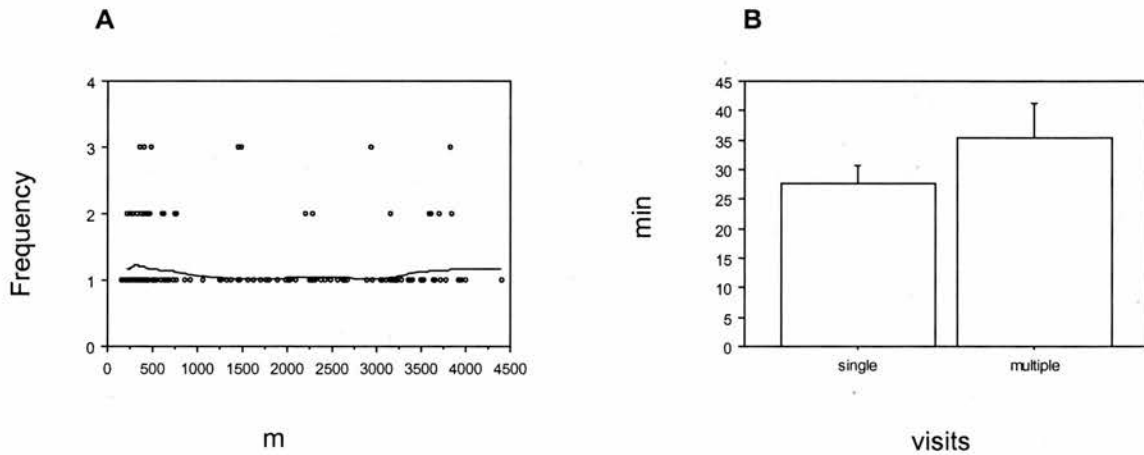
The visibility of corkwood trees, which became highly preferred in April, falls between the visibility categories established in this chapter. With 5-6 meters in height, they are shorter than marula trees, and their seeds are attached to their branches in the beginning of their fruiting period and fall to the ground later. The distances travelled between them are well above the average visibility on the ground, but below the visibility of the taller marula trees (Table 5.1). Therefore, I cannot entirely exclude that corkwood trees were visited at sight.

However, the number of visits to particular specimens was not dependent on their distance from the sleeping site (Figure 5.7. A), and the average reward of multiply visited trees (n=18) was significantly larger than the reward of
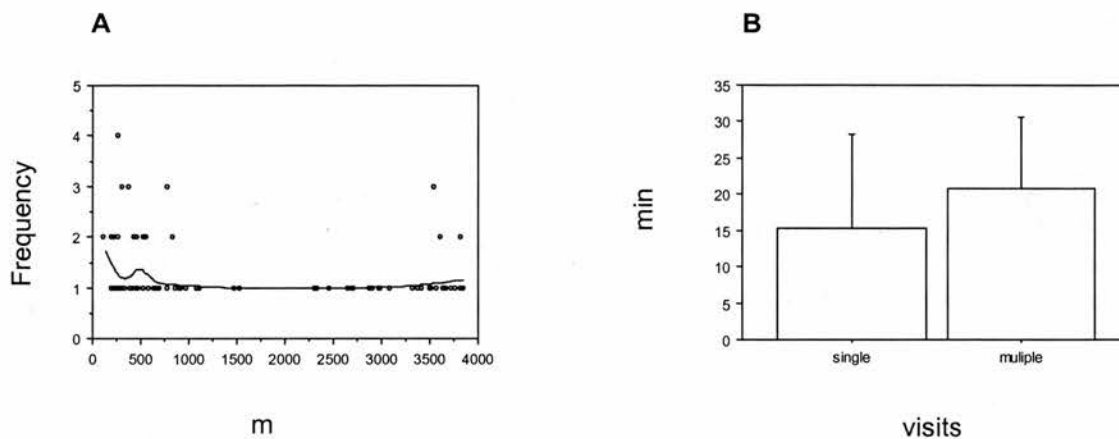
Figure 5.7. Frequency of visits to each of 76 corkwood trees as a function of their distance to the sleeping site. The line is a lowess-smoother (tension = 30). B. Reward (number of animals x time spent feeding) of singly and multiply visited specimens.

A

B

Frequency (y-axis, 0 to 5) vs m (x-axis, 0 to 4000)

min (y-axis, 0 to 35) for single and multiple visits

m

visits

trees that were visited on a single occasion only (n=58, Figure 5.7. B, square root transformed data, unpaired t-test, df=74, t=-2.116, p=0.04).

The Kloof group's main food consisted of grewia berries during the second dry season. Bushes are approximately 2-3 m in height. The distances travelled to reach them were significantly larger than visibility on the ground, and also larger than visibility to tree crowns (Table 5.1.).

I recorded a total of 97 visits to 91 Grewia bushes. 85 bushes (93.4%) were visited on a single occasion, and only 6 bushes (6.6%) were visited twice. Figure 5.8. A shows that multiple visits only occurred to bushes that were far from the sleeping site. Also, the average reward (number of animals x time spent feeding) per visit was larger for multiply visited specimens, compared to

Figure 5.8. Distance from sleeping site and average reward per visit of singly and multiply visited grewia bushes.
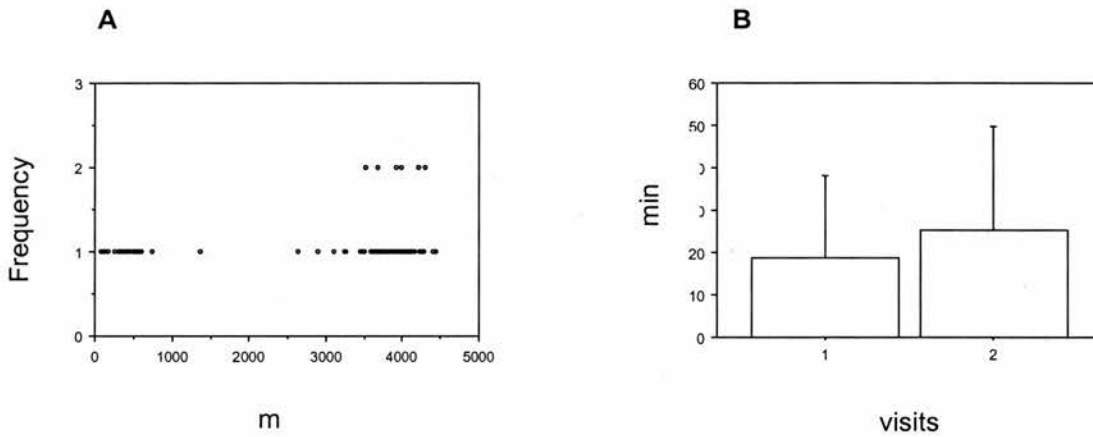
singly visited ones. However, this difference was statistically not significant (unpaired t-test with square root transformed data, df=89, t=-0.769, p>0.05).

The two water holes were the only limited resources in the plain. Since the probability of meeting them by chance were small, I tested whether they were approached from a distance that was larger than the distance from which the trees associated with them could be seen. I took 450 m as the hypothesised distance from which the baobab and nyala trees were visible from the ground. Median distance travelled to the water holes in the plain was 971 m. A one-sided t-test revealed that this difference was significant (df=50, t=5.823, p<0.001). I take these results as the best evidence so far that the Kloof group can find resources on the basis of memory in the plain.

b) Visibility on the hill

In contrast to the plain, visibility on the hill was highly variable, depending on the locations of the food sources. I recorded 173 path segments to resources on the hill with known visibility. In 15 cases, the next resource was visible from the last one. Among the remaining 158 segments, the distance covered without visual access to the next resource ranged between 21 and 1817 m. In order to test whether visibility had an impact on the path linearity, I plotted two measures of visibility against directedness of the paths. The first measure was the absolute distance over which the resource had not been visible. The second was the ratio between the distance travelled without visual contact and the overall distance of the path. Under the assumption that visibility of the resources was important for the baboons, I expected (1) that resources that were visible over long distances were approached in a more linear way and faster than resources that became visible only from short distances, and (2) that resources that were visible for a large portion of the path were approached more directly and faster than resources that were visible for a small portion of the path.

Neither the distance travelled without visual contact to the resources (dry: b = -0.054, R2 = 0.001; wet: a = - 0.407, R2= 0.018, both p>0.05) nor the distance travelled without visual contact relative to the overall distance to the resource (dry: b = -0.107, R2=0.01, wet: a = 0.034, R2=0.001, both p>0.05; linear regressions) significantly affected directedness of the path segments. Thus, with respect to path linearity, the Kloof group approached resources that were visible over large and short distances in the same way.

Similarly, travel speed was not affected by visibility. The Kloof group moved at 17.8 m/min before visually perceiving a resource on average, and at 17.4 m/min afterwards. These values did not differ statistically from each other (paired t-test, df=145, t=0.774, p>0.05). This also applied when I tested the outward movements separately (df=87, t=1.009, p>0.05).

The above analysis has shown that many of the path segments during the first part of the dry season 2001 were significantly directed. This was the time when kooboo berries were available on the S and SW foot of the hill. I recorded a total of 34 visits to 18 kooboo berry bushes. 11 bushes (61.1%) were visited on a single occasion, 4 were visited twice (22.2%), and three bushes were visited on 4, 5 and 6 occasions each. Note that unlike the food sources in the plain, the distribution of kooboo berries was confined to a narrow area on the S and SW slopes of the hill.

Four of these bushes were situated in a small forest-like patch of approximately 1.5 ha in size on the SW slope of the hill, the 'sable forest'. The Kloof group returned to this place to feed on kooboo berries in the early mornings on 13 days between end of May and mid- August 2001, but visited alternative patches situated on the S slopes on the hill on other days in the same time period. The journeys to the sable forest led either directly across the hill, or followed the N foot of the hill. In addition, the study group sometimes approached it from South, after visiting a separate patch of kooboo berries (Figure 5.9). The 2D-distance from the sleeping site of the sable forest was approximately 1700 m, but it became visible only from a distance of maximally 200 m.

Figure 5.9. Paths to the sable forest (SF) in the early mornings on 13 days (black lines). Journeys either directly led across the hill, via the Southern kooboo berry patches, or along the N foot of the hill. Large dot. Sleeping site, smaller dots: kooboo berry bushes. Thick line: Visibility borders. Dashed lines: 20m contour lines. The figure only shows the paths leading to the bush first visited, and does not show how other kooboo berry patches were approached.
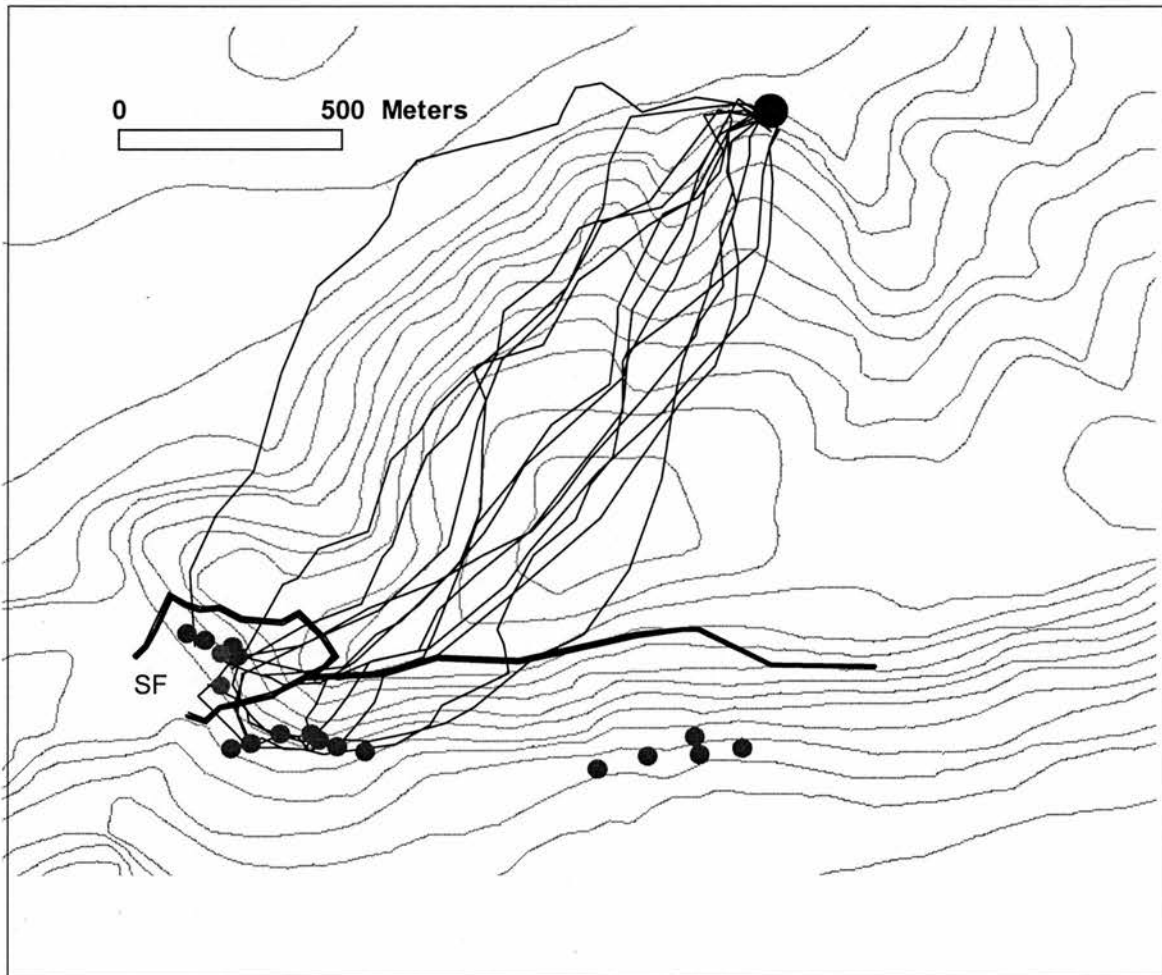
5.4. Discussion

With this chapter I have aimed to shed some light on the strategies the Kloof group used to find their resources, with an emphasis on the cognitive pro-

cesses which are minimally required to produce the observed movement patterns. I considered simple searching strategies such as random walking or strategic search, and the use of vision and spatial memory as possible means by which distant resources may be located.

The Kloof group predominantly walked in a directed way from one resource to the next in winter, but 40 % of their movements between resources were undirected in summer. Chapter 4 has already shown that this was partly due to the increased group density in the N plain, which forced the study group to take detour paths on many occasions. But it was also obvious that food was abundant during that time, allowing the Kloof group to forage widely dispersed, and to mainly travel-feed. As a consequence, I did not capture resource places that were smaller than those offering a reward to less than 3 animals for less than 2 min.

On the other hand, more than 80% of the paths between resources were directed in winter, and around 60% in summer, suggesting that mechanisms other than randomly walking around must be involved in the Kloof group's foraging. The bearings of the paths between resources were directed over large time periods, both during the journeys away from the sleeping site as well as when approaching it. In order to do so, the Kloof group must at least have remembered the approximate direction which they had travelled on days before when leaving the sleeping site, and must have been able to reverse this direction to reach the sleeping site in the afternoons.

The mountain fig fruiting season suggested that the Kloof group not only remembered an approximate course, but the exact bearing which they had taken on previous days (Figure 5.3. B). From the sleeping site, they headed towards a fig tree with identical bearing on 12 out of 13 mornings, and the bearing of the remaining morning deviated with only 5 degrees. The next chapter will reveal that this fig tree was not visible from the sleeping site. This is the second piece of evidence that the mountain fig season is of special interest for investigating cognitive mapping. I will do so in the following chapter.

On the other hand, I found evidence that vision may well be important to the Kloof group when the marula trees and knobthorn acacias were flowering. Evidence for this came from two sides. First, the bearings of the paths leading from one tree to the next were randomly distributed, and the next resources were situated within the distance from which they could be spotted by the keen baboon eyes.

This was also the case in January, when marula fruit became available in large quantities next to their sleeping site. However, distances walked to marula trees were well beyond the distances from which they could be seen in February and March, when the closer trees became depleted. This was the time when the Kloof group roughly walked towards NW during their outbound journeys, suggesting that they had at least mapped the approximate direction of additional marula fruit sources.

However, they also walked towards NW in the time when corkwood kernels and grewia berries became available later in the year, and then foraged in a similar area. Since marula, corkwood and grewia plants were abundant in the plain, but became depleted in the course of the season, remembering and then holding an approximate bearing and following a food density gradient could well explain the observed movement patterns.

There is some evidence that they may have remembered some particularly rewarding marula trees. First, the distances of the trees from the sleeping site was not a predictor of the number of visits to a particular tree. And second, revisited trees gave larger rewards on average than trees that were visited only on a single occasion. But I cannot exclude that the baboons remembered the approximate direction of previous rewards, and were attracted to the same large trees by vision whenever they passed by. The low frequency of revisits to particular marula trees supports the latter notion, and this argument also holds for the subsequent time periods, when corkwood kernels and grewia berries were available in the same area.

However, spatial memory must have been involved in finding the two highly limited resources in the plain, the two water holes. The previous chapter has revealed that the study group approached the water holes in very straight lines, unusually fast and over long distances. They did so in a flexible way, from many different directions. The present analysis shows that they did so long before they could see any proximate cues that were associated with them, such as the high baobab and nyala trees. Locating places without

perceiving associated landmarks fits the strictest of definitions for cognitive maps, sensu Tolman (1948) and O'Keefe & Nadel (1978). This certainly warrants further investigation. I will therefore examine the paths leading to water holes in more detail in chapter 8.

Evidence for spatial memory also comes from the Kloof group's ranging on the hill, where I knew visibility of each resource individually. On one hand, visibility altered neither path linearity nor travel speed, suggesting that direct visual stimuli from the resources played at most a subordinate role. Also, the Kloof group repeatedly visited a small and remote area on the hill to feed on kooboo berries, the sable forest. The area was not visible to them for the most part of their journey, but they approached it in a flexible way, either by walking across the hill, by approaching it from other kooboo berry patches situated to the South, or by following the N foot of the hill. Since repeated visits to a small, hidden food patch is strong evidence for cognitive mapping, I will investigate the journeys to the sable forest in more detail in chapter 8, together with those to the water holes.

Chapter 6 Travelling among multiple destinations

6.1. Introduction

The previous chapters have revealed that many baboon food trees at Blouberg were abundant over large areas of their range, such as marula trees and grewia bushes. The specimens next to the sleeping site became depleted in the course of time, so that the animals needed to visit a more distant, but large area where these resources occurred in large quantities. I have proposed that to find them, the baboons minimally needed to memorise an approximate bearing that they had travelled before. Other resource sites such as kooboo berries or water holes were confined to a few small areas. But these areas yielded large rewards, so that only one or two of them needed to be visited per day. The high frequency of revisits to these areas as well as the flexible way by which they were approached suggested that the Kloof group had memorised their exact locations.

However, the distribution and size of reward of some resources at Blouberg differed from those investigated so far. Mountain fig trees (Ficus glumosa) were comparatively rare, and each tree only offered a few ripe figs per visit to each animal. As a consequence, the study group visited several distant trees in quick succession on a given day. Chapter 4 and 5 have revealed that their ranging patterns during the mountain fig season differed from those at other times of year. Path linearity was unusually high and there was evidence that the day-to-day movements were repetitive. In this chapter I will now examine the ranging patterns during the mountain fig season in more detail.

The question as to how animals travel among multiple destinations has been of considerable interest in recent years (reviewed in Janson, 2000). This task is far from being trivial. On one hand, the overall travel distances are to a large extent affected by the order in which destinations are visited. On the other, destinations may differ in reward or other intrinsic features, and remembering past experiences may be necessary for optimising the overall energy gain.

Interestingly, there is no simple mathematical algorithm available to date which guarantees computation of the shortest path between many points in two dimensions (Janson, 2000). This has led to the notion that animals and humans adopt 'satisficing' rather than optimal solutions to the problem; that is, accepting solutions which are 'good enough' to survive and reproduce rather than necessarily optimal (Simon, 1981; Chown, 1999b). This consideration has been the basis for developing several hypothetical 'rules of thumb' that animals and humans alike may apply when consecutively visiting multiple destinations. For example, 'always visit the nearest tree', the simplest possible rule of thumb, has produced fairly short travel distances among several goals in computer simulations. Other rules take the amount of gained energy at each destination into account, in addition to travel distance (reviewed in Janson, 2000).

There is evidence that primates make efforts to reduce their travel effort when walking among multiple destinations in the lab. Chimpanzees *(Pan troglodytes,* Menzel, 1978) and vervet monkeys *(Cercopithecus aethiops,* Gallistel &

Cramer, 1996; Cramer & Gallistel, 1997) were tested in the 'travelling sales-
man' task. They were allowed to observe an experimenter hiding food items in
their enclosures, and then were released into the area. Test animals of both
species did not simply follow the route the experimenter had walked to hide
the rewards, but tended to minimise the overall distance travelled. When larg-
er rewards were hidden on one side of the enclosure, both chimpanzees and
vervets first visited the larger patches, and left the side with the smaller re-
wards for later. The vervets seemed to apply a nearest-neighbour rule. How-
ever, in one of the experiments, they were given the opportunity to minimise
their overall distance when visiting a further location first, and waited with
visiting the nearest neighbour for later. They did so in 20 of the 26 trials. The
results suggested that that vervets are able to look ahead not only to the next,
but to the second next step of their journey, and thus to 'plan' a simple route.

Also, the above experiments revealed an interesting difference between the
chimpanzees and vervet monkeys. Whereas the chimpanzees found up to 18
hidden food items, the vervets found maximally 6. Cramer & Gallistel (1997)
therefore proposed that monkeys and apes dramatically differ in the amount
of information they can keep in mind at a time.

On the other hand, field workers always felt that monkeys memorise large
numbers of out-of-sight locations (Milton, 1981; 1988; 2000; Garber, 1988;
1989; Menzel, 1991; Janson, 1998), but hard data that support this notion are
scarce. The best evidence so far comes from capuchin monkeys (*Cebus
apella*, Janson, 1998), who travelled between 15 artificial feeding sites in a

way suggesting that they had memorised their locations (but see discussion of this experiment in section 5.1.). They strongly preferred to visit nearest-neighbour platforms, and favoured resources with larger amounts of food over such with only relatively small rewards.

Also, moustached *(Saguinus mystax)* and saddleback *(Saguinus fuscicollis)* tamarins in the lowland forest of Peru travelled among 10 flowering manil trees *(Symphonia globulifera)* in a way that suggested goal-directedness (Garber, 1988). They visited 2-8 trees per day, and kept travel distances short. They visited the nearest manil tree in 86%, and the second nearest tree in 3% of the cases, suggesting that they may have applied a 'nearest-neighbour' rule to a large degree. In the remaining 11% of the feeding bouts, however, distance between trees did not affect the choice of the feeding sites. In these cases the tamarins bypassed the nearest trees, but visited preferred trees that were situated further away and yielded larger amounts of nectar.

In both of the above studies, it remains open as to what degree the decisions of the monkeys were based on memory, and to what degree they foraged at sight. However, they suggest that the nearest-neighbour rule seems to have some validity, and that previous experiences at rewarding locations additionally influence their choices.

The above proposed strategies for finding food in natural environments are highly sophisticated from a cognitive point of view. Flexibly applying a near-

est-neighbour rule to out-of-sight resources requires a capacity to represent all resource places at a time, and to compare the distances to each destination at any location. Rules of thumb that take differential patch size into account implicitly assume that animals are able to remember the past experiences at all places in addition to travel distance, and then to choose among the best options. Whether animals and humans have the corresponding cognitive prerequisites for doing so needs to be critically reconsidered.

In this chapter, I examine how the Kloof group travelled among multiple destinations during the mountain fig season. I do not wish to explicitly test any of the proposed rules of thumb, but simply ask whether the observed movement patterns can be explained by simpler cognitive mechanisms, such as a thorough knowledge of only a few resource places. I therefore examine path flexibility and hypothesise that multi-destination routes are learned rather than subsequently integrated. Also, I investigate whether all destinations were purposefully approached, and whether the study group anticipated their goals well before they could see them.

6.2. Methods

Since the start of data collection in May 2001 I had recorded the locations of 50 mountain fig trees *(Ficus glumosa)*. This was likely to be the whole population that was present in the Kloof group's home range. Mountain figs became highly attractive to the baboons during a 3-week period between late Decem-

Table 6.1. Distribution of observation time during the mountain fig season.

	Number of days	h of observation
Whole days	7	78.8
Half days	5	31.0
Fragments	1	1.5
Total	13	111.3

ber 2001 and early January 2002. During that time, I followed the study group on 13 days for a total of 111.3 hours. Table 6.1 indicates how observations were distributed over the days.

I examined the visibility of all fig specimens by the 'plastic bag method', as described in section 5.2. for the resources on the hill.

The Kloof group did not feed from all the fig trees they encountered through-out the day. I therefore distinguished between 'approaching', 'passing by' and 'visiting' a fig tree, by looking post hoc at each of the recorded paths relative to the distribution of the trees. An approach was scored when the recorded path came within 30 m of a specimen, regardless of whether this was followed by a visit or not. I scored a 'visit' when at least three animals started feeding from a specimen. When this criterion was not fulfilled, I scored this tree as 'passed by'. For calculating the approach rate to fig trees, I counted the num-ber of approaches per h, after discounting the time during which the study group was stationary from total observation time (e.g. rested, or fed at a resource).

Table 6.2. Identity and percentage of first and second food type consumed on 36 mornings before, during and after the mountain fig season. ♦ = abundant food types. See Appendix 1 for common names of the food plants.

before		during		after	
B. albitrunca ♦	29.2%	F. glumosa	100%	S. birrea ♦	70.8%
M. accuminata ♦	25%			H. monopet. ♦	12.5%
Ximenia spp ♦	8.3%			F. tettensis	8.3%
G. livingstonei	8.3%			F. glumosa	8.3%
F. tettensis	8.3%				
F. glumosa	8.3%				
E. magalismont.	4.2%				
Insects ♦	4.2%				
A. anthelmintica ♦	4.2%				

Under the assumption that the study group anticipated which resources they were going to visit when still at their sleeping site, I expected the onset of the journeys to depend on the abundance of the food types subsequently visited. I therefore investigated the abundance of the first two resource types visited in the early mornings prior, during and after the mountain fig season. Table 6.2. reveals that on 12 mornings before the mountain fig season (mid-November to mid-December), the Kloof group visited a wide variety of food types, and showed no preference for any particular food sources. On 12 mornings after the fig season (early January - early February), they mainly visited marula trees (Sclerocarya birrea), which were abundant. Mountain figs were the only limited food source during that time. I therefore hypothesised that if the ba-

boons anticipated where they were heading to, they should leave the sleeping site early when foraging for mountain figs, and later when they were foraging for more abundant food types.

I defined departure time as the time when the last animal had left the sleeping site area, accurate to 5 min. A failure of the tape recorder prevented me from unambiguously reconstructing departure time on one day. I therefore discarded this day from analysis.

Departure time from the sleeping site is likely to depend on the time of sunrise. I therefore used the NewMoon software, which allowed me to compute time of sun rise at the coordinates of a prominent rock situated immediately above the sleeping cliff. I then defined departure latency as departure time relative to sun rise.

Temperature is also likely to affect the onset of the journeys in the mornings. For example, it was evident that the animals left the sleeping site early during the hot summer months, and rested in the shade around midday. In contrast, they rested well until the sun had risen after cold winter nights, and then abstained from resting during the day.

Therefore, I performed an Ancova, with departure latency as dependent variable, day temperature as a regressor and abundance of food type as a factor. All other statistical tests were two-tailed, except a single exception which is mentioned in the text.

6.3. Results

Mountain fig trees were confined to the North-facing slopes of the hill, and occurred in an area of approximately 1.6 x 1.2 km within the baboons' home range. Figure 6.1 also shows the locations of the sleeping sites of 4 neighbouring baboon groups. Although I was unaware of the home range sizes of these groups and the distribution of additional mountain fig trees therein, it was evident that not only the study group, but also their neighbours were attracted to the fig trees.

Members of the Kloof group, mainly juveniles and subadult males, sometimes visited either of two figs which were situated within the sleeping site area in the early mornings. These figs seemed to be of little attractiveness to the remainder of the group.

The baboons climbed the hill in the early mornings, and first visited a series of figs they could not see from the sleeping site. They chose a highly repetitive route to these figs on all 13 days of observation (Figure 6.2.). From the sleeping site, this route led the animals towards South, and at fig B turned West. Shortly before arriving at the two figs F, their movement patterns became more variable. This was the point when the animals switched their feeding strategy. They exclusively fed on figs while travelling on the repetitively used route, but later intermittently visited patches of abundant grass corms *(Brachiaria spp)*, or milkplums *(Englerophyum magaliesmontanis)*, for example. In the course of the day, the animals sometimes visited the flat area in the

Figure 6.1. Distribution and inter-visibility of 50 mountain fig trees *(Ficus glumosa)*. Dots represent the locations of all known specimens. Black lines connect those specimens which were inter-visible. Fig A and D were visible from each other, but Fig C was only visible from Fig D, and not from Fig A. Grey lines are 20m contour lines. Grey area: sleeping site area of the Kloof group. Triangles: sleeping sites of four neighbouring baboon groups.
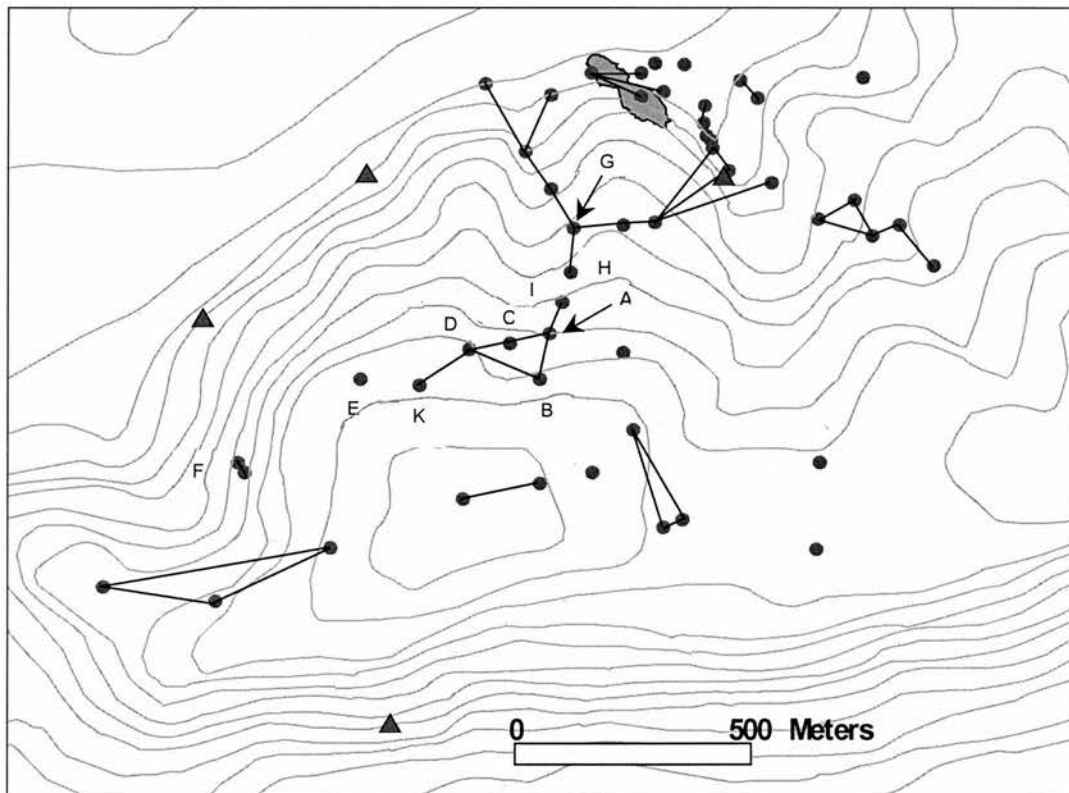
vicinity of their sleeping site. In the following, I will refer to the repetitively used path as 'the route'.

In addition to the two fig specimens that were situated within the sleeping site area, 10 mountain fig trees were situated along the route. The baboons did not visit all of them but only 2 - 4 specimens per morning (Table 6.3.).

Figure 6.2. Baboon ranging patterns on 13 days during the main fruiting season of mountain figs. B and F refers to the labels of two figs in Figure 6.1.
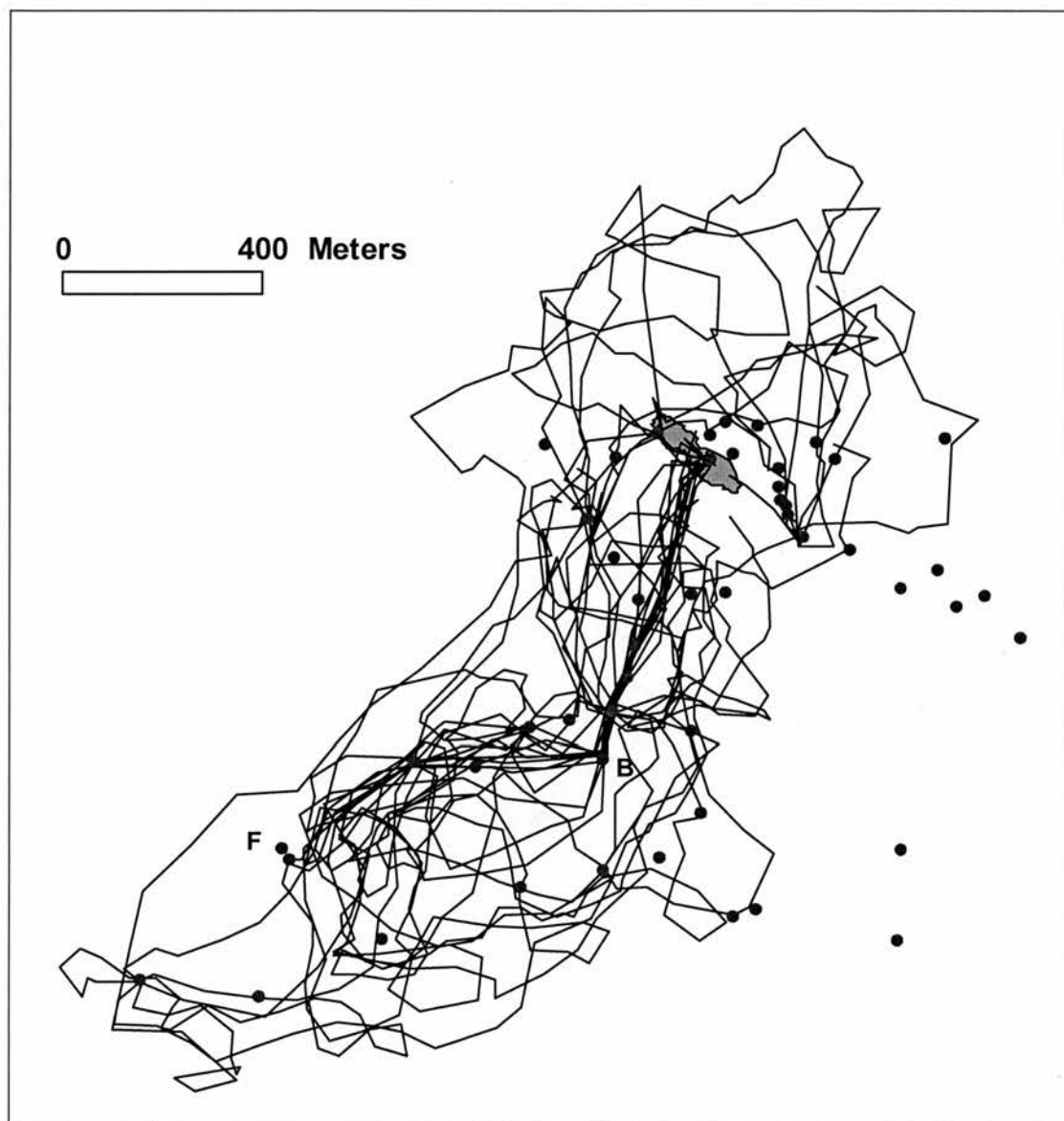
Table 6.3. Total number of visits to each of the 10 mountain fig specimens A - K along the route, number of visits in the early mornings, total feeding time (number of animals x time spent feeding), average feeding bout length ± SED and number of instances when trees were bypassed at a distance of maximally 30 m.

Fig	A	B	C	D	E	F	G	H	I	K
Total no of visits	19	9	1	4	10	2	0	2	1	1
No of early visits	13	9	1	4	9	2	0	2	1	1
Total feeding time (min)	384	178	37	76	258	30	0	48	5	19
Mean bout length (min)	20.2	19.8	37.0	19.0	25.8	15.0	-	24.0	5.0	19
SED	8.4	9.5	-	10.9	17.0	9.9	-	26.9	-	-
Bypassed	3	2	3	3	4	3	11	11	18	9

During the 7 days of data collection throughout the day, the Kloof group visited 8.0 ± 1.9 figs per day on average. Visits were confined to 27 (54%) of the 50 known specimens. 7 of the 23 unvisited trees were situated outside their ranging area during the fig season (Figure 6.2.). The remaining 16 specimens were sometimes approached, but then bypassed.

Total foraging time on the hill was 97 h. During that time, the study group approached 2.7 ± 1.4 figs per hour on average. In order to estimate how many approaches resulted from chance, I calculated the number of approaches to figs during 13 randomly chosen days prior to the fig season (August - October 2001), when the baboons foraged for other food types and showed no interest in figs at all. This resulted in an approach rate of 1.5 ± 0.4 mountain figs per h. I took this as a base-line value which was likely to occur by chance when

Figure 6.3. Approach rate to figs outside fig season, on and off the route (A), path linearity (B) and travel speed (C) on and off the route. Star: significant difference from base-line value.
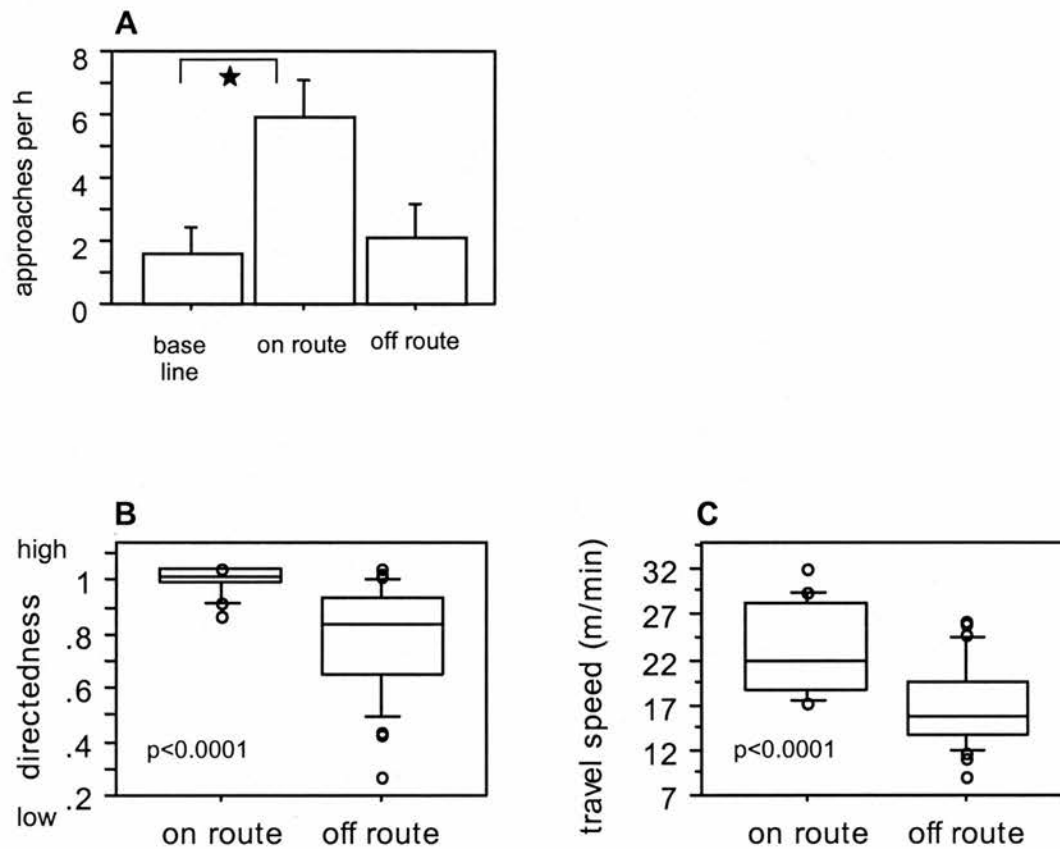
foraging on the hill. Subsequently I compared this value with the approach rate during the mountain fig season.

Significantly more fig specimens were approached during the fig season compared to the 13 days outside the fig season (unpaired t-test, t=-3.103, df=24, p=0.0048; Figure 6.3.). This was mainly due to the high approach rate to the figs on the route, which was 5.9 ± 1.2 approaches per h. In contrast, the approach rate to the figs off the route was only 2.1 ± 1.1 per h. I therefore

performed an Anova with the base-line approach rate, the approach rate to figs on the route and the approach rate off the route as factors, and then investigated whether the approach rates to figs on and off the route differed from the base-line value by means of the Dunnett test (Zar, 1999). This revealed that only the approach rate to the figs on the route significantly differed from the base-line value, but not the approach rate to the figs off the route (Anova: df=2, MS=77.626, F=76.711, p<0.001, Dunnett test: mean diff$_{(on route)}$=3.812, p<0.05, mean diff$_{(off route)}$=-0.501, p>0.05).

Also, ranging patterns on and off the route differed markedly (Figure 6.3). When following the route in the early mornings, travel speed was 25.4 ± 3.4 m/min on average, with approximately $^2/_3$ of the journey leading steeply uphill. As soon as the baboons left the route, travel speed dropped to 14.5 ± 2.8 m/min on average. Both path linearity and travel speed were significantly higher on the fixed route, and dramatically decreased off the route (unpaired t-tests, df=48, t=4.628 and t=9.635 respectively, both p<0.0001). Thus, both the approach rate and the ranging patterns suggest that the searching strategy for figs on and off the route markedly differed, and that the figs off the route were probably approached by chance.

In order to examine whether this resulted from differential reward provided by the figs on and off the route, I investigated their reward sizes (number of animals x time spent feeding). Overall reward size was 22.5 ± 15.8 min per fig on average, ranging between 4 and 91 min. Reward size on the route was 21.1 ± 11.7 min (n=51 visits), and reward size off the route was 24.5 ± 20.4 min on

Figure 6.4. Size of reward from figs on and off the route significantely differed in variability.
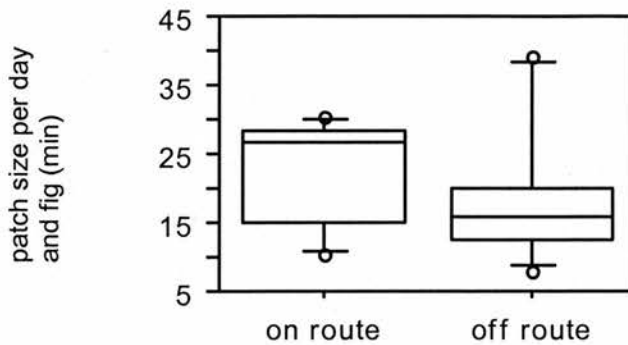
average (n=33 visits). This difference was statistically insignificant (unpaired t-test, df = 80, t=-0.938, p>0.1). However, only 1 out of 10 trees on the route, but 14 out of 33 trees off the route remained unvisited over the whole mountain fig season.

I performed a variance ratio test (Zar, 1999) to examine whether the variability of reward sizes on and off the route differed. This difference was highly significant (s_1*s_1=137.818, df=48, s_2*s_2=415.818, df=32, F=3.071>$F_{(0.001, 30, 45)}$, p>0.001). Note that I approximated F_{crit} by using df_2=30 and df_1=45 instead of the true degrees of freedom, because the table presented in Zar (1999) does not list the exact degrees of freedom of the two samples. Thus, the reward from figs on the route was more constant, whereas the reward from figs off the route was more variable (Figure 6.4.).

I suspected that this difference was due to resource depletion, caused by other groups who had already visited the figs off the route by the time the

study group had arrived. Therefore, I plotted the distance travelled by the Kloof group relative to the distance that all neighbouring groups could potentially have covered in the same time (Figure 6.5.A, B, and C). By doing this, I assumed that departure times from the sleeping sites as well as travel speed were approximately equal for all groups.

This revealed that by the time the Kloof group had arrived at fig K approximately, all other figs in their home range were likely to be visited and depleted by the neighbouring groups (Figure 6.5.C).

In order to examine to what degree the visit of a baboon group decreased the patch size for subsequent visitors on a given day, I investigated reward of those figs which the Kloof group had visited twice the same day (n=9). The time between leaving and revisiting a specimen later that day ranged between 115 and 526 min. During the first visits, resource size was 23.9 ± 8.4 min on average. It decreased to 13.2 ± 9.1 min during the second visit. This difference was significant (one-tailed paired t-test, df=8, t=2.46, p<0.02), suggesting that after a visit of a baboon group, the reward for subsequent visitors was significantly decreased (Figure 6.6.).

Finally, I addressed the question as to whether the study group anticipated their destinations. On the 36 mornings examined, the Kloof group's average departure latency (departure time relative to sun rise) was +18 min, ranging between +104 and -20 min.

Figure 6.5. Distance and direction travelled by the study group (arrow) relative to the area within which other baboon groups potentially foraged simultaneously (black circles). Small dots: Mountain fig trees. Large dots: Sleeping sites of study group (within grey area) and four additional baboon groups.
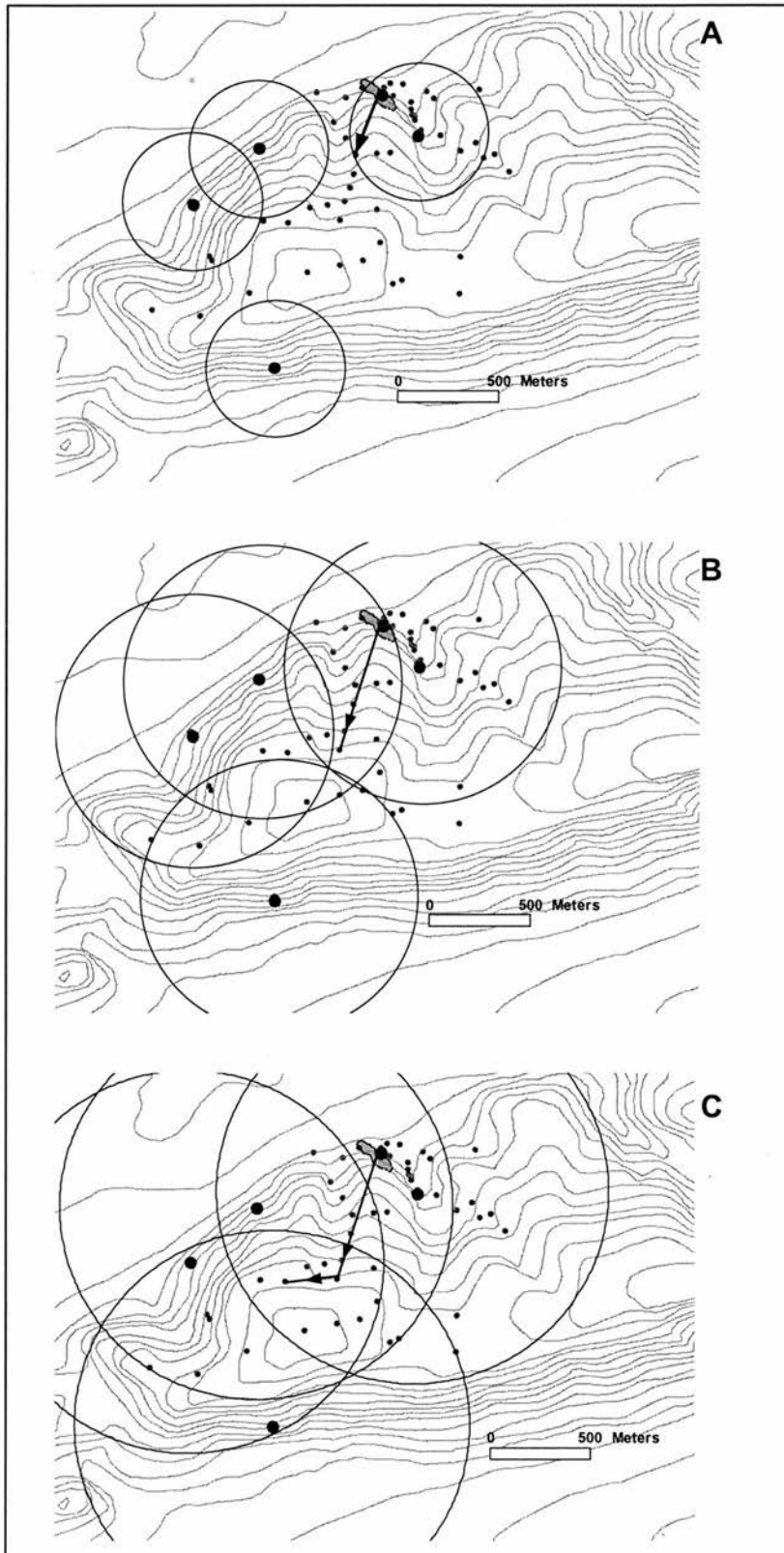
Figure 6.6. Size of reward from fig specimens that were visited twice the same day (n=9).
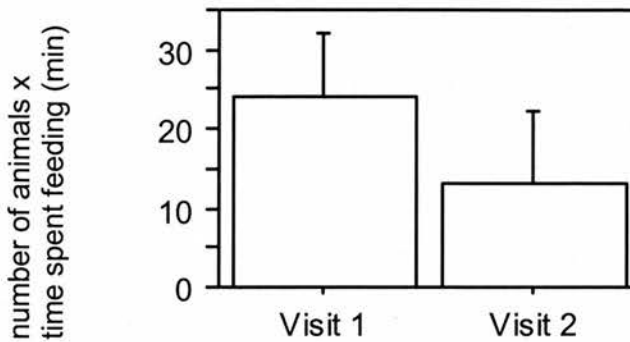
Figure 6.7A. shows that day temperature was a good predictor of departure latency. However, on a single day, departure time was exceptionally late (104 min after sun rise).

The behavioural records revealed that the Alpha male had given several roar-grunts, and had herded the females that morning. Usually, roar-grunting and herding only occurred in the close presence of another baboon group. This suggests that this morning was exceptional, and that a neighbouring baboon group delayed the onset of the study group's journey. I therefore performed two Ancovas, one including this morning, and one excluding it (Figure 6.7. A and B, Table 6.4).

Figure 6.7. Departure latency, maximum day temperatures and the abundance of the first two resources visited in the mornings. Bare circles: Departure times when next food sources were abundant (see text). Black circles: Departure times during the mountain fig season. A. Delayed departure on one morning included, n=36. B. Delayed departure excluded, n=35.

A

B
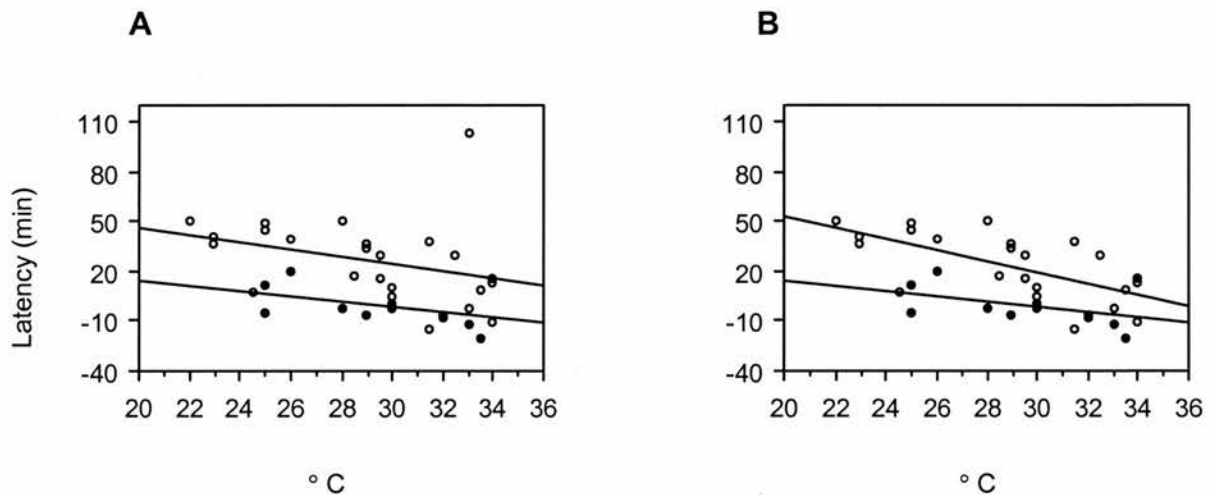
The relation between maximum day temperatures and departure latency was negative, suggesting that the study group departed earlier from the sleeping site on days with higher maximum temperatures (Figure 6.7). This effect was significant only in the analysis without the delayed departure (Table 6.4.). Also, departure latency was shorter before visits to scarce mountain figs, and longer before visits to abundant food sources. This result was apparent in both analyses, with and without the delayed departure. The fact that the interaction between temperatures and food abundance was not significant suggests that these two measures were not related to each other. Departure latencies before and after the mountain fig season did not differ from each other when the delayed departure was included (unpaired t- test, df=22,

Table 6.4. Results of Ancova with (n=36) and without outlier (n=35) for departure latency, with temperatures as a regressor and abundance of resources visited as a factor.

Ancova	Independents	F	p	Power	Fisher's PLSD
outlier included	abundance	0.402	0.53	0.092	p=0.0007
	temperatures	2.468	0.13	0.32	
	abund * temp	0.062	0.81	0.06	
outlier excluded	abundance	2.65	0.11	0.34	p<0.0001
	temperature	9.74	0.004	0.87	
	abund * temp	1.363	0.25	0.19	

t=0.706, p>>0.05), but there was a trend for earlier departure times during the marula season when excluding the outlier from analysis (df= 21, t=1.897, p=0.073).

6.4. Discussion

In this chapter I have examined how the study group travelled among several mountain fig trees *(Ficus glumosa)* with each tree only providing a relatively small reward. In particular, I examined whether they approached all trees purposefully, and anticipated their goals well before they could see them.

This analysis suggests that the animals had memorised the locations of at least some of the 50 fig trees available in their home range. The most obvious feature of their ranging was a repeatedly used, static route along which several fig specimens were situated. Inter-visibility of the specimens along this route seemed to be unimportant, suggesting that the animals did not forage at

sight, but on the basis of memory. Travel speed and path linearity along this route were high, and the trees along this route were visited with a frequency that significantly differed from chance. This suggests that these trees were approached purposefully, in a goal-directed way. Furthermore, the unusually early departure time from the sleeping site when visiting these out-of sight figs suggested that the study group represented these figs when still in their sleeping site, and was well aware of the relative scarcity of this food type. Although I could not directly show that they anticipated the exact nature of the resources they were going to visit, these findings suggest that baboons anticipate events that will take place in the near future.

However, the study group's searching strategy for figs dramatically changed in the course of the mornings. Path linearity and travel speed dropped at the end of the repetitively walked path, and the approach rate to the remaining figs suggested that the baboons approached them incidentally.

The most conservative interpretation of this finding is that the study group knew how to approach a small number of fig specimens, and did so by following a well known route. They were unaware of how to find additional specimens, but encountered them sometimes by chance. As soon as they had visited all memorised specimens, they started to feed on alternative food types that were available both on the hill and in the plain. This is consistent with the finding of Cramer & Gallistel (1997), who proposed that monkeys only store a small amount of information at a time.

However, the task the vervets were confronted with in the lab differed from the task of the study group when travelling among mountain fig trees. The vervets needed to find food items that were hidden at different locations in a small enclosure which could be seen at a glance. The Kloof group, in contrast, needed to find fig trees in a large area of their home range, and only some, but by far not all trees were inter-visible.

An alternative interpretation becomes plausible when taking inter-group competition for the scarce mountain figs into account. The dramatic change of the Kloof group's behaviour when searching for figs coincided with the time when all remaining figs were likely to be depleted by other groups. As a result, the study group was likely to have only limited interest in visiting the remaining specimens, because their reward was uncertain. Unpredictability of resources potentially shifts the ratio between travel costs and nutritional gain towards less favourable outcomes, especially when travel costs are comparatively high. Switching to other food sources when all predictable resources are visited is therefore more favourable, especially in times when alternative, predictable resources are widely available.

Supportive evidence for this latter interpretation came from two sides. First, the value of the figs off the repetitively walked route was more variable, whereas that of the figs on this route was relatively constant. And second, the reward of figs that the Kloof group visited twice a day was decreased in the second visit, compared to the first, when measured in terms of actual feeding time. Thus, mountain figs seem to be depletable. The variability in reward of

the figs off the route is likely to result from visitors that had used these figs earlier in the mornings.

Risk-sensitivity seems to be a fundamental phenomenon in the foraging decisions of most invertebrate and vertebrate species investigated so far (reviewed in Kacelnik & Bateson, 1996). When given the choice between two rewards, one of constant and the other of varying amount, the animals choose the constant option with very few exceptions, even when the amount of the two classes of rewards over time is exactly the same. In other terms, they are risk-averse. To date, the learning and evolutionary processes that underlie risk-aversion are vividly discussed (reviewed in Bateson & Kacelnik, 1998), but conclusive explanations are still lacking. Little attention has so far been given to this phenomenon in studies on primate ecology and cognition.

In summary, I have found that the study group travelled among several fig trees in a static, rather than in a flexible way. They used a well known route to reach some of the available trees, and visited the remaining trees in a way that suggested incidental, rather than purposeful encounters. This contrasts sharply with the notion of a detailed Euclidian cognitive map, but is consistent with the concept of a network map (Byrne, 1978; 2000).

However, the pronounced inter-group competition for mountain figs may have hindered a better insight into the cognitive processes of the study group. The fig trees in their home range seemed to be attractive only for a short time period in the mornings before they became depleted. Following a well known,

least-effort route may be the best option when under time pressure. Whether the Kloof group decided against visiting unpredictable fig trees in favour of alternative food sources, or whether they had not learned the locations of unpredictable resources remains open to speculation. Risk-aversion certainly warrants further investigation in future studies of primate spatial knowledge.

However, I found that the study group departed earlier from the sleeping site when foraging for scarce mountain figs than when foraging for more abundant food sources. This suggests that they were aware of the limited time during which mountain figs were available in the mornings, and thus, were planning at least the first part of their journeys.

Chapter 7 Path flexibility after unexpected disruptions

7.1. Introduction

In each of the previous chapters, I have intended to identify the simplest cognitive mechanisms for orientation that are necessary to explain the movement patterns observed in the study group. This has revealed that the baboons may have foraged at sight under certain conditions, but needed to have memorised at least the bearings or routes to resources in others. However, I have not yet explicitly addressed any questions about the nature of their cognitive maps.

In the past, several researchers have emphasised that there is only a single way to prove that animals posses the ability to compute Euclidean relations between locations. To be credited with such a powerful cognitive tool a subject must be able to perform adequate new routes under novel conditions, that is, to choose the most economical alternative path, such as a shortcut or a detour (Tolman, 1948; O'Keefe & Nadel, 1979; Dyer, 1991; 2000; Etienne et al., 1999; Byrne, 1978; 2000). Thus, a navigator possessing a vector map can plan a goal-directed path at his current location by deducing a new itinerary from the memorised spatial relationships between different locations, without the help of continuous landmark guidance.

The experimental approach to this problem has consisted of depriving the animals from seeing familiar landmarks. For example, bees have been conditioned to fly from a hive to a feeder, and then were captured and

released at a new location (Gould, 1986; Wehner & Menzel, 1990; Dyer, 1991; see chapter 1 for more detailed discussion). They failed to find the feeder when previously learned landmarks were unavailable to them. Similarly, rats were unable to swim to a hidden platform in opaque water in a maze when they were prevented from seeing the landmarks that were visible from the platform (Benhamou, 1996; see chapter 1). This was taken as evidence that neither bees nor rats possess mental representations of space isomorphic in spatial properties to the real world.

The concept of 'network maps' has been developed to explain the errors that humans commit when asked to estimate distances and angles of roads in a well known urban environment (Byrne, 1978; 2000). The test subjects were well aware of the topological connectedness of routes and their relative bearings at intersections. However, the route length estimations depended on the complexity of the surroundings and the number of turns in that route. Road angles were categorised in a surprisingly simple way: All angles in the range between 60° - 120° were remembered rather precisely as right angles. Byrne (1978; 2000) therefore proposed that the mental representations of humans who need to find their ways in an urban environment do not resemble vector maps which encompass Euclidean relations between objects, but are based on interconnected strings of codes (eg. turn right at the post office, then walk straight on, at the library turn half right, etc) that form a tight representational network. Thus, a network map contains the topological relations among locations, but lacks precise information about distances and angles.

Implicit evidence that wild primates have network map representations comes from a variety of path descriptions in the literature. For example, howler monkeys appear to use 'arboreal pathways', that is, frequently travelled routes which connect important feeding areas (Milton, 1981; 1988; 2000). The frequent use of 'street segments' which Stolba (1979) identified to analyse the routes of hamadryas baboons, and the regular and repetitive movement patterns of olive baboons (Ransom, 1981) also point towards the conclusion that these primates represent space in a network map. However, these descriptions do not necessarily exclude the possibility that primates also have vector map spatial representations.

A promising, but largely neglected approach to the problem of examining the nature of cognitive maps in animals consists of deliberately manipulating their familiar routes. The idea behind this is that cognitive mechanisms should come to light when animals need to adjust their behaviour to unexpected events en route. I base this chapter on route manipulation in order to examine the nature of the cognitive maps of my study group.

Chapter 3 has revealed that path linearity of the Kloof group depended, among other things, on the distance to groups of conspecifics. This was due to the fact that the animals avoided other groups, a common behaviour among chacma baboons (Anderson, 1981). I therefore view group encounters as natural experiments which forced the study group to leave their paths, and to find alternative ways to reach their resources. I hypothesise that the alter-

native paths should exhibit characteristic patterns according to different mechanisms of orientation, such as network maps and vector maps.

7.2. Methods

Figure 7.1. summarises the evasive manoeuvres I predicted under different cognitive mechanisms of orientation. My initial null hypothesis was that the study group had no spatial knowledge and therefore never aimed at any particular resource places. Under this assumption I expected them to leave their path as soon as they encountered another group, and to visit resource types other than those steered at initially (scenario A in Figure 7.1.).

In chapter 5, however, I proposed that the memory of an approximate bearing can explain the movement patterns to the abundant food sources in the plain, for example to marula and corkwood trees. If I was right, and that was the extent of their navigational ability, then the study group should leave their initial path after encountering another group, and then resume their bearing, so that their new path lies parallel to the path travelled before (scenario B). I expected to predominantly find this scenario when the Kloof group travelled away from their sleeping site, because of the absence of distant landmarks in this situation (see below).

If the study group had memorised single routes, as suggested in chapter 6 for the visits to some of the mountain fig trees, I expected them to bypass the danger, and then to resume their initial path to the resources (scenario C).

Figure 7.1. Hypothetical evasive manoeuvres, A without any spatial knowlege, B when remembering an approximate bearing, C+E when navigating by means of a network map, and D when navigating by means of a vector map sensu Tolman (1948; Byrne, 1978; 2000) and O'Keefe & Nadel (1979). Slim arrows: direction of movement; Bold arrow: direction from which danger emerges; Circles: resource type initially steered at; Triangles: alternative resource types.
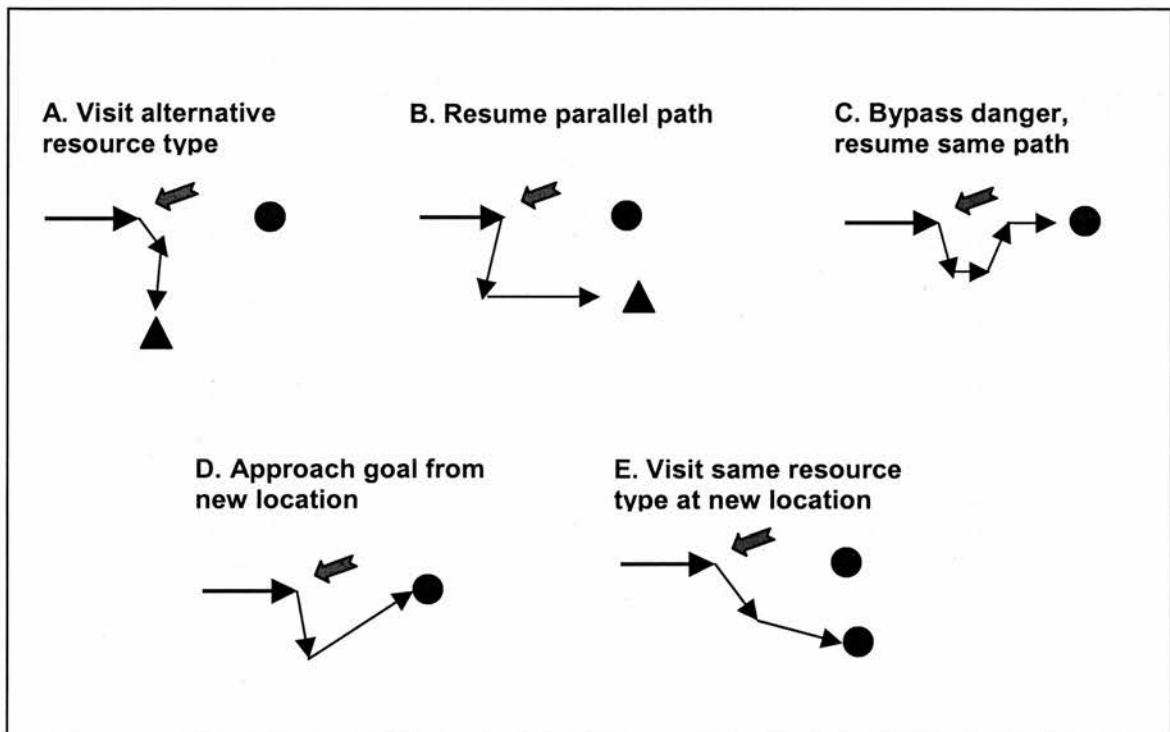
Similarly, a network map (Byrne, 1978; 2000) would tie them to the chosen routes, and I expected to find scenario C also under this assumption. However, network maps allow for more flexibility than memory of single routes. At each intersection of the paths within the network, several strings of 'commands' become available which can guide the movement to alternative resources. This should result in visits to alternative resources that are equally high in quality as the resource that was initially steered at (scenario E).

Figure 7.2. Distant landmarks in the plain were entirely lacking during the movements away from the sleeping site (A). The hill was a prominent landmark at all locations during the movements towards the sleeping site (B).
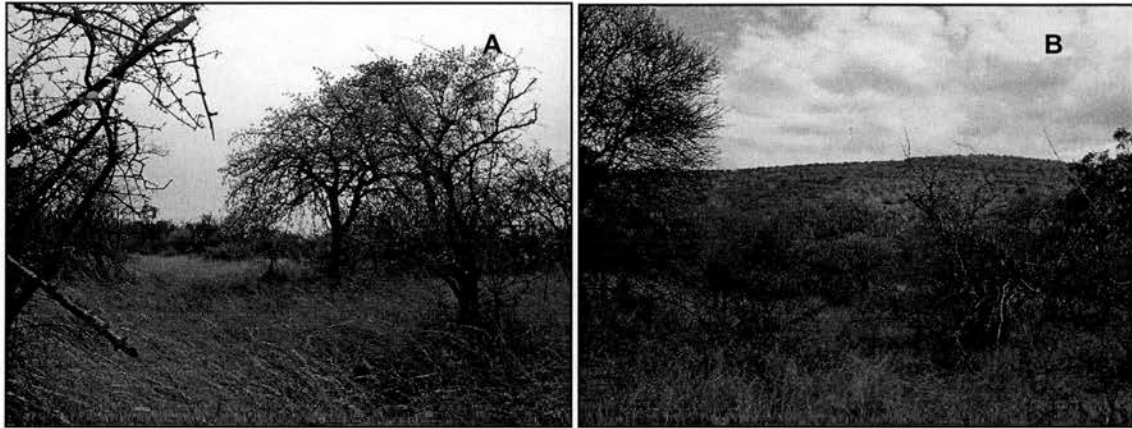
Only vector maps sensu Tolman (1948; Byrne, 1978; 2000) would allow the animals to approach a resource in a straight line from any new location, where they found themselves after an evasive manoeuvre (scenario D).

According to the definition of Tolman (1948) and O'Keefe & Nadel (1979), vector maps can only be proven when animals take novel shortcuts in the absence of permanent landmarks which potentially guide their movements. In the home range of the Kloof group distant landmarks were entirely lacking during the N-bound movements in the plain, when they were moving away from the sleeping site. During those movements, the crowns of trees and bushes built a comparatively monotonous horizon, but no other landmarks were visible (Figure 7.2.A). In contrast, the hill was a prominent distant

landmark during the inward movements. Although the sleeping site was not directly visible, the hill could have indicated the approximate bearing of the sleeping site from any location. Therefore, I expect supporting evidence for a vector map if scenario D occurred during the outward movements.

When the study group unexpectedly met a group of conspecifics at close distance, the females usually reacted in fear, by screaming and running into the opposite direction of the conspecifics. The alpha male usually roar-grunted, then followed his females, and sometimes herded them at a distance. The reaction was less pronounced when other groups were more distant. Based on their vocalisations, ie screaming and roar-grunting, I suspected that similar behaviours occurred in the other groups.

I therefore identified evasive manoeuvres by visually examining all recorded paths for pronounced changes of direction. I viewed a directional change as a response to the presence of another baboon group, when either the other group had vocalised at close distance (100 - 300 m), when the alpha male of the study group had given roar-grunts, or when he had herded his females.

Since many group encounters occurred in the vicinity of the two water holes in the plain, I examined their visibility by means of the 'plastic bag' method (see methods section in chapter 5) in austral winter, when visibility was largest. In addition, I recorded how far the tall nyala and baobab trees that were associated with them were visible. For this purpose, I walked in a large circle around the water holes and took GPS waypoints at small time intervals, so that the

enclosed area represented the maximal area within which these trees could be seen when walking on the ground.

7.3. Results

I identified a total of 34 evasive manoeuvres which occurred on 29 days between May 2001 and July 2002 (Table 7.1). Interestingly, I did not find any evasive manoeuvres during inward movements on the hill. This was partly due to the comparatively low vocalisation rate of other groups on the hill (chapter 4), indicating that the baboons at Blouberg mainly foraged in the plain. On the other hand, visibility was certainly an important factor that affected the probability of group encounters. On the hill, other groups could be spotted from larger distances than in the plain. This prevented the study group from unexpectedly meeting other groups at close distance, and probably allowed them to avoid groups well in advance.

Moreover, 4 out of a total of 7 evasive manoeuvres recorded on the hill occurred when the Kloof group arrived at the edge of its steep South-facing slope, before descending to its S-foot. The vocalisations recorded came from groups that were feeding there already. Since from above, the Kloof group could see the resources they subsequently visited, I view these instances as uninteresting for examining my hypotheses, and will not further discuss them.

10 out of a total of 27 evasive manoeuvres recorded in the plain occurred when the study group was moving away from their sleeping site. During these

Table 7.1. Number of evasive manoeuvres on the hill and in the plain, during outward and inward movements. Letters A - E indicate hypothetical evasive manoeuvres expected under different mechanisms of orientation (see Figure 7.1.).

	A	B	C	D	E	Total
outward total	**5**	**0**	**9**	**2**	**1**	**17**
hill	3	0	2	1	1	
plain	2	0	7	1	0	
inward total	**0**	**0**	**6**	**8**	**3**	**17**
hill	0	0	0	0	0	
plain	0	0	6	8	3	
Total	**5**	**0**	**15**	**10**	**4**	**34**
Total hill	3	0	2	1	1	
Total plain	2	0	13	9	3	

and all other outward movements, the animals always seemed to be confident about the direction chosen, and I never observed any animals to look back as if searching for a reference point on the hill.

7.3.1. Scenario A: Leave path, visit alternative resource type

Figure 7.3 illustrates two cases of reorientation towards new resources after a group encounter which correspond to scenario A. Both of them occurred during outward movements. The first example (panel A) shows that after leaving their sleeping site in the early morning, the study group followed a reserve road towards NW. They travelled for approximately 2 km away from their sleeping site without visiting any major resources, and then met another group. They waited for a total of 25 min, before they headed back towards SE,

and fed on dry food matter in the vicinity of the sleeping site for the remainder of the day. This example suggests that the study group was not able to by-pass the danger, but needed to wait on the spot. Presumably, the danger did not vanish, and they entirely aborted their outward trip.

Panel B (Figure 7.3) shows a similar decision. In the morning, the Kloof group departed from the sleeping site in a W direction. After 200 m, they started to steer towards NW, as if heading towards the Buffalo water hole. A first bout of herding occurred. The group then waited at two nearby locations for 10 min each, and again headed towards NW. After 300 m they met another group. They turned E, and a new herding bout occurred. They then walked straight to the remote sable forest, which was situated to their SW, at a distance of 1500m.

Again, this example suggests that the baboons were not able to bypass the danger when heading towards N from their sleeping site. Instead, they waited on the spot, presumably until the other group moved on, and then decided for an alternative resource place. This finding is not consistent with the notion of vector maps, but suggest that once the initially chosen route was blocked, the study group needed to wait on the spot. They were forced to visit alternative resource places if the block to their passage was not spontaneously removed.

But in contrast to the example in panel A, the evasive manoeuvre in panel B suggests that the animals were able to find a good alternative. From their present location, they walked directly and confidently to a frequently visited,

Figure 7.3. Scenario A: Disrupted outward movements with subsequent reorientation towards new resources. Bold line: Baboon path. Arrow: Direction from which other groups vocalised. Neat line: Reserve roads. Dotted lines: Contour lines. Grey area: Sleeping site area. Grey dots: Resting or feeding bouts. Stars: Locations where roar-grunting or herding occurred in the study group. Vis: Visibility border of the sable forest.
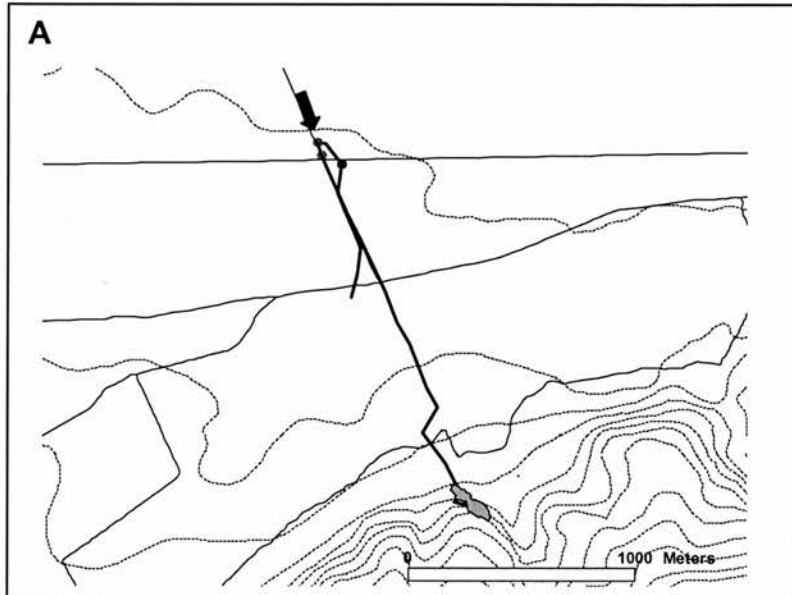
After leaving the sleeping site area the study group followed a road towards NW for approximately 2 km. After encountering another group (arrow), the movement stopped for resting (grey dots). After 25 min they walked back towards their sleeping site and spent the rest of the day in its vicinity. Path recorded in April 2002.
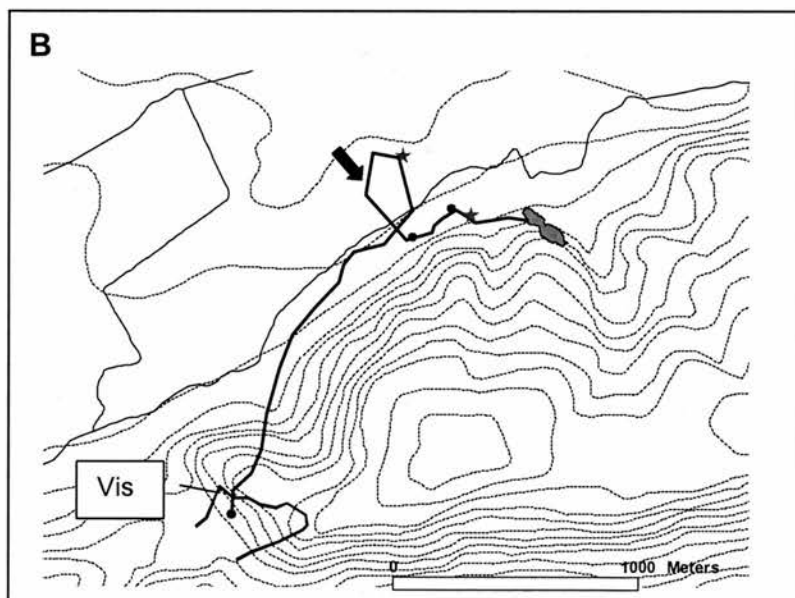
The study group left the sleeping site towards W. After 200 m, they took a NW direction, as if heading towards the buffalo water hole. A first bout of herding occurred (star). They then waited for a total of 20 min at two locations (grey dots), and again walked towards NW. After the group encounter, a new bout of herding occurred (star), and the group reoriented towards the sable forest. Path recorded in August 2001

preferred resource place that was well beyond their visual range. I had never followed the study group to the sable forest on this path before. However, they commonly used it on their way back from the sable forest to the sleeping site, that is, in the opposite direction. Thus, this route was by no means novel to the Kloof group, and therefore evidence for the presence of a vector map remains weak. The fact that they reoriented towards another highly preferred resource place from the location of the group encounter points to the possibility that a network map representation could be involved in their ranging.

7.3.2. Scenario B: Leave path, resume path parallel to initial path

I did not find any evidence for the baboons leaving their path and resuming a parallel path after a group encounter. This is evidence that, contrary to my suspicion, remembering and then holding a bearing, (suggested as the minimal cognitive requirement for explaining the outward movements in chapter 5) may not be the main means by which the animals navigated in the plain. However, it is noteworthy that the study group sometimes followed the reserve trackways during their N-bound journeys, but never did so when approaching the sleeping site area.

7.3.3. Scenario C: Leave path, bypass danger, resume same path

I recorded a total of 15 detour paths resembling scenario C, nine of which occurred during the outward movements. The examples in figure 7.4. repre-

Figure 7.4. Scenario C: Bypass danger, resume path for an inward (A) and an outward (B) movement. Consult Figure 7.3. for legend, and text for details.
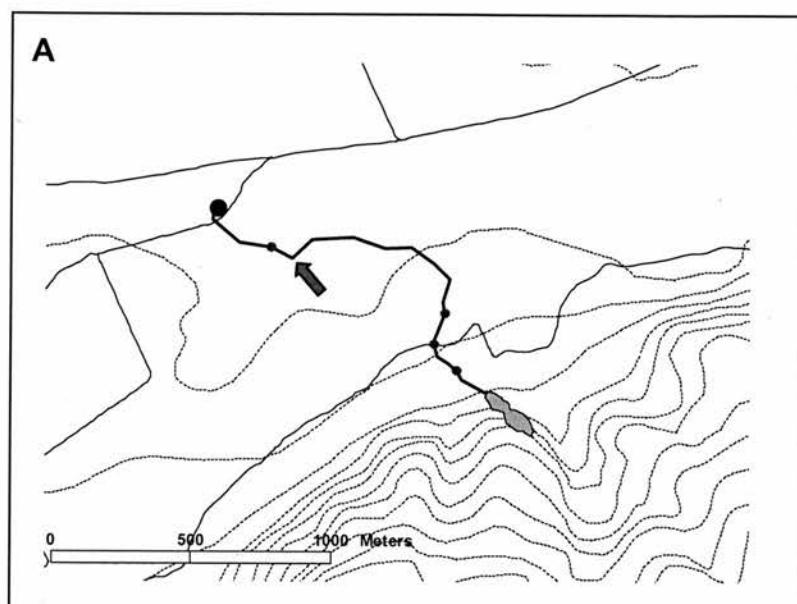
The Kloof group visited the Buffalo water hole (black circle), and then headed towards the sleeping site. Shortly after feeding at a guarri bush (grey circle), they met another group (arrow). They took a large detour path around them, and resumed their path shortly before arriving at the sleeping site.
Path recorded in May 2002
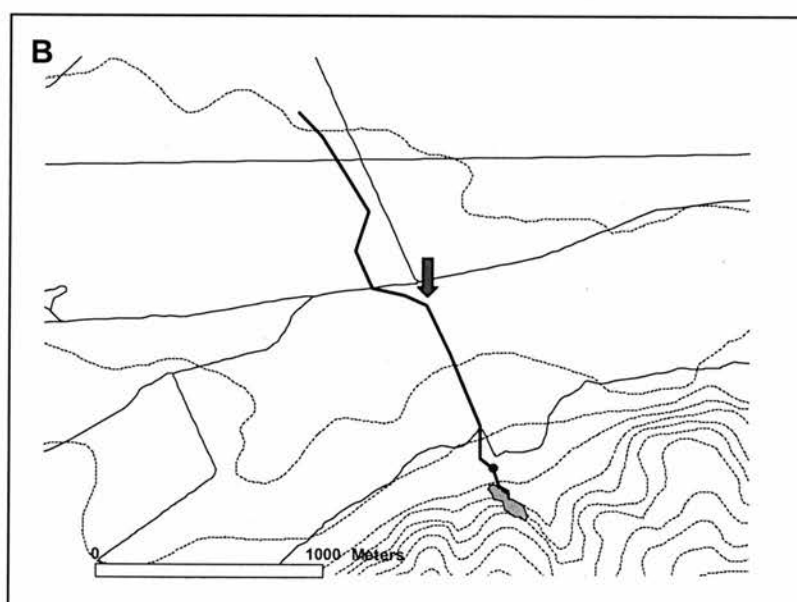
The study group left the sleeping site, fed on a marula tree (grey circle), and then followed a road towards NW. They took a short detour path around a group of conspecifics (arrow), and resumed their path leading further NW.
Path recorded in February 2002

sent the largest detours recorded. Panel A illustrates an evasive manoeuvre which occurred shortly after visiting the Buffalo water hole, when the study group was on their way back to the sleeping site in the afternoon. They walked in a large semi-circle around the danger. The maximal distance between the (hypothesised) straight-line path and the detour path was 300 m. In this area, visibility was well beyond this value. Thus, the Kloof group could not have stayed in visual contact with the initial path.

It is noteworthy that this evasive manoeuvre took place in the vicinity of the sleeping site. Although the sleeping cliff itself was not directly visible at any location, it is likely that the study group's detour path was guided by a whole range of well known landmarks closely associated with their sleeping site. Following the principle of parsimony, I suggest that this evasive manoeuvre can be explained by movement under the guidance of permanent landmarks.

A different picture emerges when looking at the detour paths during the outward movements, when visual landmarks were lacking. Panel B in Figure 7.4. illustrates an example. The Kloof group departed from their sleeping site, stopped briefly to feed on marula fruit at a nearby tree, and then followed a firebreak towards NW. After 1 km, they met another group. They bypassed it via a short detour path, before resuming the initial bearing and further heading towards NW.

The area in which this detour path was covered was an unusually open area, which obviously had been deforested some decades ago. The vegetation con-

sisted of grasses and thin bushes. Maximal visibility in February, when this path was recorded, was 143 m. This was approximately the distance between the detour path and the hypothesised straight path that day. I therefore cannot exclude that the Kloof group, while taking the detour path, always kept visual contact with the straight-line path they would have travelled in the absence of another baboon group.

In addition to this example, all other detour paths recorded during the outward movements provide evidence that the Kloof group followed well known routes in the absence of the hill as a prominent landmark. Their detour paths were larger during the inward movements, with the hill probably guiding their orientation.

7.3.4. Scenario D: Approach goal from new direction

I found 10 evasive manoeuvres in my data set which seemingly represent approaches to a resource from a new direction. However, only one of them occurred during the journey away from the sleeping site in the plain, that is, in the absence of distant landmarks (Figure 7.5. A).

The study group departed from the sleeping site in the morning towards NW that day, as if heading towards the Buffalo water hole. After they had travelled 370 m in a fairly straight line, another baboon group vocalised at close dis-

Figure 7.5. Scenario D: Approach goal from new location during outward movement. Light grey area: Area within which the nyala and baobab trees in the vicinity of the buffalo water hole were visible. Darker grey area: Area within which the water hole was visible. Grey dots within area: Water holes and tall nyala trees.
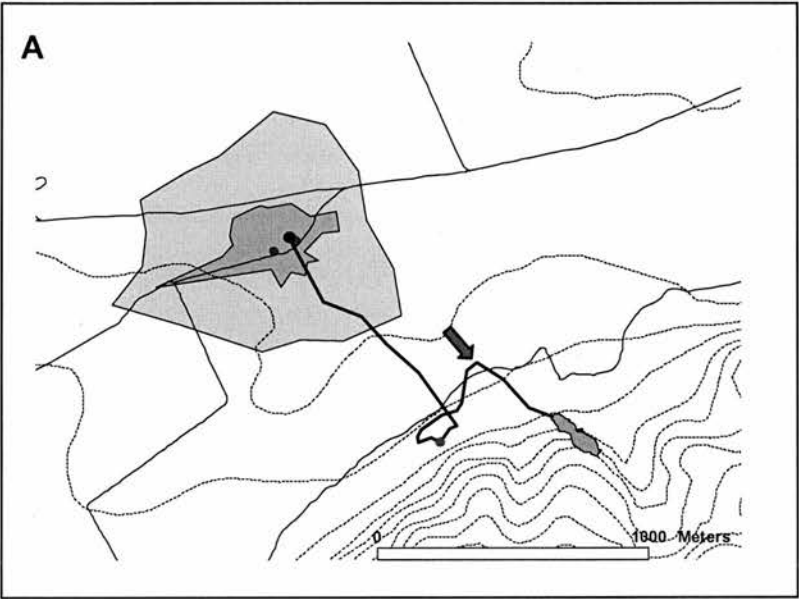
From their sleeping site, the animals walked towards NW as if heading towards the buffalo water hole. After disruption (arrow), they turned towards SW, and waited for a total of 60 min (grey dot). They then approached the water whole from this new location in a fairly straight line.
Path recorded in June 2002.
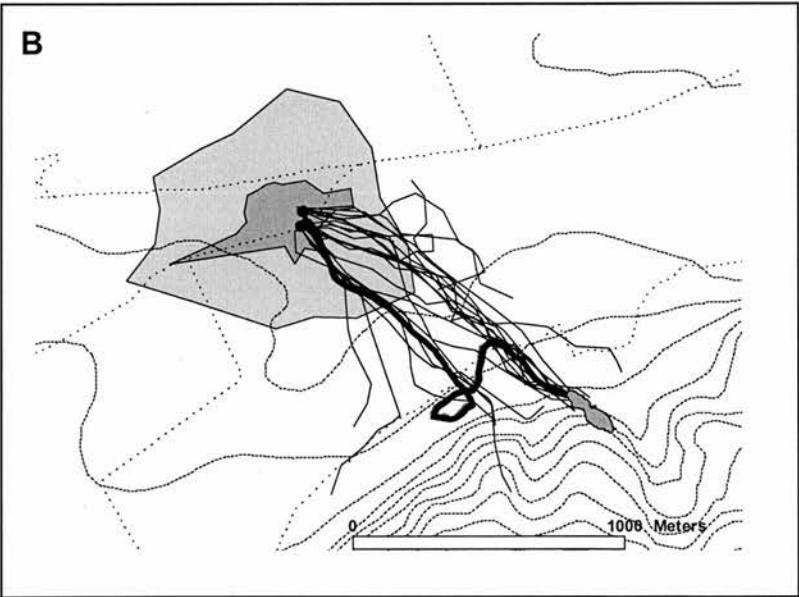
Above path relative to all undisturbed approaches to the buffalo water hole. This picture reveals that the alternative path chosen in the above example was not novel, but was frequently travelled after foraging on the hill.

tance in front of them. The study group turned SW, turned round in a small circle and then rested. An hour after the group encounter, they headed from their new location directly and in a straight line to the buffalo water hole.

So far, this is the best evidence for the presence of a vector map. I therefore investigated this path relative to the paths usually travelled when approaching the buffalo water hole from S and SE. This revealed that the alternative path chosen after the evasive manoeuvre was not novel (Figure 7.5 B). The Kloof group usually followed this route when visiting the buffalo water hole after some time spent foraging on the hill. Again, this suggests that the Kloof group navigated by means of a network map, rather than a vector map that day. During inward movements, I had recorded 6 instances of scenario D in the vicinity of the buffalo water hole. 5 of them occurred inside the visibility area of the associated nyala trees. Since reorientation could well have been guided by these proximate landmarks, I only present the remaining case which occurred further N (Figure 7.6.).

From a distant feeding area in the plain, the Kloof group travelled on a straight line towards SE, seemingly on their way to the buffalo water hole. At a distance of 800 m from the dam, another group gave two wahoo calls. The study group turned towards NW, and then towards SW, before their movement stopped for 25 min. Neither the water hole itself, nor the associated tall trees were visible from that location. The Kloof group then approached the dam from NE.

Figure 7.6. Scenario D: Approach goals from new location during inward movement.
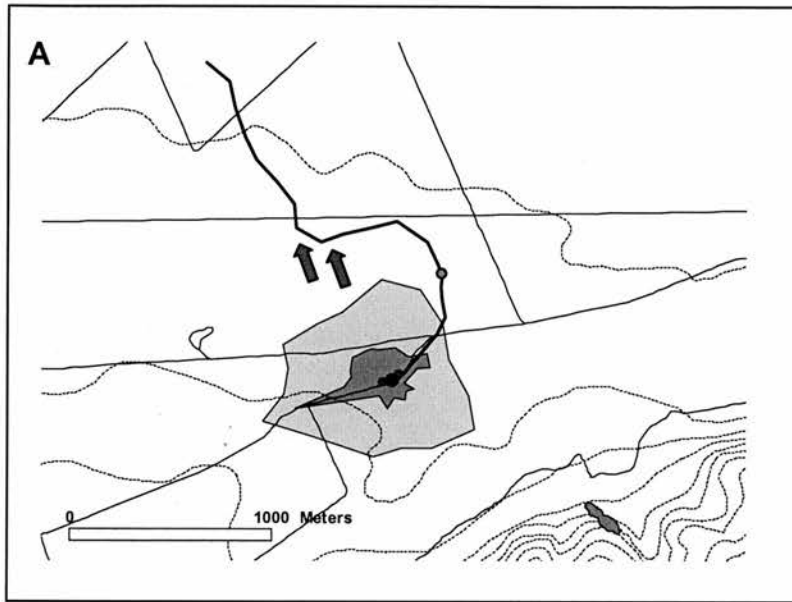
After feeding at a distant food patch in the plain, the group headed towards the buffalo water hole. After the group encounter (arrows), they approached the water hole in a semi-circle, along which they waited for 25 min. Only a small part of this detour path was situated within the detection area of the water hole, and its associated landmarks.
Path recorded in March 2002
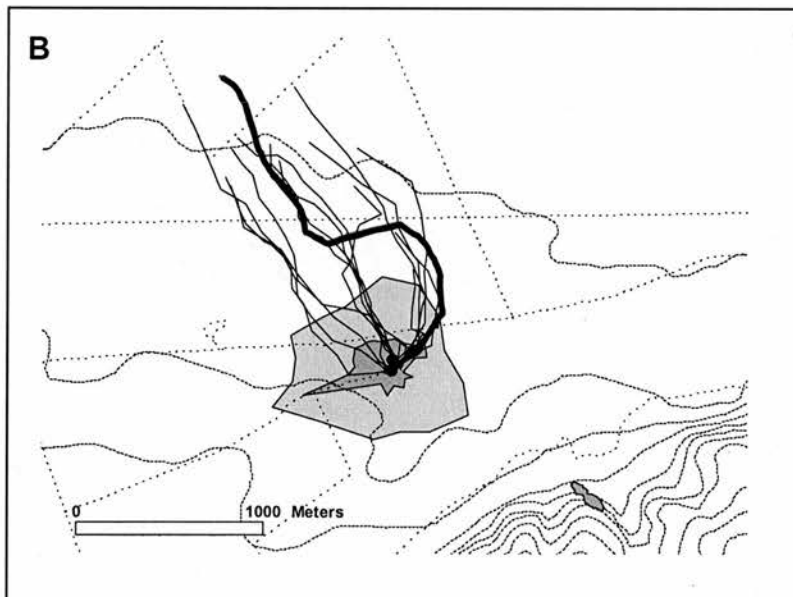
Above evasive manoeuvre relative to all undisturbed approaches to the buffalo water hole from N. The detour path was not novel, but frequently used on the way to this water hole.

Figure 7.6.B reveals that this detour path was a frequently travelled route. Again, this finding does not corroborate the notion of a vector map sensu Tolman (1948) and O'Keefe & Nadel (1979). This corroborates the finding

from the previous example that after a group encounter the animals recognised a familiar alternative route, and followed it until reaching their goal.

7.3.5. Scenario E: Visit same resource type at new location

I found 4 cases suggesting that the Kloof group reoriented towards alternative resource places which contained the same resource type as the location initially steered at. In one case, the resource type was the mupulu fruit *(Mimusops zeyheri)*, a sweet-tasting, apricot-like fruit that occurred on only 5 trees in their home range. The other instances concerned the two water holes in the plain, the buffalo and the baobab hole. In the following, I present three of the cases (Figure 7.7. - 7.9.).

The study group bypassed a mupulu tree S of their sleeping site in the early morning, after leaving their sleeping site (Figure 7.7.). They then turned SE as if heading towards a large mupulu tree situated on top of the hill. Before arriving at this tree, they met another baboon group. The alpha male herded his females, and the group then retraced their path, and rested for 15 min, before reapproaching that tree. As soon as the tree came into sight, another baboon group vocalised who was already feeding there. The Kloof group bypassed the tree and visited a third mupulu tree which was situated to their N, at the foot of the hill. This specimen was well hidden underneath the dense vegetation in a valley, and became visible only from a couple of m.

Figure 7.7. Scenario E: Reorientation towards alternative mupulu trees on the hill. Black dots: locations of mupulu trees. Only three out of a total of five mupulu trees in the study group's home range are shown. Grey dot: Location where group waited for 15 min. Grey line: distance from which the tree became visible.
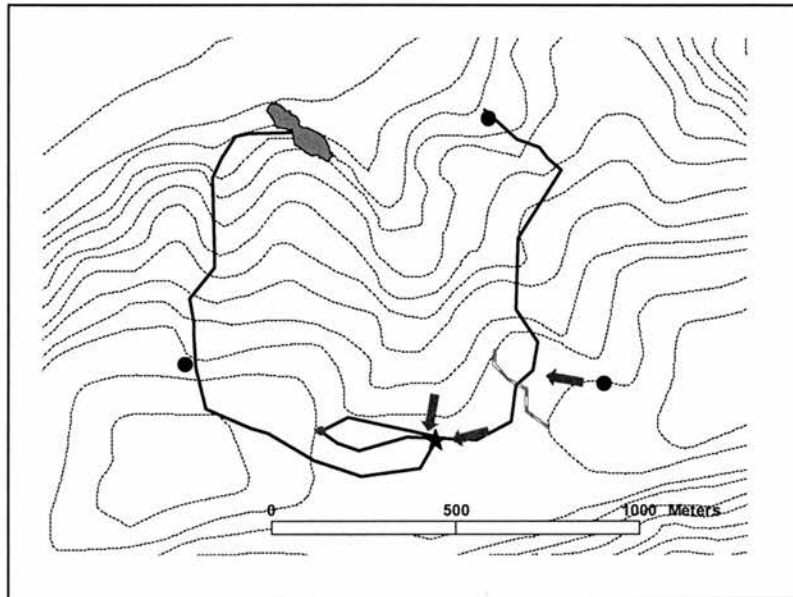
After leaving their sleeping site, the animals climbed the hill and bypassed a small mupulu tree (black dot SSW from sleeping site). They then headed towards a second tree, but met another group on their way (two arrows). After a herding bout (star), they turned back, waited (grey dot), and then reapproached the tree. At its visibility border (grey line), they encountered another group who was already feeding there (arrow). They then walked down the hill and visited a third tree E of the sleeping site.

Path recorded in August 2001

The path chosen to the third mupulu tree that morning was not very straight. However, this may have been due to the fact that when descending from the hill, the study group needed to cross a steep valley at an appropriate location. I view this path as evidence that the study group remembered the locations of alternative mupulu sources. Unfortunately, mupulus were available only for a short time period and seemed to become depleted very rapidly, so that my data do not allow for a more detailed analysis.

Figure 7.8. Scenario E: Reorientation towards an alternative water hole.
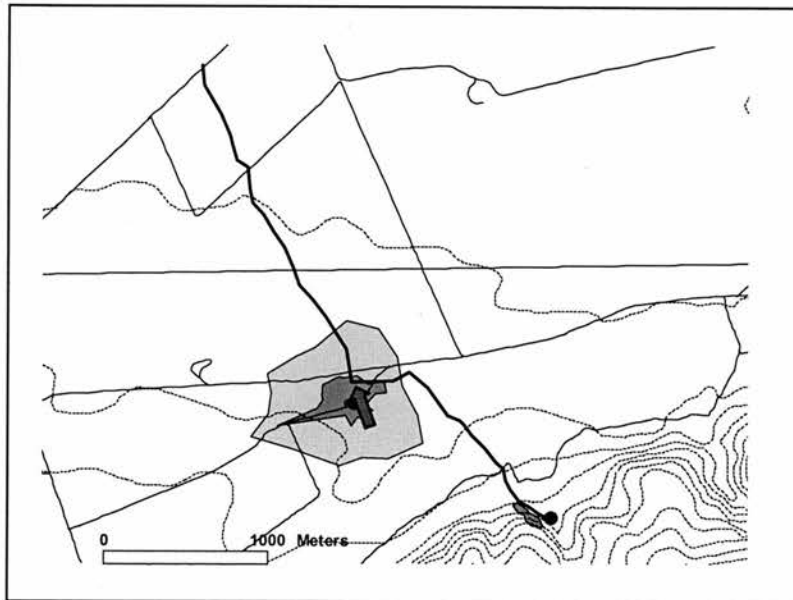
The animals approached the buffalo water hole in a long bee-line from N. Shortly before arriving, another group vocalised in front of them (arrow). The study group turned E, and then walked to the Kloof water hole which was situated next to their sleeping site. Path recorded in June 2002

The study group also reoriented towards alternative water holes. In Figure 7.8. they approached the buffalo water hole from roughly N in a long bee-line. Shortly before arriving, they met a group of conspecifics. They evaded in an E direction, and then reoriented to the Kloof water hole. However, the Kloof water hole was situated next to their sleeping site. I can therefore not exclude that they simply walked towards the sleeping site, and then recognised the cues that were associated with the Kloof hole.

Figure 7.9 shows a similar event. The baobab water hole was approached from N. After encountering a group which was already drinking there, the study group fled towards E, and then walked to the buffalo water hole. Re-orientation took place long before they could visually perceive the associated trees. Note that in this example, however, the direction of the path towards the

Figure 7.9. Scenario E: Reorientation towards an alternative water hole.
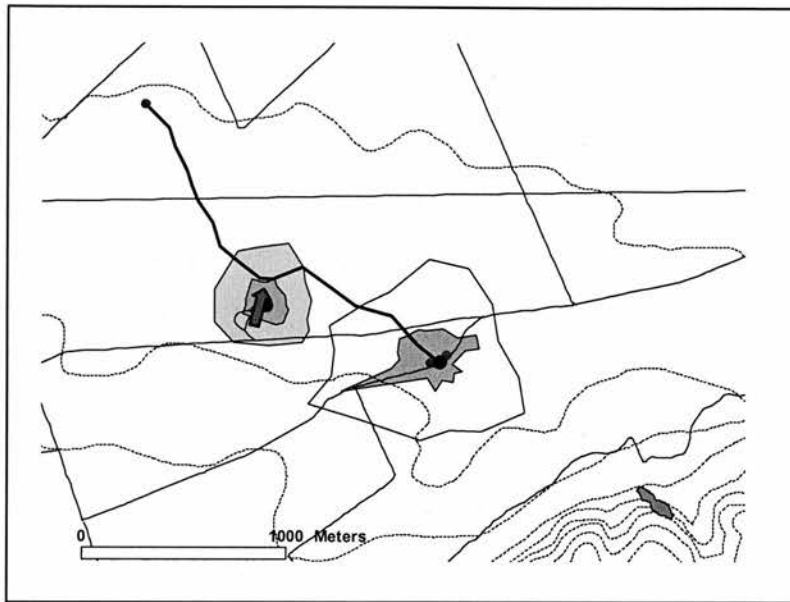
The Kloof group approached the baobab water hole on a long, straight route. The group encounter occurred at its visibility border (arrow). The animals fled towards NE, and then reoriented towards the buffalo water hole.
Path recorded in July 2002

buffalo water hole corresponds with the direction towards the sleeping site. Again, I cannot exclude the possibility that the Kloof group reoriented towards the sleeping site by means of the visual appearance of the distant hill, and then encountered the buffalo water hole by chance.

Two additional points warrant mention. First, it is striking that during all inward movements, the study group avoided other groups by walking (or running) towards E. Since their sleeping site was situated to the SE from virtually all distant resource places in the plain, I view this as evidence that they needed to keep visual contact with the sleeping-site or the associated landmarks during the inward movements.

Also, there is a striking feature common to the figures 7.6 and 7.8.-7.9. The paths used during the inward movements in the plain are all nearly parallel to

the human-built reserve roads that lead roughly from N to S. These roads were visible only from a short distance, and it is unlikely that the study group travelled with reference to them when approaching the hill. Both the roads and the baboon paths that lead roughly towards South from the more distant areas in the plain are approximately perpendicular to the hill. I therefore propose that the humans who built the roads and the baboons were guided by the same general perspective of the hill.

7.4. Discussion

The low visibility in the woodland savannah at Blouberg as well as its high baboon population density leads to an increased probability that baboon groups unexpectedly encounter each other. The females of my study group reacted fearfully to groups of conspecifics in close proximity, and fled away from them, while the alpha male usually roar-grunted, and sometimes aggressively herded his females. Based on their vocalisations, I suspected that similar behaviours occurred within the groups they encountered. However, the dominance relations among baboon groups within a population are still poorly understood. It is not known whether small groups, such as the Kloof group, are more likely to withdraw from their opponents than larger groups.

The evasive manoeuvres examined in this chapter revealed that group encounters sometimes caused the study group to interrupt their progressions, and then to wait for up to 60 min before they continued their trip, and in one

case to entirely abort their journey. However, they also reoriented towards alternative resources, took detour paths around the danger, or approached the resource places on alternative routes.

I found no conclusive evidence for vector maps sensu Tolman (1948), Byrne (1978) and O'Keefe & Nadel (1979). Large detour paths occurred only in the vicinity of the hill during inward movements, on the hill, or next to the water holes, where learned landmarks were likely to guide their orientation. In contrast, prominent landmarks were absent only during the outward movements in the plain. In this situation, groups of conspecifics could sometimes be bypassed via small detour paths, during which visual contact with the presumed straight-line path was always possible. In all other instances, the Kloof group either needed to reorient towards alternative resources or to follow alternative, but familiar, routes in order to reach their resource places.

Although my data base was limited, this strongly suggests that the Kloof group navigated on the basis of a network map representation (Byrne, 1978; 2000). Evidence for network maps comes also from other baboon and primate groups (Milton, 1981; Garber, 1989). Stolba (1979) based a large part of his analysis of hamadryas baboon movements on frequently used path segments. Altmann & Altmann (1970) pointed out that the yellow baboons who ranged in the vast plain of the Masaai-Amboseli game reserve 'move often along habitual routes'. Ransom (1981) states for olive baboons that

'the most outstanding feature of range use by the Gombe troops was their extremely regular and repetitive daily movement patterns. Throughout the study period both B and C troops followed basically circular daily routes that began and ended at the sleeping area (...). For long periods of time these routes varied, for the most part, only in the direction taken, ie. clockwise or counterclockwise'.

The fact that primate groups often travel along known routes provides, of course, no conclusive evidence for the lack of vector maps. However, the amount of time and energy lost by the Kloof group as a result of group encounters is striking. It seems that a vector map would have allowed them to react in a more flexible way, and thus to optimise their energy balance. In contrast to urban settings, some natural environments, including most forest and woodland habitats, theoretically allow individuals to walk from any point A in a straight line to any point B. Thus, natural selection would favour individuals possessing the ability to compute Euclidean relations among important locations over those who lack such skills. It therefore appears that baboons may lack the genetic variation that allowed the development of the computational device for a vector map.

In this light, the question arises whether any mammals, humans included, have vector map abilities. Evidence for vector maps has remained weak for all animal species investigated so far (present study; Benhamou, 1996; Dyer, 1991; Wehner & Menzel, 1990). Adult humans have been shown to predominantly use network map representations in order to find their ways in

familiar urban environments (Byrne, 1978; 2000). However, the question of whether humans entirely lack the ability to represent space as if viewed from a bird's perspective has remained open, and future research is needed to investigate whether their spatial representations may under some conditions take the form of a vector map.

Chapter 8 Change point analysis: the Jupp test

8.1. Introduction

Thus far, I have examined the ranging behaviour of the study group from several different perspectives. I have investigated the ecological factors that affected path characteristics (Chapter 3 and 4), which revealed that food availability and the high baboon population density at Blouberg significantly affected ranging. Chapter 5 and 6 have suggested that baboons travel to some resources in a goal-directed way, and anticipate the resources long before they can perceive them with their senses. Also, I have examined path flexibility after unexpected disruptions of the journey (Chapter 7), which suggested that the study group used network maps rather than vector maps for finding important resources. In this final chapter of data analysis, I intend to illuminate the movement patterns of the study group from an additional, more technical perspective.

To date, statistical methods for analysing ranging patterns of animals are limited. For examining path linearity, Batschelet (1981) presents a straightness index, in addition to the measure r which I used in previous chapters. Both measures provide useful tools for a purely descriptive apporach to the problem of path linearity. However, when it comes to the question of cognitive processes, their merits are limited. As stated before, many different mechanisms of orientation can result in linear movements, and evidence for the underlying cognitive processes remain ambiguous. For a refined analysis of movement patterns, additional variables need to be considered.

In this chapter I present a novel statistical procedure which was developed in cooperation with Prof. Peter Jupp, Department of Statistics at St Andrews University. The initial idea behind this procedure was that *change points* (CPs) in animal paths may provide interesting insight into the mechanisms of orientation and group movement. That is, we intended to find the locations at which paths significantly change direction, and then to examine whether certain behavioural, ecological or topological features are typically associated with directional changes.

The techniques used to investigate this question are novel to a large degree. I will therefore first present the statistical background of the test for change points (in the following named 'the Jupp test'), and process two sets of paths, one generated artificially and one observed in my study group. By this means, I intend to investigate its properties as well as its weaknesses and strengths.

8.2. Methods

8.2.1. The nature of the Jupp test

The Jupp test for finding change points is derived from the two-sample Watson-Williams test for circular data (Batschelet, 1981). The purpose of this latter procedure is to test whether the mean angles of two samples differ significantly from each other. Its null hypothesis states that the mean angles do not differ.

Briefly, the idea of the Watson-Williams test is to compare the scalar lengths of the resultant vectors R1 and R2 of two samples with the scalar length R of the combined sample. If the sum of R1 and R2 approximately equals length R, then the deviation of the mean angles of the two samples is small. In this case, H0 cannot be rejected. In contrast, the more length R differs from R1 + R2, the more the mean directions of the two samples deviate from each other (see Batschelet, 1981, pp. 96).

In other words, the Watson-Williams test compares the angular variances of the two samples with the angular variance of the combined sample. If the two samples completely overlap, then the variance of the combined sample is not different from the variance of the two samples. In contrast, if the two samples differ in their mean directions, then the variance of the combined sample is considerably larger than the average of the two samples (Batschelet, 1981).

The Kloof group's foraging paths are represented as chronological series of GPS readings, collected in regularly-spaced sample times throughout the days. For the purpose of finding CPs in these paths, the Jupp test is applied iteratively. We initialise the test at the location of an important resource, for example at a water hole. We then run the test 'backwards in time' along the path until the first significant directional change is found. Note that this CP occurred *before* the animals reached the resource, and represents a significant change of direction *towards* the resource.

At each location k of a path, we determine the directional variance of a sample of k preceding and a sample of q subsequent vectors. We compare the directional variance of both sample k and sample q with the directional variance of the combined sample k+q. If the test fails to find a significant directional change at location k, we proceed to the next location k+1 and test it for a CP. We repeat this procedure until we find the first significant directional change at location k+n. That is, we 'move' the stats procedure over the path until we find a significant directional change.

Note that k corresponds to the number of vectors between the starting point of the test (eg the water hole) and the location under test. Therefore, k increases linearly with the number of locations tested. In contrast, q denotes the number of vectors we wish to use as the reference sample, and its value remains constant.

In more technical terms, the Jupp test considers the following hypothesis at each location

$$H_k: F_1 = F_2 = \ldots F_k \quad F_{k+1} = \ldots = F_{k+q} \qquad k = 1, n - q.$$

('the directional variability of the vectors before location k is different from the directional variability of the vectors after location k')

It denotes the change point as the first value of k for which the null hypothesis H_k0 is rejected in favour of the alternative hypothesis Hk. Thereby, the null hypothesis can be written as

$$H_k0: F_1 = F_2 = \ldots = F_k = \ldots = F_{k+q}$$

(' the directional variability of the vectors before and after location k do not differ from each other').

For each location k under investigation, we use the test statistic

$$W = (R1 + R2 - R)(k + q - 2)/(k + q - R1 - R2).$$

We reject H0 at position k if

$$W > F_{(1, k+q-2, \alpha)}.$$

We then conclude that the mean directions of the vectors before and after location k deviate significantly from each other.

Figure 8.1. illustrates the two first steps of the Jupp test, applied to an imaginary path, at location k=2 and k=3 with q=1. Note that when using q=1, we compare the directional variability of a sample of k vectors with the direction of a single vector. We are therefore not able to test location k=1, since at this location only 2 vectors are available, one before and one after

Figure 8.1. Basic mechanism of the Jupp test for finding change points in foraging paths with q=1. The first two steps of the test are shown. Bold arrows point to the locations under test. (A) A path to a fig tree is described by the vectors between subsequent locations. The direction of the vectors indicate the travel direction of the animals. (B) We start the test at location k=2 and compare the direction of vector V3 with the directions of vectors V1 + V2. R1 is the scalar length of V1+V2, R2 is the length of V3, and R is the length of V1+V2+V3. The null hypothesis H_20 states $R1 + R2 \cong R$. If we can reject H_20, we have found the first CP in this path, and we stop testing. In contrast, if H_20 cannot be rejected, we test the next location k=3. (C) At k=3, we compare the direction of vector V4 with the directions of vectors V1 + V2 + V3. H_30 is $R1 + R2 \cong R$. In this step R1 is the length V1 + V2 + V3, R2 is the length of vector V4, and R is the length V1 + V2 + V3 + V4. Again, if we can reject H_30, we have found a CP. Otherwise we continue testing the next location, until we reject H_k0 for the first time.
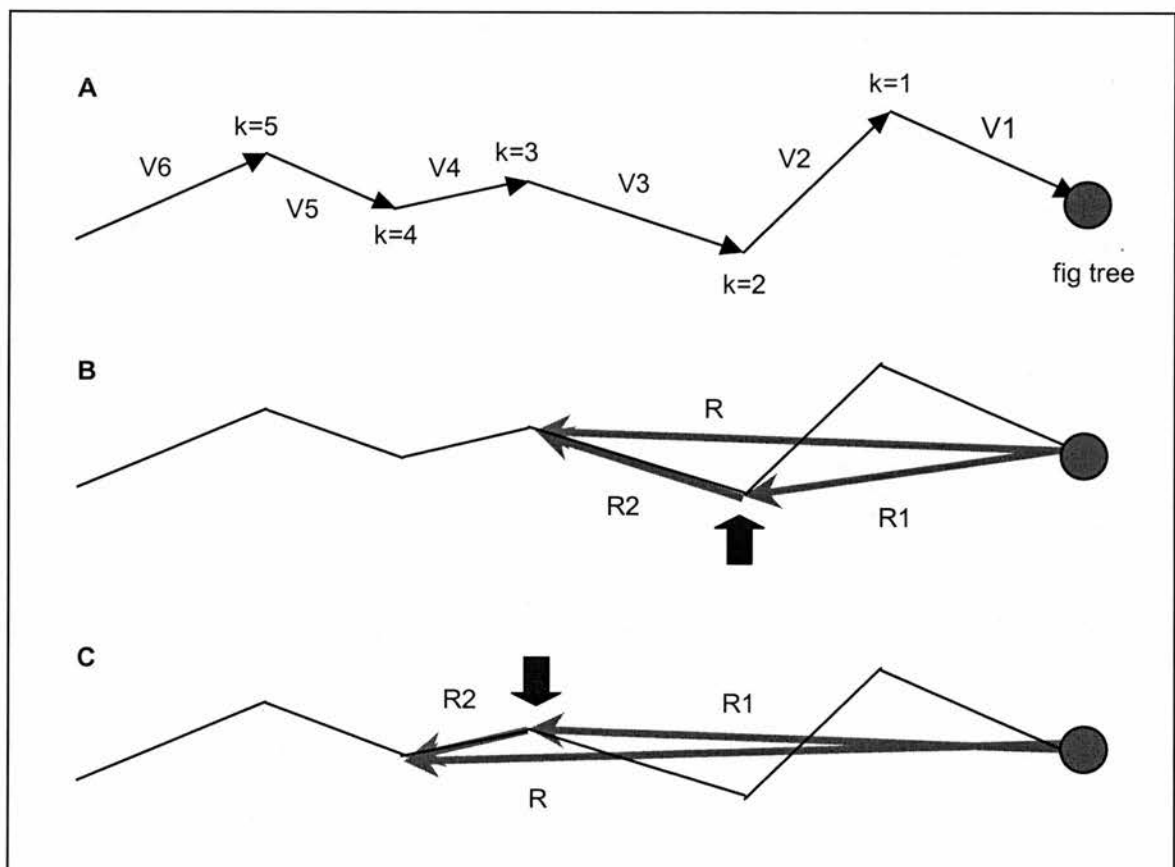
Figure 8.2. First and second step of the Jupp test with q=2. Bold arrows: locations under test (A) In order to test the first location k=1 before the fig tree, we build the resultant vectors R1= V1, R2=V2+V3, and R = V1+V2+V3. $H_1 0$: R1 + R2 $\cong$ R. If $H_1 0$ cannot be rejected, we continue testing. (B) Test of location k=2. Here, we compare the scalar length of the vectors R1= V1 +V2 and R2=V3+V4 with the vector length R= V1 + V2 + V3 + V4. Again, $H_2 0$ is R1 + R2 $\cong$ R. If we reject $H_2 0$, the procedure stops here, otherwise we continue testing until we can reject $H_k 0$ for the first time.
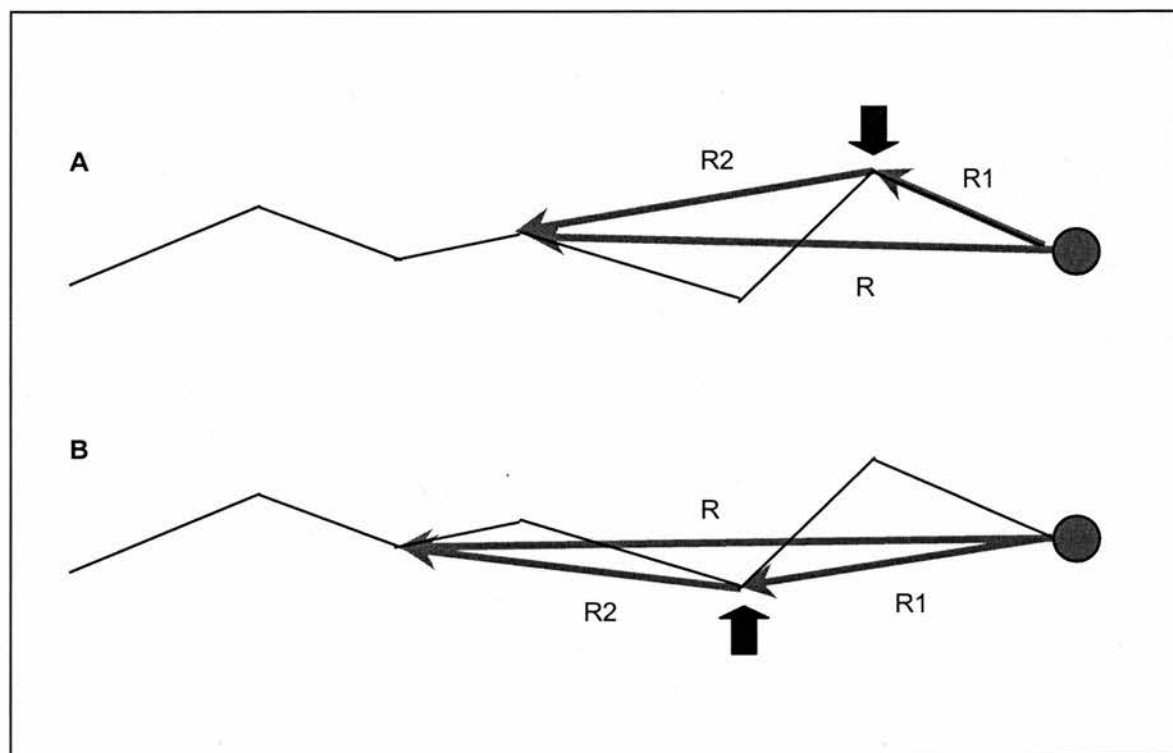
location k. Figure 8.2. shows how the Jupp test performs the tests at the two first locations k=1 and k=2 when using q=2.

8.2.2. Theoretical considerations

The Jupp test was initially designed for q=1. However, this procedure had the disadvantage that the first location before the starting point of the procedure could not be tested (see above). We therefore considered varying the value of q. Since the power of any statistical procedures increases with increasing sample size, q should theoretically be as high as possible. However, q denotes the sample size of the vectors situated *after* the location under test (when looking backwards in time). Large q-values therefore increase the possibility of finding significant directional changes as a result of path linearity after, rather than before the location under test. However, our main interest lies in confirming that the variability of the vectors in sample k is small. Moreover, high values of q increase the possibility of failing to detect genuinely low variance in sample k, because of spurious variance in sample q (e.g. if the baboons were previously wandering on a circular path, before heading directly towards the resource). In order to optimise this trade-off, I will consider several q-values in the next section 8.3.

Inevitably, also the size of k contributes to the power of the procedure. It lies in the nature of this test that we subsequently add vectors until we find a significant result. Thus, the size of sample k increases while testing a single path, and inevitably so does the power of the test. As long as all change points are likely to occur at a similar distance from the starting point, this should not pose a severe problem. However, if the CPs occur next to the starting point in some paths, and far from it in others, direct comparison of the two results should be undertaken with caution.

When testing a single path, we repeatedly consider the null hypothesis of the Jupp test. This potentially increases the danger of falsely rejecting the null hypothesis in any of the steps. From a purely statistical point of view, this suggests that significance levels lower than 5% should be chosen. On the other hand, low significance levels increase the danger of missing any directional changes that may in fact be meaningful from a perspective of the animal's behaviour. In the following two sections, I will therefore closely observe the effect of using several different significance levels.

A last point that warrants a note is the fact that the Jupp test reduces vectors to unit vectors. This may cause a loss of important information in the data. In the case of the Kloof group, travel speed of outward and inward movements differed significantly. Consequently, vector length is also different, because time was held constant during GPS data collection. But since travel speed seemed to gradually decrease towards the afternoon rather than to markedly vary from one GPS reading to the next, I view these differences in vector length as unimportant for interpreting the results.

8.3. Testing a set of artificial data

I tested a set of simple, artificially created paths with the purpose of examining the properties of the Jupp test. Paths A – F (Figures 8.3. - 8.5.) contain 13 data points each. The starting points of the paths are situated on the left of the panels, the resources – and therefore the starting points of the Jupp proce-

dure - on the right. I performed a total of 4 test runs on each of the paths by using the test variants with q=1, 2, 3, and 4. I considered significance levels of 5%, 1% and 0.1%. I computed each variant of the Jupp test in a separate Excel file.

8.4. Results

Path A exhibits a pronounced directional change at location ID 7. The vectors of the two segments before and after this location contain low directional variability. Results of the Jupp test were consistent across the different test variants (Table 8.1.). The variants with q=1 and q=2, found a significant CP at location ID 7 (p<0.01). However, both the q=3 and the q=4 variant found a CP at ID 8 (p<0.05), that is, slightly too early . In addition, they indicated a highly significant directional change at location ID 7, with p<0.001.

The results of the q=3 and q=4 variants can easily be understood when looking at location ID 8 in figure 8.3.A. At this location sample k consists of the vectors between R and location ID 8, and sample q of the vectors between location ID 8 and ID 5 (q=3 variant) or ID 4 (q=4 variant) respectively. The main direction of the vectors in the two samples differ from each other. However, in sample q the direction of the vector between location ID 7 and ID 8 differs from the direction of the subsequent vectors. Therefore, the q=3 and q=4 variants rejected H0 with a comparatively high significance level of 5%, whereas they rejected H0 at the next location ID 7 at p=0.001.

Figure 8.3. Artificial paths A and B. Path A is characterised by two straight segments of differing direction, with a pronounced CP at location 7. The vectors of path B change direction very subtly, until the overall directional change reaches 140°. Numbers: ID numbers of locations. S: Starting point of the path at position ID 1. R: resource place = position ID 13 = starting point of the Jupp test.
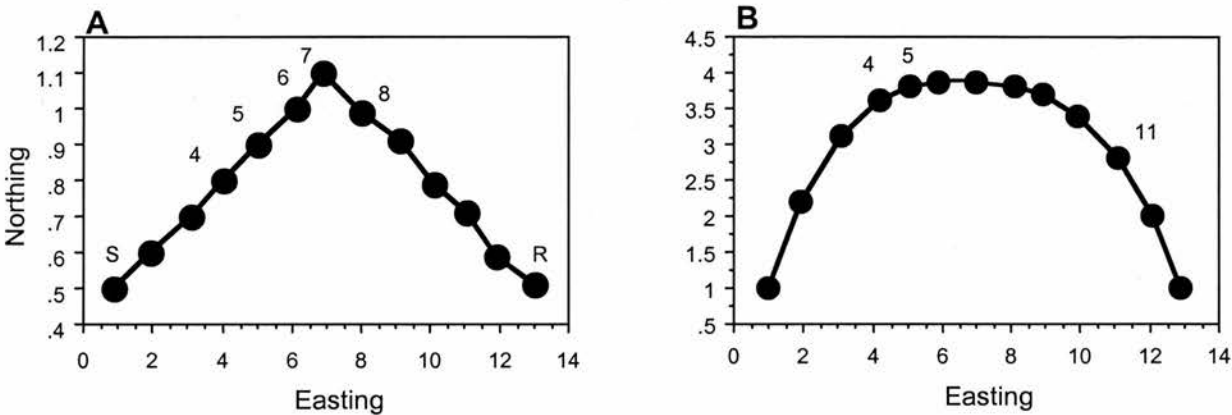
Therefore, I propose that we need to observe the test statistics W in relation to the critical values F particularly closely when using test variants with higher values of q. Instead of simply viewing the first location k with W › F_{crit} as a CP, we need to examine the test statistics of the following locations k+1, k+2, ..., k+q. If the difference between W and F_{crit} further increases, then the location with the largest difference between W and F_{crit} is likely to be the 'true' CP. In contrast, if the difference between W and F_{crit} decreases, location k is likely to be the CP. In the following I will refer to this observation as 'decision rule 2' (in contrast to the 'decision rule 1', which refers to the initial plan of viewing the first location with W › F_{crit} as the CP).

Table 8.1. Results of 4 variants of the Jupp test for path A and B. Variants include q=1, 2, 3 and 4. Significance levels of 5%, 1% and 0.1% were considered. Numbers represent the ID numbers of the locations where a CP was found. NC: No change point found along the path.

Path A	p=0.05	p=0.01	p=0.001	Path B	p=0.05	p=0.01	p=0.001
q=1	7	7	7	q=1	NC	NC	NC
q=2	7	7	7	q=2	5	NC	NC
q=3	8	7	7	q=3	11	4	NC
q=4	8	7	7	q=4	11	5	NC

It is impossible to intuitively tell where path B changes direction, although the directional difference of the first and the last vector is approximately 140° (Figure 8.3B). Correspondingly, the test results were ambiguous. The q=1 variant did not find any CPs, whereas the remaining variants did (Table 8.1). The q=2 variant indicated a significant directional change at location ID 5 ($p < 0.05$), and the test statistics W of both the q=3 and q=4 variants exceeded F_{crit} at location ID 11 already (both $p < 0.05$). In addition, they found a CP at location ID 4 and 5 respectively (both $p < 0.01$).

This example illustrates that test variants with q-values higher than 2 are more powerful, and therefore more likely to detect subtle directional changes than variants with low values of q. Thus, if we wish to perform a fine-grained analysis of directional changes in animal paths, we need to choose comparatively high q-values.

Figure 8.4. Artificial paths C and D. Path C is characterised by a straight segment followed by a segment of steady, subtle directional change. Path D is composed of two segments of differing overall direction. In both segments, the variability of the data points is high.
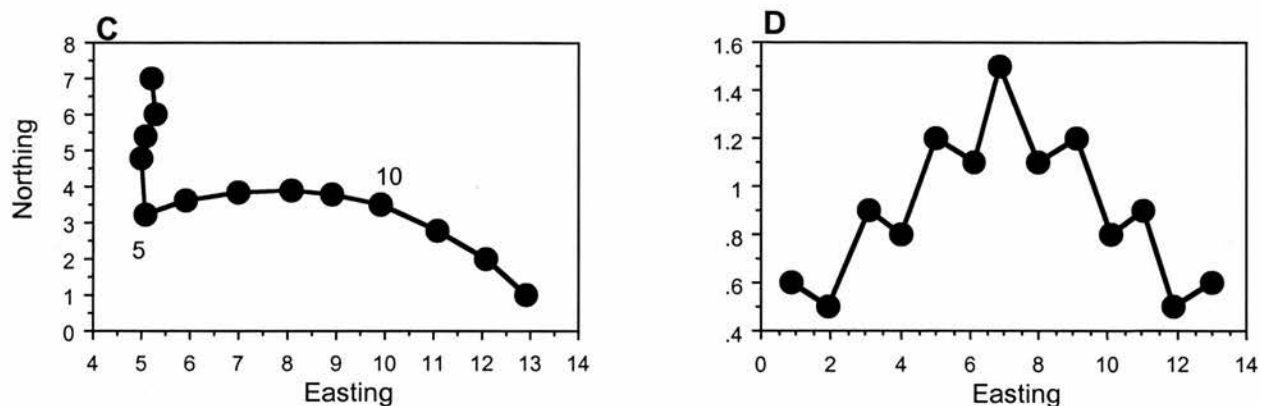
Table 8.2. Test results for path C and D.

Path C	p=0.05	p=0.01	p=0.001	Path D	p=0.05	p=0.01	p=0.001
q=1	5	NC	NC	q=1	NC	NC	NC
q=2	10	5	NC	q=2	NC	NC	NC
q=3	10	5	NC	q=3	NC	NC	NC
q=4	10	5	5	q=4	NC	NC	NC

Test results of path C were similar to those of path B. The q=1 variant found the first significant directional change at location ID 5 (p>0.05), which was a pronounced CP also from a intuitive point of view. However, all other test variants found a first CP at location ID 10 already with p<0.05. Again, this suggests that test variants with larger q-values are more likely to pick up subtle directional changes.

I designed path D (Figure 8.4) in order to examine the performance of the Jupp test when the vectors along a path exhibit large directional variability. Would any of the test variants pick up the intuitive directional change at location ID 7? Table 8.2 shows that none of them did. From this I conclude that the Jupp test gives non-significant results in two conditions. First, when paths are nearly linear, and second, when subsequent vectors exhibit high directional variability. Therefore, it seems that only those paths which are likely to exhibit low directional variability should be examined with the Jupp test.

In order to get a better feel for this issue, I designed an additional path which was similar to path D. Directional variability of the vectors in path E is slightly reduced, and it contains a clear change point at ID 7. Table 8.3. shows that surprisingly all variants of the Jupp test picked up a CP at location ID 7 ($p<0.05$). However, none of the variants rejected H0 at lower significance levels. These results suggest that in order to avoid missing any directional changes that may be important for interpretation of the data, a significance level of 5% is appropriate.

Figure 8.5. Path E and F. The variability of the vectors in path E is somewhat reduced compared to path D, but it is still pronounced in both of the path segments. Path F intuitively exhibits two directional changes, one next the goal at ID 12, and the other at position ID 7.
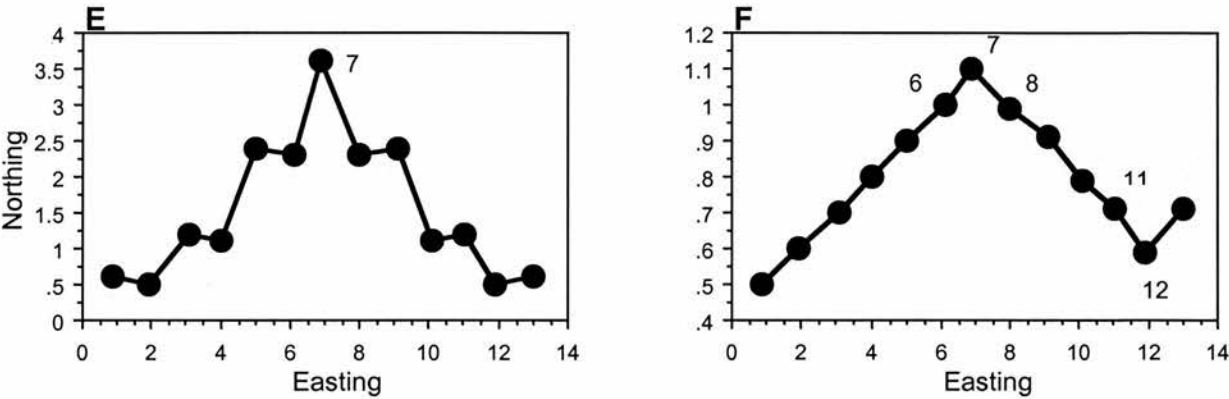
Finally, path F emphasises a similar problem (Figure 8.3.). Here, the resource place is located next to a pronounced directional change at ID 12 which contributes to a large directional variability in the first two vectors under test. An additional CP is located at ID 7. Under this condition, the q=1 variant failed to find any significant results. In contrast, the q=2 variant picked up the CP at location ID 7 ($p<0.05$), but missed the one at location ID 12. Only the variants with q=3 and q=4 were powerful enough to identify location ID 12 as a CP ($p<0.05$). This corroborates the above finding that variants with low values of q tend to miss directional changes.

8.5. Discussion

Despite the fact that the Jupp test performs multiple tests to identify a single CP, the above analyses suggest that subtle directional changes are often only found at significance levels of 5%. Since a fine-grained analysis of directional

Table 8.3. Test results for path E and F.

Path E	p=0.05	p=0.01	p=0.001	Path F	p=0.05	p=0.01	p=0.001
q=1	7	NC	NC	q=1	NC	NC	NC
q=2	7	NC	NC	q=2	7	NC	NC
q=3	7	NC	NC	q=3	12	NC	NC
q=4	7	NC	NC	q=4	12	7	NC

changes in animal paths may be crucial for obtaining insight into the cognitive mechanisms underlying their ranging, I will consider directional changes found at significance levels of 5% in the following sections.

The power of the Jupp test seemed to dramatically increase with increasing size of sample q. The methods based on q=3 and q=4 were more likely than the q=1 and q=2 variants to pick up both subtle directional changes, and CPs in the vicinity of the starting point of the test. For this reason, I will continue to use the variants with larger values of q. However, one of the disadvantages of the q=3 and q=4 variants was the phenomenon that they sometimes reacted 'too early' to directional changes. This suggested that the best way to interpret the results was to observe the test statistics W of several adjacent locations in relation to F_{crit}. When W exceeded F_{crit} over a series of locations, then the 'true' CP seemed to be at the location where the difference between W and F_{crit} was largest (decision rule 2). In the following section, I will investigate the reliability of this decision rule.

In three of the six paths examined, the test variants with q=1 did not find any CPs, although some of them were considerably prominent. This suggests that the results of the tests with q=1 should generally be viewed with caution. This may partly be due to the fact that the power of the test with q=1 is low. But also, the q=1 variant starts at k=2 only, and leaves the first location prior to the starting point untested. This potentially affects the subsequent test steps. If the first (untested) vector is in a perfect line with the subsequent vectors, directional variability of sample k remains small, and the test is likely to find a CP further away. However, if the direction of the first vector differs from the directions of its neighbouring vectors (Path F), then any CPs further down the path are likely to be missed. Obviously, the amount of variability contributed by the first vector also influences the variants using higher q-values, but the more powerful variants are more likely both to pick up the location at k=1 as a change point and to respond to later directional changes even though the early directional deviations were not viewed as significant.

With this in mind, I will now investigate the performance of the Jupp test with a set of field data. I will further employ several test variants in order to examine the Jupp procedure on more naturalistic, and thus probably less tidy paths. In particular, I will examine whether the tests of field data justify the use of the q=1 variant, and whether the above proposed 'decision rule 2' can be applied with confidence to interpret the results of the variants with higher q-values.

8.6. Testing field data - Methods

In this section, I investigate the performance of the Jupp test by applying it to two sets of field data, path A (Figure 8.6) and path B (Figure 8.10), which I randomly chose from among my data. Both paths consist of the last section of a whole day's ranging, and represent the way how the study group app-roached their sleeping site. As usual, I started the Jupp test at the 'important resource', in this case the sleeping site. I searched for the first, the second and the third directional change before the animals arrived at their goal. That is, as soon as I found the first CP, I restarted the procedure from this location, in search for the second CP before the sleeping site. I redid this procedure once, and stopped testing as soon as I found the third CP of each path.

I first labelled each GPS position of the two paths. The sleeping site was location ID 0, the reading before the sleeping site was location ID 1, the previous one ID 2, and so forth (see figures 8.6 and 8.10). Note that these numbers correspond to the k-values only in the test for the first CP before the sleeping site.

The previous section has suggested that variants with large values of q may give the most reliable results. I therefore added two more test variants to the procedure, and performed a total of 6 test variants per CP, with the q-values of 1, 2, 3, 4, 5 and 6. In order to observe the test statistic W in relation to F_{crit}, I present the corresponding values of each test variant separately in the below figures. Again I considered the critical values p=0.05, 0.01 and 0.001.

Figure 8.6. The study group used path A when travelling from a water hole (location ID 23) to their sleeping site (triangle). Numbers: ID numbers of the locations tested. Large dots: Feeding trees. Arrow: Direction of movement before reaching the water hole.
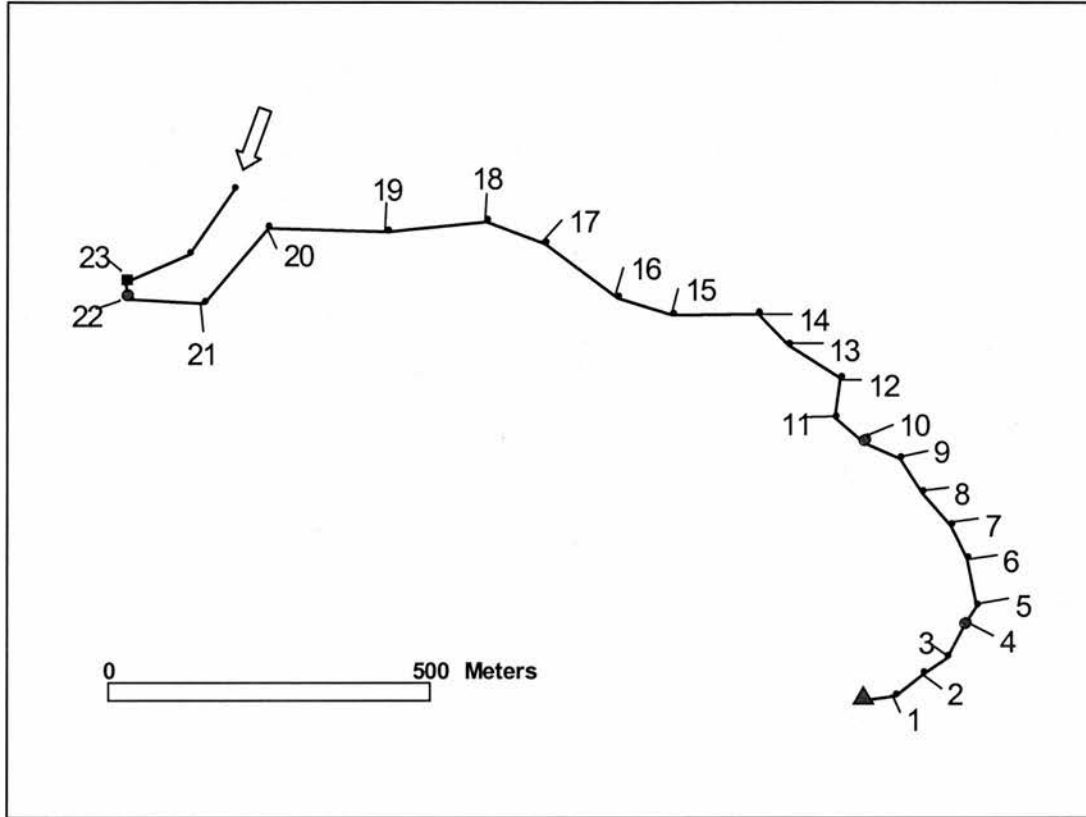
8.7. Results

8.7.1. Path A

a) First change point

I started the first set of tests at the sleeping site. The test variant with q=1 did not find a significant directional change in path A within the first 10 locations examined. W remained well below the critical values F at a significance level of 5% (Figure 8.7).

Figure 8.7. Test results for the first CP in path A. Test statistics W (black dots connected with bold line) obtained by the test variants with q=1, 2, 3, 4, 5 and 6 in comparison to their corresponding critical F-values. Only the first 10 locations under test are shown. Thin lines: Critical values for p=0.05 (left), p=0.01 (middle) and p=0.001 (right). Only the line for p=0.05 is given in the panel showing the test variant with q=1. Only the lines for p=0.05 and 0.01 are given in the panel for q=2.
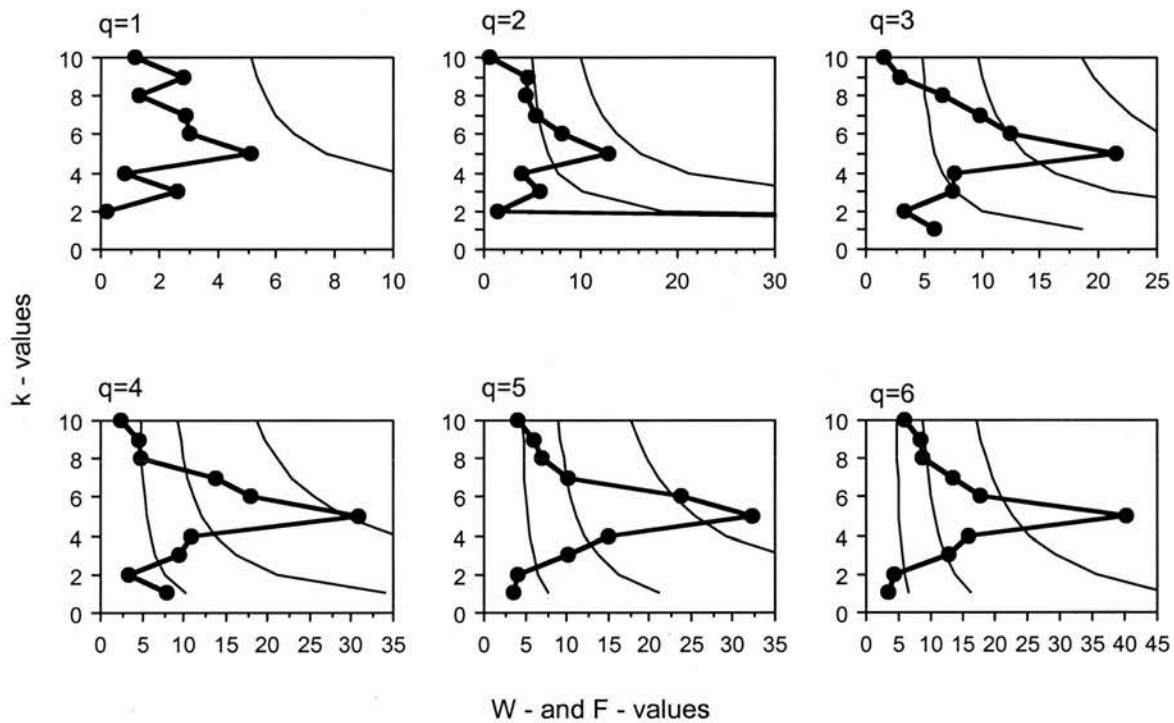
In contrast, the variant with q=2 exceeded $F_{(0.05)}$ at k=5, corresponding to location ID 5 in Figure 8.7. Note that, although not shown, W at k=1 remained below $F_{(0.05)}$. Significant directional changes at location ID 5 were also found by all other test variants, with q=3, 4, 5 and 6. But again, they tended to occur too early. W obtained with the q=3 variant exceeded $F_{(0.05)}$ for the first time at k=4, and with all other variants at k=3. Thus, when interpreting the results according to 'decision rule 1' (the CP is the location where W exceeds the

critical value for the first time), either location ID 3, ID 4 or ID 5 may be viewed as a CP, depending on the test variant. 'Decision rule 2' in contrast led to a different picture. After exceeding $F_{(0.05)}$ for the first time, the test statistics W of all variants dramatically increased over the next few values of k, and peaked at k=5. Thus, this way of looking at the results suggests that location ID 5 is the 'true' CP, and this result does not depend on either of the variants.

b) Second change point

Based on the above results, I restarted the Jupp test at location ID 5 (Figure 8.6), in order to find the second CP before the sleeping site. Location ID 6 now became the location of k=1, location ID 7 the location of k=2, and so forth. Figure 8.8. shows that the results obtained were inconsistent.

The q=1 variant found the first significant CP at k=9, which corresponds to location ID 14 (p<0.05). However, the test statistics of the variant with q=2 exceeded $F_{(0.05)}$ for the first time at k=4 already, suggesting that the first directional change occurred at location ID 9 (p<0.05).

The variant with q=3 converged with the q=1 variant and first exceeded $F_{(0.05)}$ at k=9. In contrast, the q=4 variant suggested that the first significant directional change was at k=7, that is, at location ID 12. Since W decreased after this location, decision rule 2 did not alter this finding. W of the two variants with q=5 and q=6 exceeded $F_{(0.05)}$ at k=7 for the first time. However, when

Figure 8.8. Test results of the second CP in path A. All tests were started at location ID 5. Consult Figure 8.7. for legend.

W - and F - values
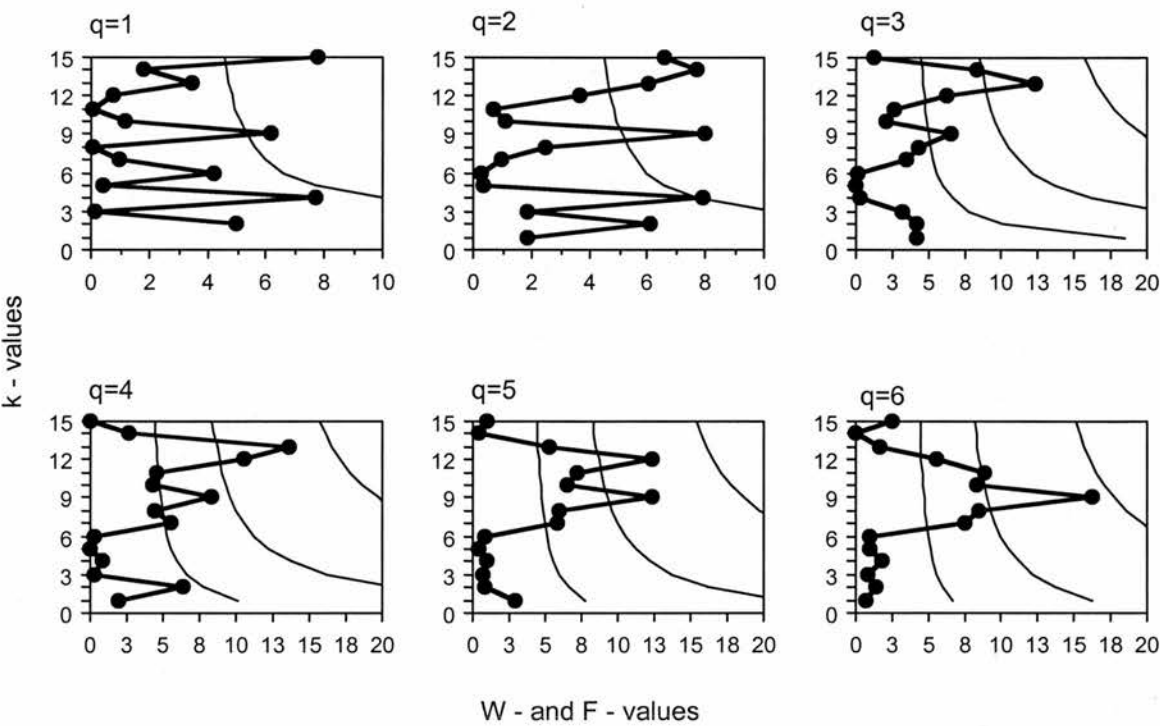
applying decision rule 2 the conclusion pointed towards a CP at k=9, that is at location ID 14 (both p<0.01).

The inconsistency of these results underline the difficulty of deciding on 'appropriate' levels of q and α. There is evidence for CPs at three locations, ID 9, ID 12 and ID 14, all of which intuitively seem reasonable results.

For example, the q=2 variant suggests that the mean direction between location ID 5 and ID 9 (sample k) is significantly different from the mean direction of the vectors between location ID 9 and ID 11 (sample q). However, when increasing q to 3, we compare the mean direction of the vectors between lo-

cation ID 5 and ID 9 with the mean direction of the vectors between location ID 9 and 12. In the latter case, the difference of variance in the two samples disappears.

Contrary to the findings of the previous section, these results suggest that increasing sample size q does not necessarily improve the chances of detecting subtle directional changes. In the above tests, the q=2 and the q=4 variants found a CP which disappointingly was not detected by the other variants. One way of solving this problem may consist of using several variants of the Jupp test simultaneously when searching for a single CP, and viewing the first location which gives a significant result by any of the variants as the CP. In the above tests, this would point to the conclusion that there is a significant directional change at location ID 9.

c) Third change point

Although I was not able to unambiguously identify the second CP in path A, I restarted the Jupp test from location ID 14, in search for an additional CP. The q=1 variant indicated that the first significant directional change occurred at k=6, that is, at location ID 20 (p<0.05, Figure 8.9). The test statistic W of the q=2 variant peaked at k=9, but the directional change at location k=8 was highly significant with p<0.001. Thus, decision rule 1 led to the conclusion that location ID 22 is a CP, whereas location ID 23 is a 'true' CP according to decision rule 2.

Figure 8.9. Test results for the third CP in path A. All tests were started at location ID 14.
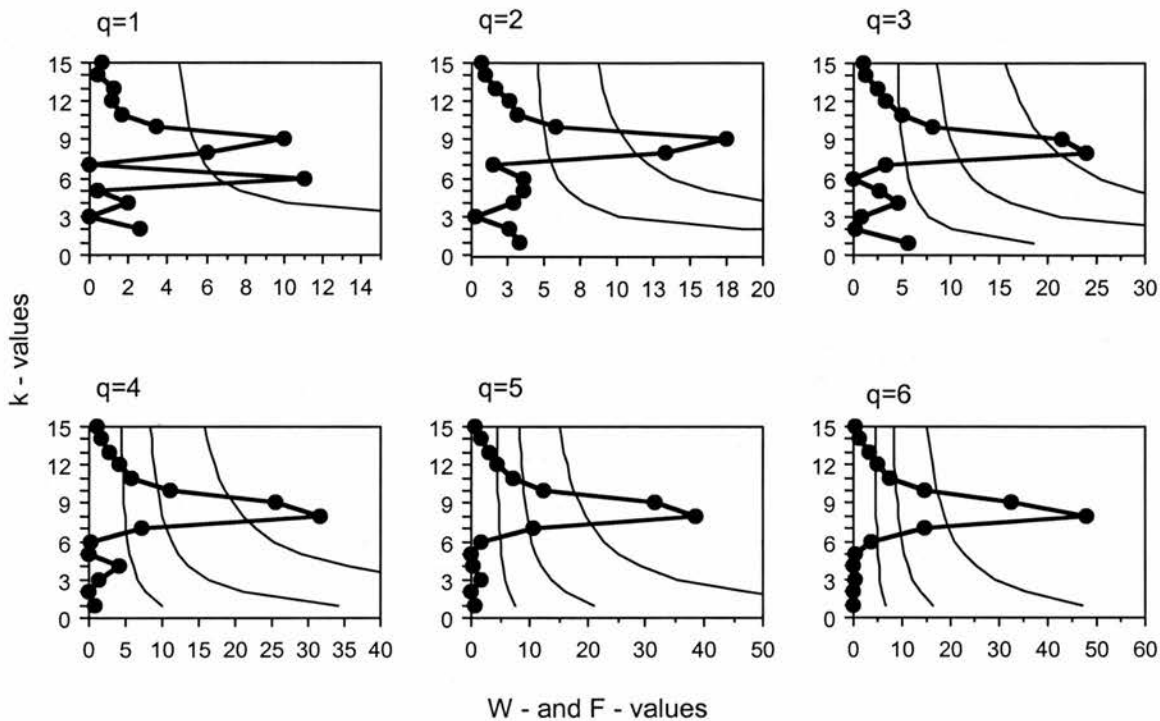
The variant with q=3 found a significant directional change at k=8, and

therefore pointed towards the conclusion that location ID 22 was a CP. The

remaining variants with q=4, 5 and 6 were significant with p<0.05 at k=7.

Thus, decision rule 1 suggested that a CP is present at location ID 21,

whereas decision rule 2 led to the conclusion that k=8, and therefore location

ID 22, should be viewed as the 'true' CP. This is the first evidence that the

q=1 variant needs to be included into the change point analysis. It was the

only variant to identify location ID 20 as a CP, whereas all other variants

found CPs at either of the following locations. Thus, the most conservative

conclusion is that the path segment starting at location ID 14 changes

direction for the first time at location ID 20.

Table 8.4. ID numbers of CPs in path A found by tests with q-values of 1, 2, 3, 4, 5 and 6. Two different decision rules for interpreting significant results were applied. Decision rule 1: the CP is the location where W exceeds F for the first time. Decision rule 2: the CP is the location where the difference between W and F is largest in a series of significant test results. All results that were significant at p<0.05 are shown.

CP 1	Rule 1	Rule 2	CP 2	Rule 1	Rule 2	CP 3	Rule 1	Rule 2
q=1	-	-	q=1	14	14	q=1	20	20
q=2	5	5	q=2	9	9	q=2	22	23
q=3	4	5	q=3	14	14	q=3	22	22
q=4	3	5	q=4	12	12	q=4	21	22
q=5	3	5	q=5	12	14	q=5	21	22
q=6	3	5	q=6	12	14	q=6	21	22

Table 8.4. summarises the results of the above tests and emphasises the different conclusions that I derived from the two decision rules. It shows that decision rule 1 (the CP is the location where W exceeds F for the first time) leads to the same conclusions as decision rule 2 (the CP is the location where the difference between W and F is largest in a series of significant test results) with test variants of low values of q. However, decision rule 2 may be applied to the variants with q-values of 3 or larger, because they tend to find CPs 'early'.

Figure 8.10. Path B led from a water hole (rectangle, location ID 30) to the sleeping site (triangle). Numbers: ID numbers of the locations tested. Large dots: Feeding trees. The arrow indicates the direction travelled by the study group.
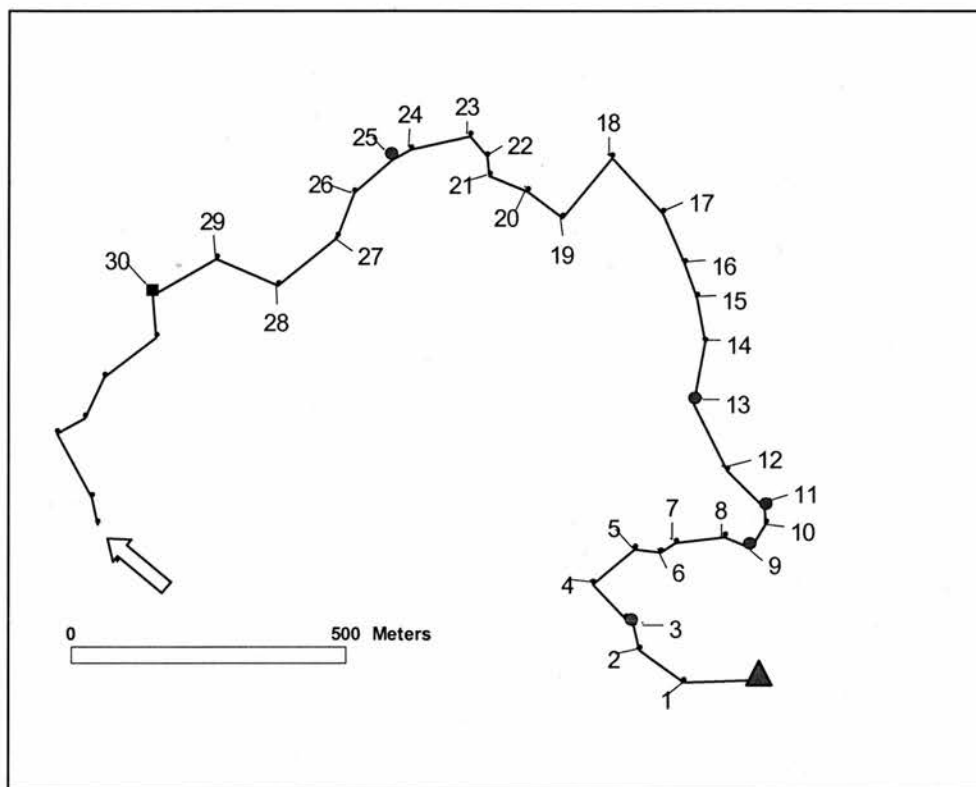
8.7.2. Path B

a) First change point

The tests for the first CP before the sleeping site in path B gave rather consistent results across different test variants (Figure 8.11). Nevertheless, the test with q=1 failed to detect a CP at a significance level of $p<0.05$ within the first 15 locations under test. In contrast, the q=2 variant found a significant directional change at k=4, that is, at location ID 4 with $p<0.05$. Both the q=3 and the q=4 variant confirmed this result ($p<0.01$ and $p<0.001$ respectively).

Figure 8.11. Test results of the first CP before the sleeping site in path B.
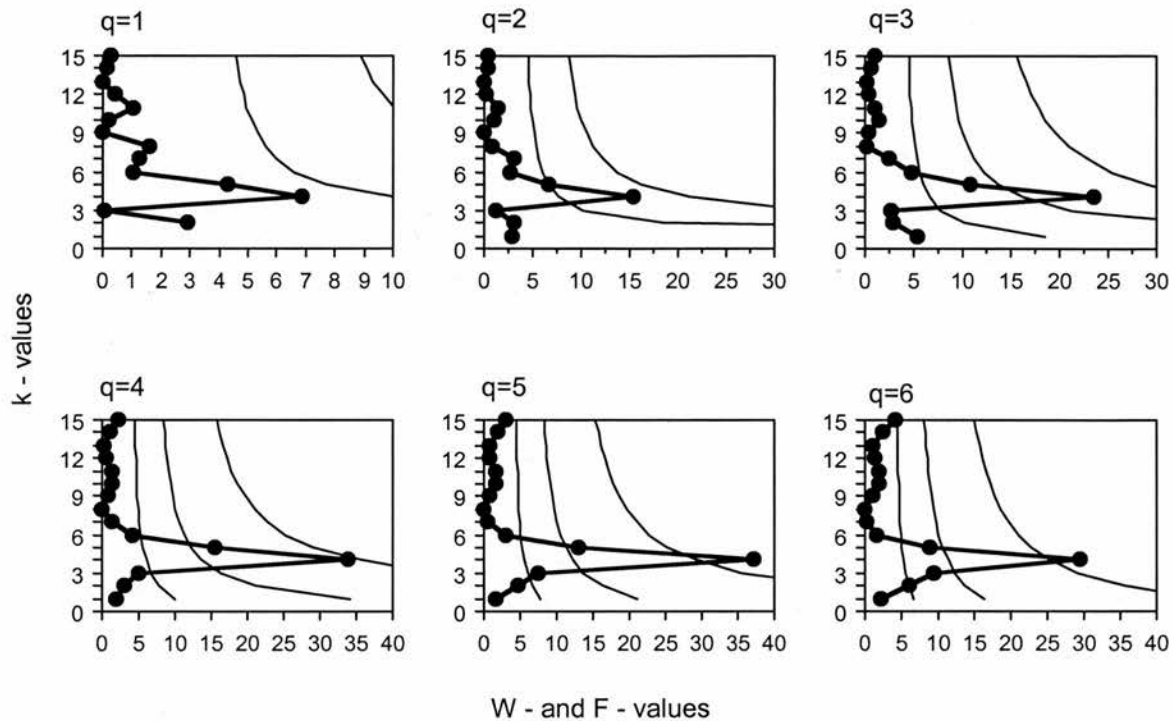
Again, in the test variants with q=5 and q=6 W exceeded $F_{(0.05)}$ earlier, namely at k=3 and k=2 respectively. That is, decision rule 1 for these variants points to the conclusion that the first CP before the sleeping site is at location ID 3 or ID 2 respectively. But again, decision rule 2 suggests that the 'true' CP is at location ID 4. Thus, location ID 4 can be viewed as the first directional change before the sleeping site with confidence.

b) Second change point

I restarted the Jupp test at location ID 4, in search of the second CP before the sleeping site. Figure 8.12 reveals that the test with q=1 found the first

Figure 8.12. Test results of the second CP in path B. All tests were started at location ID 4.
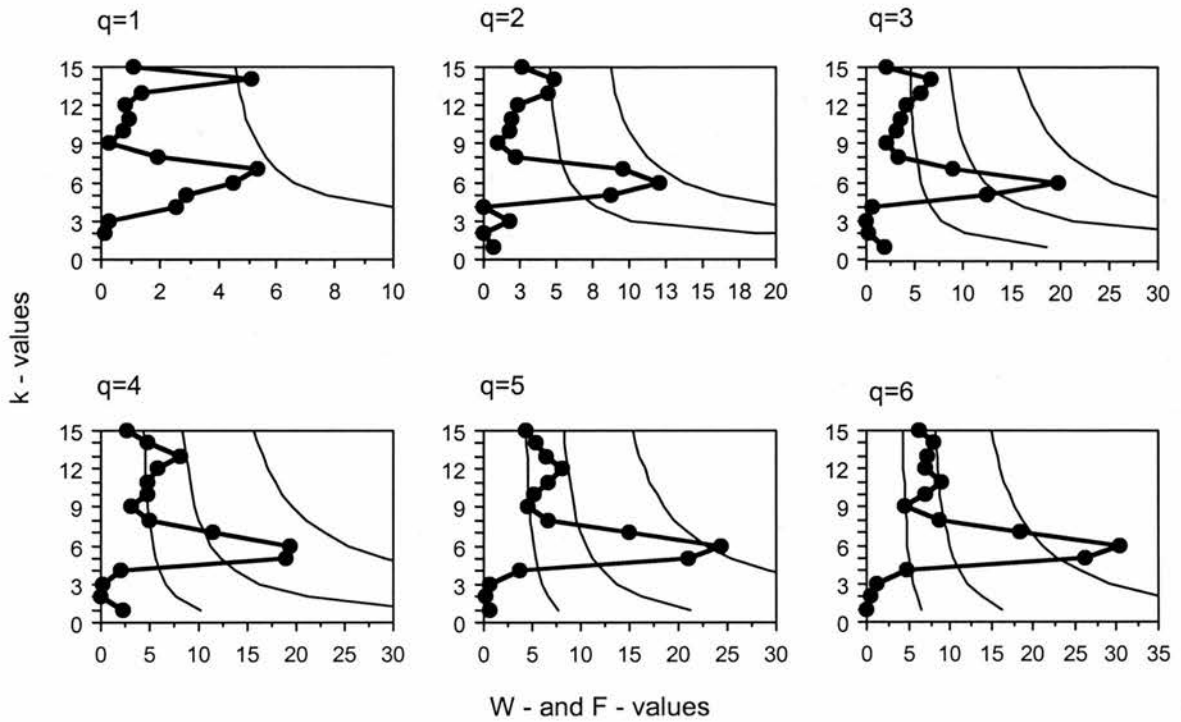
significant directional change at k=14 (p<0.05), corresponding to location ID

18. The test variants with larger q-values found a CP earlier. All test statistics

W exceeded $F_{(0.05)}$ for the first time at k=5 (decision rule 1), suggesting that

location ID 9 can be viewed as the second CP. This result was significant at

p<0.01 for the test variants with q=4 and q=5 , whereas the test with q=6 was

significant at p< 0.001. However, decision rule 2 suggested that H0 could be

rejected with even smaller significance levels at k=6, and that location ID 10

can be viewed as a CP.

c) Third change point

In order to find the third CP before the sleeping site, I restarted the Jupp test at location ID 9. The test variant with q=1 gave a highly significant result at k=9, corresponding to location ID 18 (p<0.01). In contrast, the test statistics of both the q=2 and the q=3 variant already exceeded $F_{(0.05)}$ at k=8 (ID 17). However, decision rule 2 suggested that the 'true' CP was at k=9 (ID18). Interestingly, the q=4 variant found a significant directional change at k=8, but did not pick up a CP at k=9. Thus, both decision rules for the q=4 variant led to the conclusion that location ID 17 should be viewed as a CP.

The q=5 variant was significant at k=7 already, suggesting that location ID 16 is a CP. Again, applying decision rule 2 did not alter this result. And finally, the test statistics W of the q=6 variant exceeded $F_{(0.05)}$ for the first time at k=8, but decision rule 2 led to the conclusion that there is a significant directional change at k=9, which corresponds to location ID 18.

Table 8.5. summarises the results of the three tests performed along path B. Generally, the results corroborated the previous finding that the q=1 variant sometimes ignores CPs that are picked up by other test variants. On the other hand, the q=1 variant detected abrupt directional changes of only a single vector that the remaining variants missed.

Figure 8.13. Test results of the third CP in path B. All tests were started at location ID 9.

k - values

W - and F - values
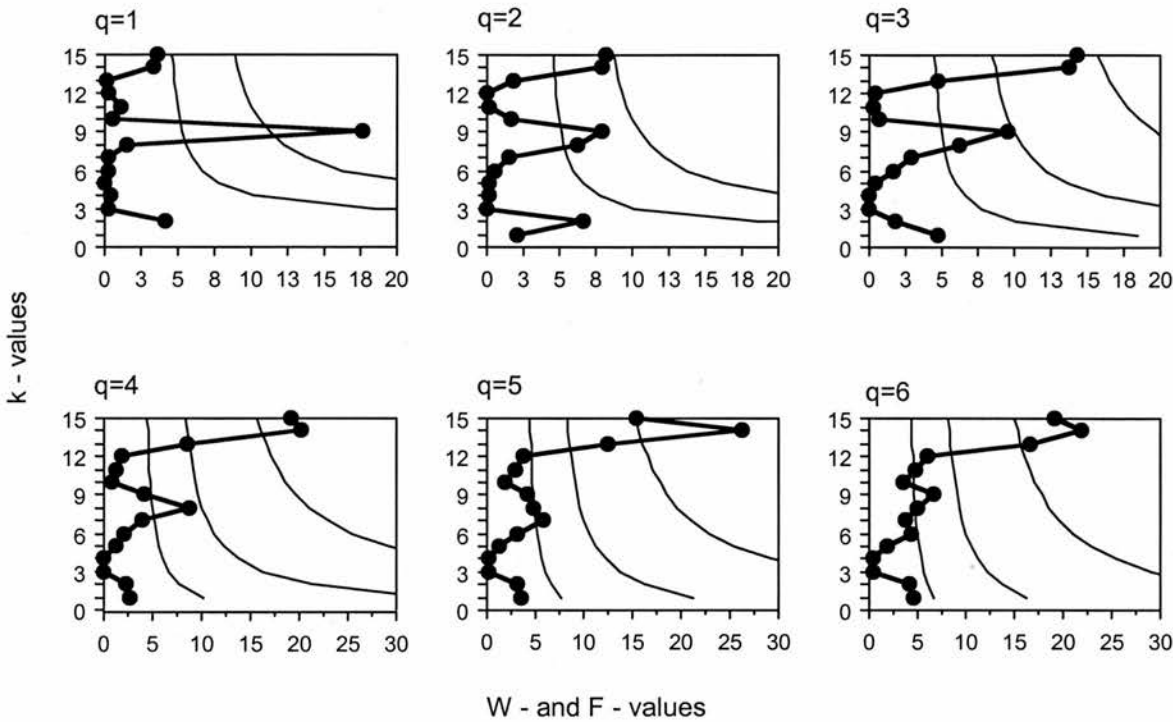
The q=2 variant found directional changes as reliably as the variants with higher values of q. However, and as expected, its power seemed to be considerably lower. Variants with q-values beyond 2 tended to find CPs 'early', that is, one, two or even three locations before the intuitively 'true' CP. For these variants the decision rule 2 may provide more accurate results than decision rule 1.

Table 8.5. ID numbers of CPs in path B found by tests with q-values of 1, 2, 3, 4, 5 and 6. Two different decision rules for interpreting significant results were applied. Decision rule 1: the CP is the location where W exceeds F for the first time. Decision rule 2: the CP is the location where the difference between W and F is largest in a series of significant test results. All results that were significant at $p < 0.05$ are shown.

CP	Rule 1	Rule 2	CP 2	Rule 1	Rule 2	CP 3	Rule 1	Rule 2
q=1	-	-	q=1	18	18	q=1	18	18
q=2	4	4	q=2	9	10	q=2	17	18
q=3	4	4	q=3	9	10	q=3	17	18
q=4	4	4	q=4	9	10	q=4	17	17
q=5	3	4	q=5	9	10	q=5	16	16
q=6	2	4	q=6	9	10	q=6	17	18

8.8. Discussion

In this section I have investigated six change-points in two 'real' baboon paths with the aim to find the most appropriate levels of q to apply to field data. The results revealed that in order to perform a fine-grained analysis of animal paths, several variants of the Jupp test need to be simultaneously applied. Variants with smaller q-values were more likely to detect subtle directional changes which consisted only of a few vectors. In contrast, variants with q-values up to 6 were more powerful, but detected only pronounced directional changes. Thus, variants with larger q-values provide stronger evidence for significant directional changes, but tend to ignore more subtle changes, such as small detours that may consist of only a few vectors.

Also, there remained some open questions as to the best interpretation of the results when using larger values of q. Test variants with large values of q sometimes reacted too early to directional changes in the paths. It therefore seemed appropriate to investigate the test statistic W at the locations immediately following the first significant result. Instead of viewing the location as a CP whose test statistic W first exceeded the critical values, I proposed to take the location with the largest positive difference between F and W into account, when a series of locations gave significant results. This interpretation seemed to be appropriate under some, but not all conditions.

On the other hand, variants with small values of q tended to give results that were significant only at comparatively low levels of α. The tests with q=1, especially, sometimes did not respond in a satisfactory way, but tended to miss change points that tests with larger q-values detected. On the other hand q=1 was the only test variant that found pronounced directional changes of single vectors which other test variants tended to miss.

The Jupp test may need modification before it can be applied to animal paths with more confidence. Nevertheless, I will experimentally apply its present version to a set of field data in the next section of this thesis, with the aim of highlighting the potential merits of such a statistical tool for further research on animal ranging and cognitive mapping.

8.9. Testing baboon foraging paths - Methods

Chapter 4 has revealed that outward paths towards fruit sources and movements towards water holes were characterised by a high degree of linearity and high travel speed. This suggested that advance planning was most likely to occur in these situations. Based on these findings, I applied the Jupp test to the outward paths leading to two food patches, the distant grewia field in the Northern plain, and the sable forest on the SW slope of the hill.

In addition, I examined the paths leading to both the buffalo water hole in the plain, and the kudu water hole on the hill. The Kloof group approached the kudu water hole during inward movements only. Since outward movements were more linear and faster than inward movements (chapter 4), I investigated the inward movements towards the buffalo water hole only. By doing so, I intended to make sure that the two data sets were comparable. Also, I excluded all approaches to the buffalo water hole when the Kloof group had met another group and was forced to take detour paths.

The previous section of this chapter has shown that the Jupp test is sensitive to directional changes, and sometimes picks up change points in the vicinity of the starting point of the procedure, the important resource. Change points in the vicinity of the resources are likely to be locations from where the resources were visible. However, the main interest of this chapter is to find change points that cannot be attributed to direct visual stimuli. I therefore tested each path twice, once for the first and once for the second CP before the water hole.

Based on the results of the previous sections, I used q-values of 1, 2, 3, and 6. Significant results with the variants with q=1, 2 and 3 indicate minor directional changes of only a few vectors, whereas the variant with q=6 reveals major directional changes that the other variants may not detect. When the variants gave different results, I viewed the location closest to the water hole as the 'true' CP. I interpreted the results according to 'decision rule 2'. That is, when a variant found a series of significant results, I viewed the locations as true CPs whose difference between the test statistic W and the critical value F was largest.

At each CP I then examined whether behavioural and topological features were typically present, according to the criteria listed in table 8.6. I included all vocalisations of the study group in this analysis. Doing so does not imply that vocalisations are necessarily causes of directional changes; rather, members of the study group may vocalise as a result of directional changes of the paths, for example because this causes them to lose visual contact with the remainder of the group.

In section 8.3, the Jupp test failed to find any CPs when the directional variability of the vectors in the paths was high. I therefore calculated the r-values (a measure of straightness; Chapter 4, Batschelet, 1981) of the paths segments between the resources and the corresponding first CPs, and between the first and the second CPs post hoc. By this means, I intended to differentiate between paths with high and low directional variability.

Table 8.6. Behavioural and topological features investigated at the CPs.

Feature	Definition
Visibility	Water hole and/or associated landmarks directly visible from CP.
Topological structures	Arriving at, following, leaving or crossing roads, former crop fields (plain) or canyons (hill).
Feeding trees	CP at feeding tree, before arriving at tree (CP located 1 GPS reading before tree), or after leaving it (CP located 1 GPS reading after tree).
Other groups	Vocalisation of other groups during 4 min prior to and 4 min after arriving at the CP.
Resting	CP at resting place, before arriving at resting place (1 GPS reading prior to resting place) or after leaving resting place (1 GPS reading after leaving resting place).
Vocalisation	Vocalisation of either of the groups' members during the 4 min preceding and 4 min following the CP.
No features	Neither behavioural nor topological features at or around CP.

8.10. Results

8.10.1. Outward movements

a) Plain

I recorded a total of 27 approaches to the distant grewia field in the N plain (Figure 8.14.). The Jupp test revealed that 17 (63%) of the first CPs were situated within the detection area of the resources (Table 8.7.), suggesting that in these cases the Kloof group adjusted their movement when they could see the resource. 13 of the first CPs (48%) were located next to a road or a

Figure 8.14. First and second change points of 27 outward paths to the distant grewia field.

Dots: Locations of resources; rectangles: first change points; stars: second change points;

dotted lines: reserve roads. Dashed circle: Intersection of 8 paths.
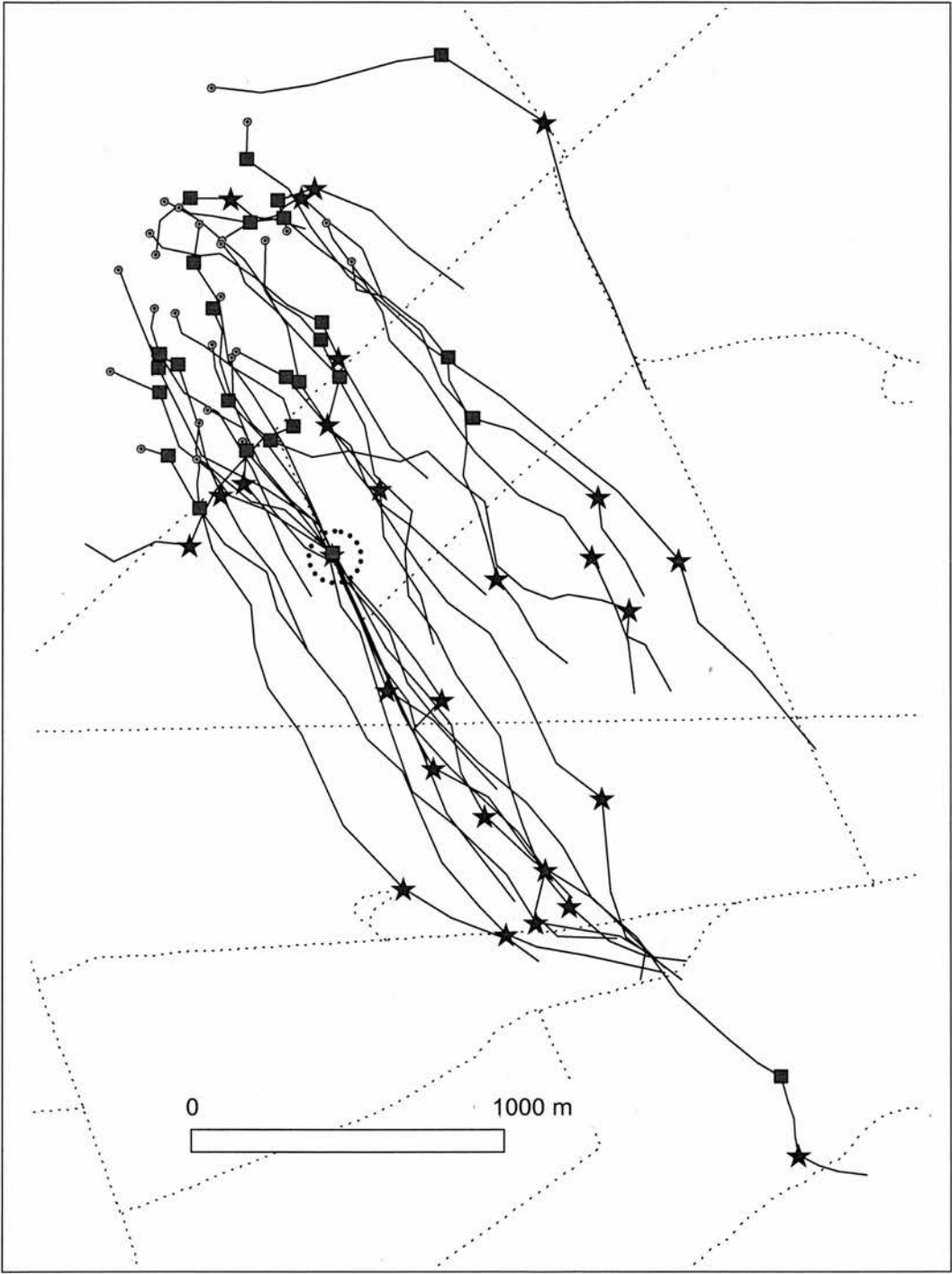
fire break, which could hint at the fact that the study animals may have taken these topological features as cues to reorient (Table 8.7.).

Other feeding sites coincided with the first CPs on 14 days (52%). Since the Jupp test picks up directional changes prior to resources, this suggests that the animals walked in straight lines from one resource to the next. Members of the Kloof group vocalised at the locations of 12 CPs (44%).

15 (56%) of the second CPs were situated next to roads and fire breaks, which corroborates the suspicion that these topological features may have served as cues for the study group to reorient themselves in the otherwise feature-poor N plain. None of the behaviours considered in this analysis occurred at high frequencies at the locations of the second CPs, suggesting that none of them was typically associated with directional changes of the paths.

An additional feature in figure 8.14. warrants a note. Eight paths intersected at a single location (marked with a dashed circle), and the Jupp test found a significant directional change at this location in two of them. Behavioural data revealed that the animals never fed or stopped for other purposes at this location. I was unaware of the importance of this location when following the animals, probably because of the lack of any conspicuous features at that place (but it was situated on a reserve road). However, the Kloof group seemed to use this location as a reference point, from where they decided to either continue along the road, or else to head in a NW direction.

Table 8.7. Topological features and behaviour exhibited at first and second CPs before the grewia and marula field (n=27). Numbers indicate frequency of occurrence. Note that more than one of the below categories can apply to each CP. Assumed detection area of a tree crown was 340 m, based on Chapter 5.

Behaviour and topology	1st CP	2nd CP
CP within detection area	17	2
CP next to topological structure	13	15
Other groups	8	6
Feeding site	14	8
Rest	0	0
vocalisations Kloof group	12	7
No evidence	0	0

b) Hill

I recorded a total of 14 approaches to the sable forest, which was situated on the NW slope of the hill (Figure 8.15.). In contrast to the grewia field in the N plain, only two of the first CPs occurred within the detection area of the forest. However, 5 more CPs were situated close to its visibility border, suggesting that that some unknown landmarks next to the forest may have guided the animals' reorientation.

Eight (57%) of the first CPs were situated at feeding sites, where the Kloof group had stopped prior to visiting the sable forest. This suggests that the animals walked in a goal-directed way from one feeding site to the next. In contrast to the paths in the plain, only 5 (36%) of the first CPs were situated

Figure 8.15. First and second change points of 14 approaches to the sable forest. Dots: Locations of kooboo berry bushes; rectangles: first change points; stars: second change points; dotted lines: 20m contour lines; Vis: Visibility border of the sable forest.
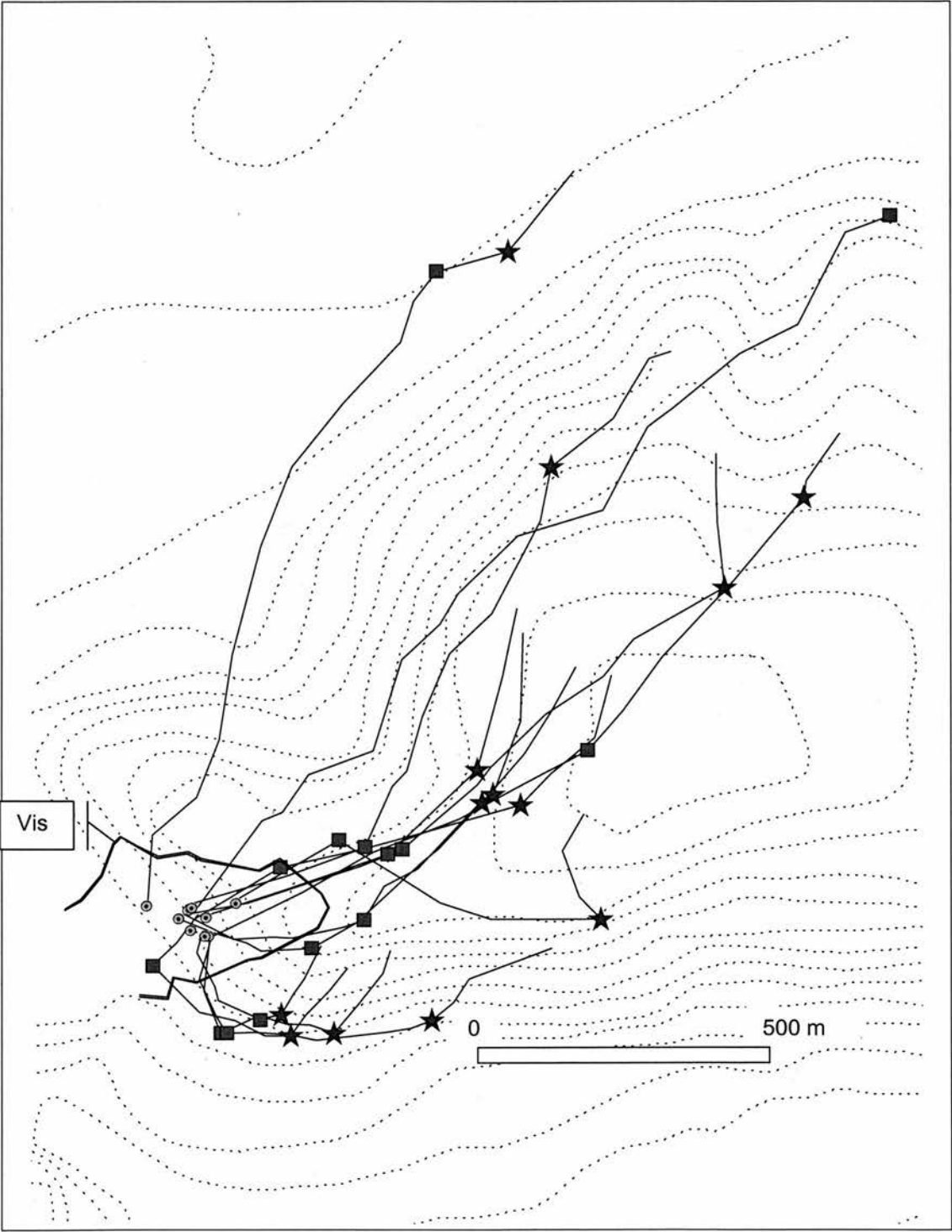
Table 8.8. Topological features and behaviour exhibited at first and second CPs before the sable forest (n=14). Note that the first CP of one of the paths was at the sleeping site, so that the corresponding second CP could not be calculated. Numbers indicate frequency of occurrence. More than one of the categories below can apply to each CP. Number in brackets: Number of CPs both within and next to the detection area of the forest.

Behaviour and topology	1st CP	2nd CP
CP within detection area	2 (7)	0
CP next to topological structure	5	8
Other groups	1	0
Feeding site	8	9
Rest	0	0
vocalisations Kloof group	1	1
No evidence	2	2

next to topological features such as the foot of the hill or the border of a canyon.

However, eight of the second CPs (62%) were situated next to a topological structure, suggesting that the animals used such features also on the hill. On 9 (70%) days, the second CP was situated at a feeding site, where the Kloof group had stopped for feeding. Again, this suggests that from these locations, the animals walked towards the sable forest in a directed manner.

8.10.2. Inward movements

a) Plain

When moving towards their sleeping site, the Kloof group approached the buffalo water hole in the N plain on 15 days in the absence of other baboon groups. The corresponding paths are given in Figure 8.16, together with their CPs. They approached the buffalo water hole on two frequently used main pathways, but sometimes took alternative, less frequently travelled routes.

The first CPs occurred within the detection area of the water hole or its associated landmarks in 11 out of 15 paths (73%). However, four CPs were situated outside this area, suggesting that from these locations the animals approached the buffalo water hole in a directed way without perceiving any corresponding cues. Two of the CPs outside the detection area were situated along one of the frequently travelled paths, whereas the other ones were located to their E and W.

Nine of the first CPs (60%) were situated next to a road or the borders of former crop fields (Table 8.9), suggesting that these structures may be important cues for orientation. Table 8.9. additionally summarises the behavioural records found at the CPs. None of the recorded behaviours systematically correlated with the CPs.

When the tests were restarted at the locations of the first CPs, 3 (20%) of the 15 subsequent CPs were situated within or very close to the area from which the buffalo water hole and the associated landmarks were visible. All other

Figure 8.16. Change points of 15 inward paths leading to the buffalo water hole. Bold lines: Baboon paths. Rectangles: First CP per path before the water hole. Stars: Second CP. Dotted lines: Reserve roads and fire breaks. Grey areas: Structures in vegetation caused by deforestation. Circles: Buffalo water hole (dam and marshy area next to it). Enclosed area labelled 'Vis': Area within which the water hole and/or the associated tall trees were visible.

Table 8.9. Topological features and behaviour exhibited at first and second CPs before the buffalo water hole (n=15). Numbers indicate frequency of occurrence. Note that more than one of the below categories can apply to each CP.

Behaviour and topology	1st CP	2nd CP
CP within detection area	11	3
CP next to topological structure	9	8
other groups	4	3
feeding site	4	10
Rest	2	0
vocalisations Kloof group	2	5
No evidence	2	1

CPs occurred well outside this area. 8 CPs (53%) were situated close to a topological structure, such as a road or the borders of an abandoned crop field (Table 8.9.). On two occasions, two CPs of different paths were situated at the same location, suggesting that the Kloof group adjusted their bearing at these locations on different days. Interestingly, 10 CPs (67%) were situated at the locations where the Kloof group had previously fed. Again, evidence that other behaviours were associated with the CPs remained only weak.

b) Hill

In contrast to the buffalo water hole, which was visible from a distance in the plain, the kudu water hole was not. It was situated in a natural rocky pool on the hill with a surface area of approximately 2 m x 1m. Rain water

accumulated in the kudu hole during the rainy season and remained available well beyond the start of the dry season. The kudu water hole could be spotted only when arriving at the edges of the pool. However, a wide variety of land-marks was present on the hill, including the structures of the valley where the kudu hole was situated and several prominent trees. It was impossible to find out which of them could possibly have guided the animals' orientation towards this water source. For example, a fig tree which was situated next to the kudu water hole could be spotted from a distance of 200 m maximally.

Seven out of 14 CPs occurred within a circle of 200 m around the kudu water hole, that is, in the area within which a prominent fig tree next to the pool was visible (Figure 8.17.). The water was visible from neither of them. Two CPs to the S of the kudu hole were situated at the same location, suggesting that the Kloof group changed their bearing at the same spot on two different days. Only four CPs were situated next the borders of a valley, and only 2 CPs were situated at locations where the animals had fed prior to approaching the water hole (Table 8.10.).

Five of the second CPs were situated next to a topological structure, four of them along a reserve road SW of the kudu hole and one at the border of a valley. Only four CPs were situated at a feeding site (Table 8.10.). Neither of the other behaviours investigated seemed to be systematically associated with directional changes.

Figure 8.17 Change points of 14 paths leading to the kudu water hole. Rectangles: First CPs. Stars: Second CPs. Bold lines: Paths. Slim lines: Reserve roads. Dotted lines: 20m contour lines. Grey areas: Approximate shape of two valleys in the Kloof group's home range.
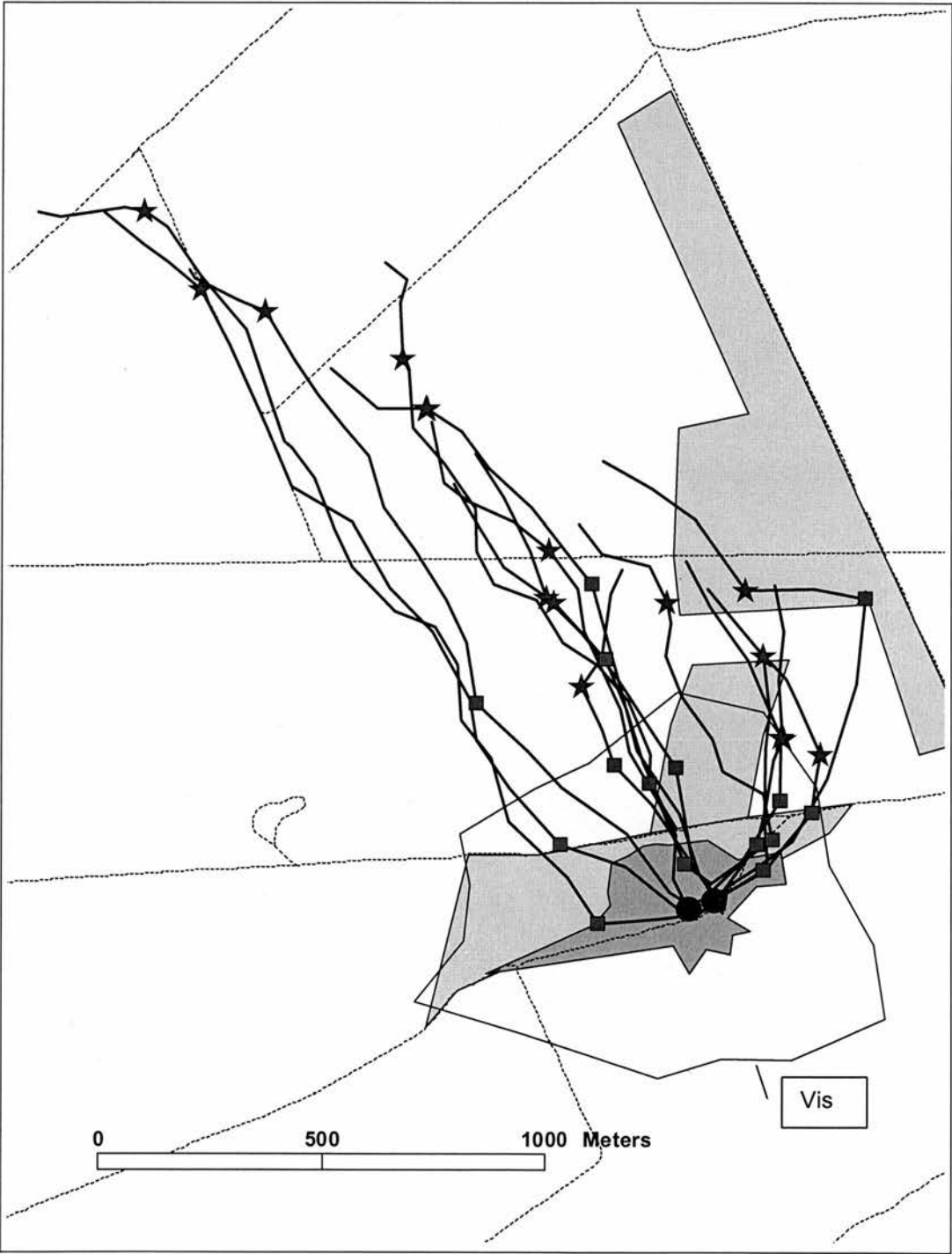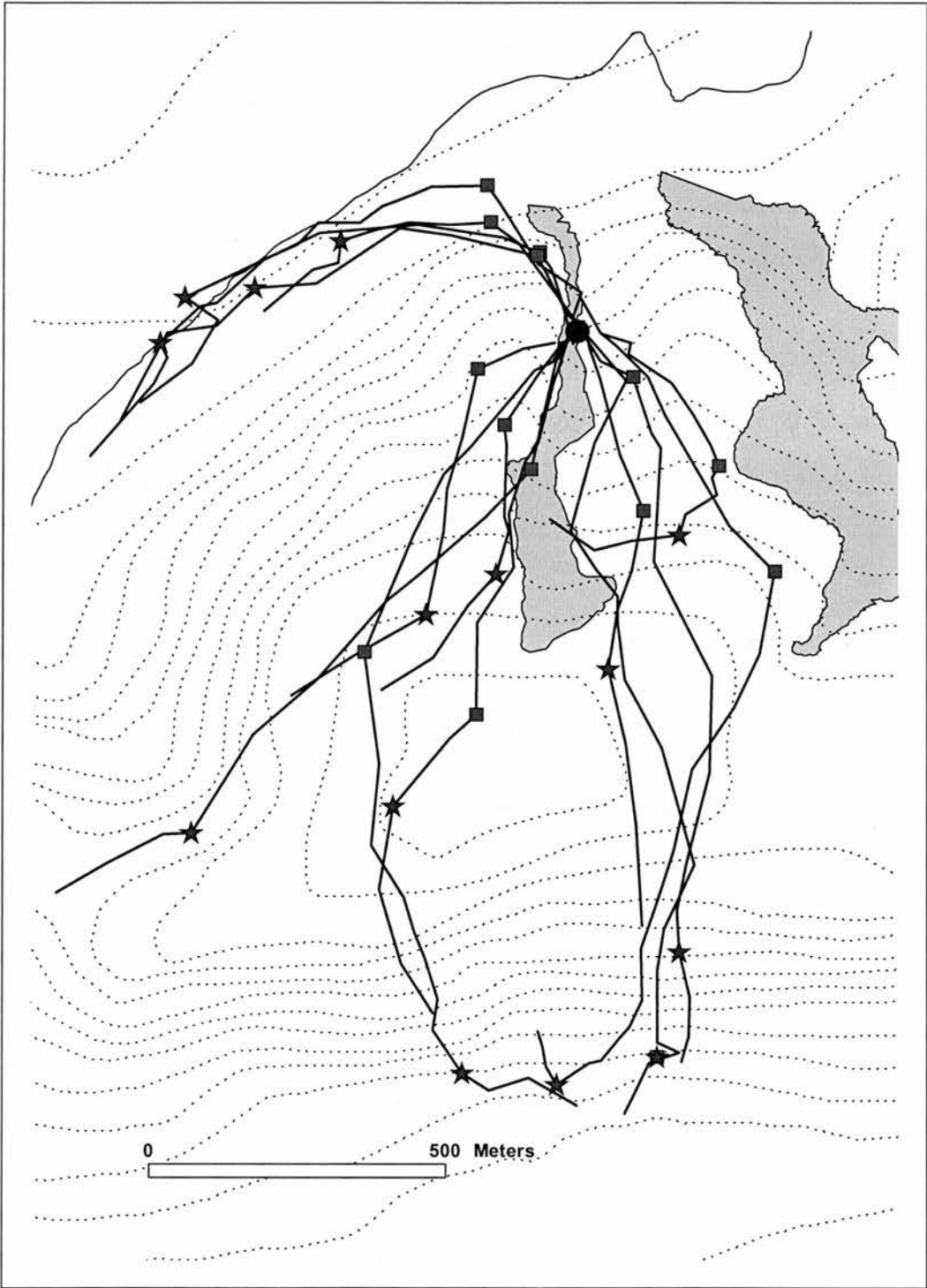
Table 8.10. Topological features and behaviour exhibited at first and second CPs before the kudu water hole (n=14 paths). Numbers indicate frequency of occurrence. Note that I was not aware of particular prominent landmarks associated with the kudu water hole, but the area as a whole was well structured.

Behaviour and topology	1st CP	2nd CP
CP within detection area of water	0	0
CP next to topological structure	4	5
Other groups	1	0
Feeding site	2	4
Rest	1	2
Vocalisations group members	4	6
No evidence	5	3

Figure 8.18. illustrates the straightness of the path segments between both the target resources and the corresponding first CPs, and between the first and the second CPs in relation to the number of vectors in the segments. It reveals that the path segments between the resources and the first CPs were typically short, whereas the segments between the first and the second CPs were longer. This is evidence that the study group navigated towards their resources in rather straight lines over long distances, but adjusted their bearing when in close proximity of the resources, probably because the resources themselves or associated landmarks came into sight.

The only exception to this pattern appears to be the sable forest, where the segments between the two CPs were short, and some of the segments be-

Figure 8.18. Straightness of path segments between resources and first CPs (dots), and between first and second CPs (triangles) as a function of the number of vectors in the path segments. Note that the number of vectors also corresponds to the number of 5min intervals in a segment.
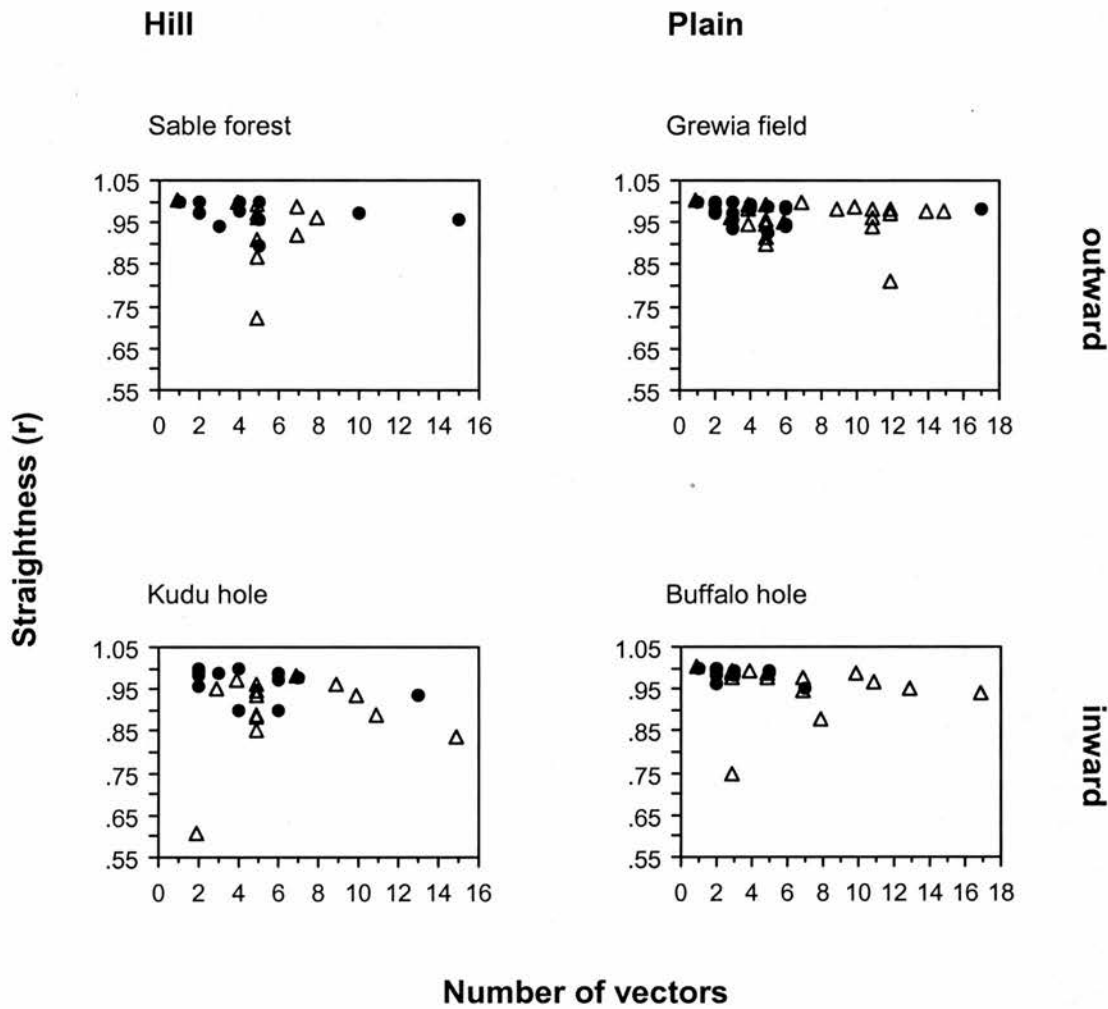
tween the forest and the first CP were long. Figure 8.15 reveals that the second CPs on four days were situated at the foot of the hill, only at a short distance from the first change points of the corresponding paths. Kooboo berries occurred in this region in a narrow belt of bushes, and the Kloof group visited the sable forest only after extensively feeding on these resources. This

caused very small numbers of vectors between the first and the second CPs. On the other hand, the Jupp test found no significant directional change in one of the paths, suggesting that the animals walked directly from their sleeping site to the forest.

Figure 8.18 also reveals an outlier in each of the panels. The corresponding test results should be viewed with caution, because they are likely to be due to the fact that the Jupp test tends to miss directional changes in paths with high directional variability and should be ignored. Therefore, plotting a measure of the directional variability of the path segments between the starting point of the test and the location of the CP seems important for interpreting the results of the Jupp test in general.

8.11. Discussion

With this chapter I have aimed at developing a new approach to the analysis of animal foraging paths and the cognitive mechanisms of orientation. In co-operation with Prof. Peter Jupp I have developed a statistical tool which focuses on the directional changes of paths. The idea behind this test was that the locations where paths significantly change direction can reveal important insights into the way how baboons orient themselves in space.

However, the results I obtained remained somewhat ambiguous. Using an entirely new statistics procedure leaves open many questions as to the de-

gree of its meaningfulness unless large amounts of data have validated it. Nevertheless, the Jupp test is an interesting approach to the wide field of unanswered questions in the context of animal ranging.

My analyses have shown that the test performs well for relatively straight paths that contain only few directional changes. Under these conditions the results were independent of the values of q, and different test variants gave the same results. Also, the Jupp test seemed to be very sensitive to subtle directional changes under this condition.

However, when the directional variability of the vectors under test increased, the test variants with differing values of q tended to give differing results. I could not think of any biological reason that would better justify the use of certain values of q than others. Therefore, interpretation of the results became problematic. In the third section of this chapter, I have decided to apply several test variants to each path, and to view those locations as 'true' change points which were closest to the starting point of the test (eg. a water hole, or a former change point), irrespective of the test variants used. By doing so, I have attempted to find the first location at which the baboons changed direction, no matter of whether these changes consisted of only a single vector or more.

Bearing in mind that this statistical tool may need to be optimised in the future, I view the results with some reservation. However, the test results from a total

of 70 paths leading to two feeding areas and two water holes point towards some interesting conclusions.

When approaching the grewia field and the buffalo water hole in the plain, the Kloof group often changed direction at a distance from the resources ('second change points'), and then held their bearing over large distances up to several km. An additional change point often occurred shortly before arriving at the resources ('first change points'). This suggests that the animals walked in a directed way over large distances, and remembered the approximate directions of the resources. However, their course was not entirely accurate, so that they needed to adjust it when in sight of their goals. Also, they did not follow fixed routes, but approached their resources in a flexible way. Walking over large distances in a directed manner and adjusting the bearing shortly before arriving is not consistent with the notion of network maps (Byrne, 1978; 2000), since a network map predicts relatively fixed routes along known landmarks. Rather, the observed movement pattern suggest that some sort of compass is involved in orientation, with which the animals can set a course, and then hold it over large distances, as observed in homing birds (Kramer, 1959; reviewed in Wiltschko & Wiltschko, 1998). Since prominent landmarks were lacking during the outward movements towards the grewia field, this result points toward the conclusion that vector knowledge could be involved in the wayfinding of baboons.

Change points often occurred in the vicinity of roads, firebreaks and borders of former crop fields in the plain. This suggests that the Kloof group have used

conspicuous cues for reorientation in the course of their journeys in the plain, where orientation must inevitably be difficult, given both the monotony of the landscape and the restricted visibility. This finding is consistent with the network map hypothesis.

Also, change points at topological features were less frequent on the hill, which offered a wide variety of cues for navigation, such as slopes or the views to the neighbouring mountain and over the plain. This richly structured environment is likely to have allowed the animals to move more freely, compared to the plain, because a wide variety of reference points could potentially guide their orientation at any location.

Several baboon paths conspicuously intersected at some locations (Figure 8.14 and 8.16), and the Jupp test indicated directional changes at these locations in some paths. This corroborates the above finding that the study group recognised landmarks along their paths, and that they used them as reference points for their journeys. Intersections of paths are clearly expected under the assumption of a network map, that is, such intersections could represent the 'nodes' of the network.

In summary, the Jupp test found several converging lines of evidence suggesting that the study group represented space in a network map (Byrne, 1978; 2000). However, there was some evidence that the study group may have applied vector knowledge when approaching the distant grewia area and one of the water holes in the plain. This contradicts the finding from the

previous chapter of this thesis. A vector map would allow the animals to take efficient and novel detour paths after group encounters, but the study animals seemed not to be able to find appropriate detour paths when familiar routes were blocked. Thus, there is good evidence the study group navigated on the basis of a network map, but evidence for the use of vector knowledge in baboons is only weak. Future experiments are needed to confirm the presence of vector maps in baboons.

Chapter 9 Discussion

9.1. Introduction

In recent years, the study of primate cognition has stressed the question about the contexts in which primate brain enlargement and intelligence may have evolved. Several hypotheses have been proposed in the past, which included competition and cooperation in long-term social relationships (Byrne & Whiten, 1988; Whiten & Byrne, 1988; Whiten & Byrne, 1997), ecological demands (cognitive mapping: Clutton-Brock & Harvey, 1980; Milton, 1981; 1988; extractive foraging: Parker & Gibson, 1977; technical skills in foraging: Byrne, 1997; arboreal clambering: Povinelli & Cant, 1995) and life history parameters (Dukas, 1998; van Schaik & Deaner, 2003). Tests of these hypotheses have usually aimed at finding the hypothesis that best explains variation in brain size across species (eg. Dunbar, 1992; Barton, 2000; Byrne & Corp, 2004). The results have generally supported social explanations, and rejected ecological parameters as possible pace-makers of cognitive evolution.

In contrast, researchers who investigated insects, birds and small mammals have brought to light an astonishing variety of highly specialised cognitive abilities of their study animals (reviewed in Shettleworth, 1998; Balda et al., 1998; Dukas, 1998; Healy, 1998), leading to the view that animal minds contain a wide variety of adaptively specialised cognitive modules. For example, Shettleworth (1998), stated that

'the mind is like a Swiss army knife, a general-purpose tool made of many specialised parts'

The variety of the cognitive processes involved in orientation is particularly rich, reaching from the relative simple process of path integration to the sophisticated concept of cognitive maps (reviewed in Shettleworh, 1998; Wiltschko & Wiltschko, 2003). However, despite a handful of publications that proposed cognitive maps for primates (Altmann & Altmann, 1970; Sigg & Stolba, 1981; Sigg, 1986; Milton, 1981; 1988; Boesch & Boesch, 1984; Garber, 1989; Kummer, 1992), our understanding of how primates find their resources is strikingly poor. It was the aim of this thesis to start filling this gap, with an emphasis on the claim that primates rely on cognitive maps. In this final chapter I review the main findings of the present study, and highlight some potential avenues for future research.

9.2 Ecology and ranging

The diverse woodland biome at Blouberg produces a wealth of energy-rich food sources containing a wide variety of fruit and seeds. This rich food supply coupled with the permanent occurrence of water explained the high baboon population density in this area. With 25 members, the Kloof group was among the smallest baboon groups know to me. Group sizes of 60 - 70 individuals were common, and reached 107 members in one of the groups.

The most striking feature in the ranging of the Kloof group was their sleeping site fidelity throughout the 24 months of my field work. This seemed to be the rule rather than the exception among the Blouberg baboon population, suggesting that safe cliffs and trees occurred only in restricted numbers.

With an average of 7.7 km the daily foraging journeys of the study group were long in comparison with baboon groups of similar size in other populations. Season did not affect the distance travelled per day, although rainfall and consequently biomass production at Blouberg was highly seasonal (Chapter 2). Both results were best explained in the light of sleeping site distribution. At least six additional baboon groups regularly slept along the Northern foot of the hill at Blouberg, lined up over a distance of less than 5 km. The groups used the adjacent areas intensely, and rapidly depleted their preferred food sources. This forced the animals to forage in more distant areas.

9.3. Spatial memory

The study group left large parts of their home range unvisited over extended time periods. For example, they foraged on the South- and Southwest-facing slopes of the hill during the dry season 2001, but never returned to this area during the following 13 months. Also, they visited one of the water holes only after 14 months of data collection. These findings converge with those of three other field studies on baboons which also reported a seasonal usage of entire home range areas (Kummer, 1968; Whiten et al., 1987; Hill, 1999). This suggests that baboons need to memorise some resource places over large

portions of the year or even longer time spans, and that they possess well developed long-term spatial memory capacities.

In order to examine whether the study group needed to represent large-scale space to find distant resources, I tested several simple searching strategies which have frequently been proposed in the past (e.g. Bell, 1991; Garber & Hannon, 1993; Janson, 1996), such as random walk, systematic search and following direct visual stimuli (Chapter 5). The movements of the study group were significantly directed during large parts of the year. Only mental representations of large-scale space could explain the repeated visits to some resources, in particular to a remote, forested area at the SW foot of the hill, to a large patch of grewia bushes in the plain, and to the water holes.

The present study is the first to systematically control for direct visual stimuli of the resources. On the hill, I recorded the locations from which 173 resources became visible along the paths travelled. Neither path linearity nor travel speed was affected by whether the resources were in sight. Though negative results should generally be interpreted with caution, these findings suggest that vision played only a subordinate role during the foraging journeys of the study group.

In contrast to the Blouberg hill, the Northern plain was relatively featureless and human observers often had difficulties to orient themselves in this area. When ranging in the plain, the study group seemed to forage by sight during some, but by far not all time periods of year. Remembering a bearing of pre-

vious rewards and holding it over several km was minimally necessary to explain the repeated movements to the distant, apparently very productive area which was situated to the NW of the sleeping site.

9.4. Goal-directedness

In chapter 4 I investigated the path characteristics based on path linearity, travel speed and distance travelled from one resource to the next, and some of the factors affecting these measures. Following the intuitive idea of Sigg & Stolba (1981), Kummer (1968; 1992) and Pochron (2001), I assumed that goal-directed movements are characterised by bee-line paths coupled with high travel speed. This approach revealed that the movements away from the sleeping site in the mornings during the dry season, as well as those towards the water holes, were the straightest and covered at the highest speed, and thus were the best candidates for goal-directed movements.

Evidence that baboons do approach resources intentionally came from the finding that the study group did not feed on different food types in accordance with the food's availability. During the dry season, they fed on fruit items significantly more often than on seeds in the early mornings, whereas they used seeds occurring in the vicinity of the sleeping site as fall-back foods in the afternoons. In order to reach their preferred fruit sources they needed to bypass the seed sources in the early mornings. Bypassing visible, potential seed sources in favour of more rewarding, but out-of-sight fruit sources

strongly suggests that the baboons anticipated the rewarding fruit feeding sites, and approached them in a goal-directed manner.

However, path linearity and travel speed were not always appropriate indicators of goal-directed movements. The sleeping site was probably the most limited resource of the Kloof group, and only goal-directedness could explain the fact that they returned to a single location every night. However, the corresponding path linearity and travel speed were significantly lower than those of movements towards food and water sources. This phenomenon clearly warrants a note of caution for further research. Sleeping sites seem to differ from food and water sources in that their value to the animals dramatically increases around the time of nightfall. The study group always arrived in its vicinity well before dusk and seemed to take advantage of the remaining hours of daylight to feed or to socialise in the area. Therefore, concurrent path linearity and travel speed only indicate goal-directedness to resources whose momentary value is high relative to other resources. It seems reasonable to assume that high travel speed and directed movement reflect goal-directedness, but low travel speed and undirected movement do not necessarily imply that movements were less goal-directed.

Yet another factor significantly affected path linearity and travel speed. When other groups of baboons were present in the vicinity of the study group, path linearity decreased, whereas travel speed increased. When other groups were close, they bypassed resources they would have visited in their absence. This reflects the tendency of baboon groups to avoid each other at some study

sites (Anderson, 1981; but see Hamilton et al., 1975), probably as a response to male competition for females or the risk of infanticide (reviewed in Henzi & Barrett, 2003).

Thus, researchers who aim at investigating the properties of primate ranging in the future need to be aware that path characterisitcs (Chapter 4) and home range use (Chapter 3) can be affected by factors other than resource distribution and predation risk. Especially with respect to predation risk, this has important implications. Several studies (Cowlishaw, 1997; Hill; 1999) have recently found that small groups tend to spend more time in areas that seemed to yield less nutritional income than other areas, areas where the large groups preferentially foraged. This was viewed as an adaptation of small groups to the increased danger of being attacked by predators. My data, however, suggest that the home range use of the small Kloof group was affected by the presence of larger groups. In order to avoid confounding group avoidance and predator avoidance strategies, more research on the nature of intergroup relations is needed.

9.5. Planning abilities

It is only a small step from claiming that baboons travel in a goal-directed way by means of mental representations of large-scale space to the statement that they plan their foraging journeys. Two kinds of questions may be stressed in this context: 1) How far do they plan ahead? and 2) how fine-grained are such plans?

On days when the study group foraged for the highly preferred but scarce mountain figs *(Ficus glumosa)*, they departed significantly earlier from their sleeping site than on days when they foraged for abundant food sources. This effect remained when day temperature and time of sun rise were accounted for. This is evidence that they anticipated the abundance and probably also the nature of the resources they were going to visit when still at their sleeping site, even though they could not see them directly. Thus, the study group and baboons in general do plan at least parts of their journeys.

During the mountain fig season, they visited 2 - 4 fig trees per morning in a way that suggested goal-directedness, that is, in (nearly) straight lines and at high speed. However, path linearity and travel speed then significantly decreased, and they approached a number of additional fig trees at a frequency that did not differ from chance.

The most conservative interpretation of these findings is that the animals only remembered the locations of a few mountain fig trees, and were effectively unaware that more specimens were available to them. This interpretation converges with the findings of Cramer & Gallistel (1997), who proposed that monkeys in the lab only store a small amount of information at a time.

However, the reward of the fig trees was largest in the early mornings, but was significantly decreased after a visit of a baboon group. The finding that the study group ceased to forage exclusively for mountain figs and started to feed on alternative food sources at the time when all available figs were likely

to be depleted by the neighbouring groups supported a slightly different interpretation. My data showed that mountain figs that were visited in a goal-directed way yielded a relatively constant reward over time, whereas the remaining trees gave highly variable rewards, which probably depended on whether they had been visited earlier by other groups. The movements of the study group during the mountain fig season could therefore best be understood as a response to risk (Kacelnik & Bateson, 1996). The study group seemed to decide on alternative food sources as soon as the value of the unvisited figs became unpredictable. Although risk-aversion is wide-spread in animals across different orders (Kacelnik & Bateson, 1996), very little attention has been paid to this phenomenon in the primate learning and foraging literature.

The baboon movements during the mountain fig season suggested that they anticipate at least the first part of their journey in the mornings. However, these data did not permit an answer to the question of whether they planned over larger time frames. Earlier studies on primate ranging and feeding strategies have stressed the complexity of many primate environments and the need to forage selectively in order to cover their nutritional needs (eg. Barton, 1989; Milton, 1981; 1988; 2000). Implicitly or explicitly, these researchers have suggested that this complexity requires complex mental abilities, and the need to look several steps ahead.

In this context, I take a somewhat different point of view. During my field work, I was impressed by the daily routine of my study group, even during the winter months when food was scarce. Roughly, they approached a rewarding re-source place (either single or multiple patches of kooboo berries or a large patch of grewia berries), then visited a water hole later in the day and sub-sequently walked back to their sleeping site (Figure 3.2). When assuming that all intermittent resources were encountered by chance, a relatively simple plan that covers entire days could well explain these movements. In particular, such a plan does not require that the animals look several steps ahead. How-ever, the relatively simple home range structure of my study group with only a single sleeping site and abundant food supplies may not be representative of all baboon habitats. Studies that focus on movements of groups instead of individuals in additional baboon populations are therefore needed to shed more light on their planning abilities in the future.

9.6. The nature of baboon cognitive maps

The highly repetitive route on which the study group approached the first mountain figs in the early mornings was striking. This raised the question of whether travelling along well known routes was a response to the increased inter-group competition over mountain figs, or whether it is a more general movement pattern, which may hint at the fact that baboons use 'network maps' (Byrne, 1978; 2000), and do not represent space in 'vector maps' (Tolman, 1948; O'Keefe & Nadel, 1979).

I viewed group encounters as natural experiments to test the two hypotheses (Chapter 7). This revealed that in the presence of prominent landmarks next to their sleeping site, the study group took comparatively large detour paths to reach their goals. However, when landmarks were lacking, they either re-mained in visual contact with their initial path, or travelled along alternative, but frequently used routes. In addition, it was striking that group encounters were coupled with waiting periods of up to 60 min, and in one case even with the abortion of an entire journey.

These findings strongly suggest that baboons do not represent space in a vector map. This is remarkable, since any ability to do so should clearly be favoured by evolution, as the loss of time and energy of the Kloof group during group encounters impressively demonstrated. The nature of their evasive manoeuvres suggested that they use landmarks that are closely associated with important resources, but use a network map to find their ways in large-scale space (Byrne, 1978; 2000). I therefore propose that previous claims for vector maps in monkeys (Altmann & Altmann, 1980; Sigg & Stolba, 1981; Garber, 1989) and in apes (Boesch & Boesch, 1984) need to be carefully reconsidered.

Landmark use is common in animals, including insects, fish, cephalopodes, birds and mammals (reviewed in Cheng & Spetch, 1998; Collet & Zeil, 1998; Braithwaite, 1998). During landmark matching, animals are believed to com-pare a memorised view of single landmarks or landmark configurations at the goal location with the current view. When moving towards the goal, the dis-

crepancy between the current view and the learned view decreases, and it vanishes at the goal location.

In chapter 8, I have presented a novel statistical tool with the purpose of putting forward the analysis of animal movement. The idea behind this procedure was that change points in animal paths may provide interesting insight into the cognitive processes of orientation and group movement. In particular, this procedure addresses the question at what point along their routes the animals start to head towards important resources.

The Jupp test for finding change points is based on the principles of an existing parametric test for circular data. One of its advantages is that testing can be performed in Excel worksheets. However, there remain some questions open as to its performance. In particular, it was difficult to decide on the size of reference sample q, against which sample k, the vectors between the location of interest and the resource, is tested.

Several test runs on both artificial and real data revealed that the results obtained are largely independent of sample size q as long as the paths under test are relatively straight. This suggested that the corresponding results of the Jupp test can be accepted with confidence. However, when testing sets of vectors that exhibited larger directional variability, different test variants tended to give differing results.

The solution to this problem was obtained by performing multiple tests per path with several test variants of varying sample size q, and to view the first locations as change points which gave a significant result with either of the variants. By doing so, I kept the test's sensitivity to directional changes as high as possible in order to avoid missing any meaningful directional changes. This procedure was appropriate for the predominantly straight paths of the Kloof group. However, a different solution may be necessary for testing the paths of species with different ranging patterns.

In contrast to conventional statistic procedures, the Jupp test leads to less stringent interpretations with more conservative significance levels. This is due to the fact that liberal significance levels are more likely to find a difference between the two samples k and q than more conservative ones. The Jupp test is therefore more sensitive to directional changes when liberal significance levels are used. Therefore, I used a comparatively high p-value of 5%, although multiple test steps are needed to find a change point in a single path.

I applied this procedure to a total of 70 paths leading to important resources, two areas offering fruit sources and two water holes. The baboons typically walked in a directed way towards their resources. They did not follow fixed routes, but held an approximate bearing over long distances. However, this direction was not exact, and needed to be adjusted shortly before arriving at the resources. Also, change points were often situated in the vicinity of topo-

logical structures such as roads or former crop fields, suggesting that the animals navigated with respect to these cues. Furthermore, up to eight paths intersected at certain inconspicuous locations, with some paths exhibiting significant directional changes at the intersections.

The finding that the baboons travel over large distances in straight lines, and adjust their bearing shortly before arriving does not support the notion of network maps. Rather, it points towards the conclusion that the study group remembered an approximate, fixed bearing towards their resources, or navigated on the basis of Euclidean knowledge when travelling in the featureless, plain area of their home range. Only translocation experiments in large-scale space can unambiguously prove this finding.

9.7. The question of communal decision-making

With this thesis, I have intended to gain some insight into the mental processes that underlie the ranging of a group of baboons in a natural environment. Implicitly, I have viewed 25 adult and juvenile individuals of both sexes as a single organism that finds its way in space, and I have neglected the fact that the relevant mental processes take place on an individual rather than on a group level. Thus, I have neither addressed any questions as to the identity of the animals whose mental processes we are looking at, nor as to the social processes that are likely to take place in the context of communal ranging.

Our understanding of the mechanisms of group coordination and communal decision-making in primates and other animals are still very poorly understood (reviewed in Byrne, 2000). To date, several converging lines of evidence point towards the conclusion that more than a single individual is involved in the ranging decisions of baboon groups, and that some individuals are more influential than others (Kummer, 1968; Stolba, 1979; Dunbar, 1983; Byrne et al., 1990). Older males were found to be most influential in hamadryas *(Papio hamadryas;* Stolba, 1979) and mountain baboons *(Papio ursinus;* Byrne et al., 1990), whereas the dominant females have been shown to take the final ranging decisions in gelada baboon groups *(Theropithecus gelada;* Dunbar, 1983). For savannah baboons, a single qualitative observation is available. It suggests that the dominant female was most influential in a group of olive baboons *(Papio anubis;* Rowell, 1972). Savannah baboon females are probably more experienced with respect to the layout of their home ranges than males, because they usually remain in their natal group throughout their lives. In contrast, the males migrate, and thus change their home ranges at least once per life-time. However, empirical data on the decision processes in savannah baboons are still missing, and the claim of female leadership needs to be confirmed in future research.

9.8. Summary

In summary, this thesis has aimed at investigating the way how baboons re-present important locations in large-scale space. The study group predomi-nantly travelled in linear movements over large distances to fruit sources and

water holes, which suggested goal-directedness. Among several hypotheses of varying cognitive sophistication, extensive spatial memory remained the only explanation for their ranging over prolonged time periods. Moreover, I found evidence that they planned their foraging journeys and anticipated the nature of their resources as well as their availability.

Several lines of evidence suggested that baboons use network maps to find their resources. Time pressure as a result of inter-group competition for limited mountain figs forced the study group to follow highly repetitive routes on many subsequent days. During evasive manoeuvres from other baboon groups they took known paths in the absence of prominent landmarks. Intersections of paths of many days at single locations and change points in the vicinity of roads and firebreaks suggested that they used these cues for reorientation.

However, in the featureless plain area of their home range, the study group travelled over large distances in straight lines, and adjusted their bearing shortly before arriving. This finding is inconsistent with the notion of a network map, but points towards the conclusion that vector knowledge may be involved in how baboons find their resources.

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Appendix 1. List of important baboon foods at Blouberg Nature Reserve

English name	Latin name	Part eaten	Time of year
Red acacia	*Acacia gerardii*	Pods	June-July
Knob-thorn acacia	*Acacia nigrescens*	Pods	March- May, August
		Flowers	September
		Leaves	September
Scented-pod acacia	*Acacia nilotica*	Pods	July
Three-hook thorn	*Acacia senegal*	Flowers	August
Umbralla acacia	*Acacia tortilis*	Pods	April
Worm-cure albizia	*Albizia anthelminica*	Flowers	September, October,
		Pods	October, November
Purple hook-berry	*Artabotrys brachypetalus*	Fruit	December, January
Y-thorned torchwood	*Balanites maughamii*	Leaves	May - October
Shepherd's tree	*Boscia albitrunca*	Flowers	September
		Fruit	September, October
Grass	*Brachiaria spp*	Flowers	December, January
Velvet sweetberry	*Bridelia mollis*	Fruit	April, August
Sjambok pod	*Cassia abbreviata*	Leaves	November
		Pods	March, April
Velvet bushwillow	*Combretum molle*	Pods	May
Tall fire-thorn corkwood	*Commiphora glandulosa*	Kernel	February, May
Velvet corkwood	*Commiphora mollis*	Kernel	February - April
Sedge	*Cyperaceae*	Flowers	December
Sickle-bush	*Dichrostachys cinerea*	Pods	October
Grass	*Digitaria argyrograpta*	Leaves	December - January
Sumach bean	*Elephantorrhiza burkei*	Pod	December
Transvaal milkplum	*Englerophytum magalismontanum*	Fruit	November, December
Magic guarri	*Euclea divinorum*	Fruit	April - August
Large-leaved rock fig	*Ficus abutilifolia*	Fruit	May, December - February
Mountain fig	*Ficus glumosa*	Fruit	May, December - January
Small-leaved rock fig	*Ficus tettensis*	Fruit	May
Mangosteen	*Garcinia livingstonei*	Fruit	October, November

English name	Latin name	Part eaten	Time of year
White raisin	*Grewia bicolor*	Fruit	December, Januray, April
Sandpaper raisin	*Grewia flavescens*	Fruit	January - September
Silver raisin	*Grewia monticola*	Fruit	January - May
Shakama plum	*Hexalobus monopetalus*	Flowers	September - January
		Fruit	December
		Fruit, dry	March, April
Wild apricot	*Landolphia kirkii*	Fruit	June-November
Live-long lannea	*Lannea discolor*	Sap	December, January, May
Pheasant-berry	*Margaritaria discoidea*	Fruit	October, April
Bell bean tree	*Markhamia acuminata*	Flowers	October, November
		Pods	December
Moepel red-milkwood	*Mimusops zeyheri*	Fruit	September – October
Grass	*Monocymbium ceresiiforme*	Roots	May - August
Kooboo berry	*Mystroxylon aethiopicum*	Fruit	May – September
Guinea grass	*Panicum maximum*	Panicle	May
Jacket plum	*Pappea capensis*	Fruit	May
False turkey-berry	*Plectroniella armata*	Fruit	May
Kudu-berry	*Pseudolachnostylis maprouneifolia*	Fruit	April - September
Mountain karee	*Rhus leptodyctia*	Fruit	May
Common rothmannia	*Rothmannia capensis*	Fruit	October, November, February
Marula	*Sclerocarya birrea*	Kernels	March – September
		Flowers	September
		Fruit	December - February
		Sap	May - July
Cactus	*Secomone spp*	Stem	August
Grass	*Setaria spp*	Flowers	December, January
Poison apple	*Solanum panduriforme*	Bark, Root	July, August
Star chestnut	*Sterculia rogersi*	Flowers	August
Black monkey orange	*Strychnos madagascarensis*	Stem	June, July
Wild medlar	*Vangueria infausta*	Fruit	April
'Knob thorn parasite'	*Viscum spp*	Stems	July, August

English name	Latin name	Part eaten	Time of year
Nyala tree	*Xanthocercis zambesiaca*	Fruit	August
Baboon tail	*Xerophyta retinervis*	Stem bases	May, October
Sourplum	*Ximenia spp*	Fruit	November, December
Buffalo-thorn Jujube	*Ziziphus mucronata*	Fruit	April - August