

Behavioural and isotope ecology of marine-foraging chacma baboons (*Papio ursinus*) on the Cape Peninsula, South Africa

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ABSTRACT

The dominant vegetation type on the Cape Peninsula, South Africa, is an oligotrophic shrubland that supports low numbers of medium-sized and large terrestrial mammals. Of these, only the adaptable and dextrous chacma baboon (*Papio ursinus*) has learnt to supplement its diet with protein-rich foods from the marine intertidal zone. There are qualitative descriptions of this behaviour in the literature, but the relative contribution of marine foods to baboon diet, the influence of lunar cycles on exploitation and the impacts of marine foraging on ranging behaviour and activity budgets through different seasons have yet to be quantified. Furthermore, all previous studies included data from troops that had access to nutrient-rich exotic foods, which may have reduced their reliance on marine organisms. For this thesis I collected behavioural data on ranging patterns, activity budgets and diet of a free-ranging, natural-foraging troop through full lunar tidal cycles over consecutive seasons. I supplemented the behavioural data with estimates of the troop's diet composition modelled from stable isotope ratios of foods, faeces and hair samples. The troop ranged over 45.262 km² and travelled an average of 6.044 km per day over the study period. The troop's activity budget was dominated by walking and feeding behaviour, both of which peaked during the hot, dry summer months. Both spatial and behavioural data suggest that the study troop is nutrient-stressed relative to other troops in this population, and hence it was surprising that they only consumed small amounts of marine foods during all four seasons. Models incorporating $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of baboon faeces and hair confirmed that marine foods were not major dietary items for these baboons, whilst generalized additive models revealed that a range of abiotic factors negatively affect the exploitation of marine foods. Both the probability and intensity of marine foraging within a given hour declined with increasing tide height and swell height, and fluctuated depending on wind speed and direction. Intensity of marine foraging varied through seasons (it was highest in autumn and lowest in spring), and was higher on the east coast than on the west. Together, these results suggest that exploitation of nutrient-rich foods in the intertidal zone is limited by rapid, unpredictable changes in accessibility. The levels of deviance left unexplained by these models however imply that other as yet unknown factors (e.g. alkaloids in mussels and limpets) may also limit the troop's exploitation of marine foods. In conclusion, this thesis represents the first in-depth study of marine foraging, a behaviour which exemplifies baboons' remarkable behavioural and dietary flexibility. That said, the temporal unpredictability of ease of access, and potential dangers associated with harvesting this resource, appear to limit how much of this high-nutrient food resource baboons are able to utilise.

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This research complied with protocols approved by the ethics committees of the University of Cape Town, South African National Parks and the Society for the Prevention of Cruelty to Animals, and adhered to South African legal requirements.

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CHAPTER 1

Introduction and study site description

LITERATURE REVIEW

Behavioural trade-offs and activity budgets

The amount of time available for allocation to different activities is limited by the length of a primate's activity cycle each day (Dunbar and Dunbar, 1988; Hill et al., 2003). Certain activities are mutually exclusive, so the amount of time allocated to one activity can be increased only at the expense of another (McFarland, 1974). Non-human primates (hereafter referred to as "primates") are therefore forced to make behavioural choices between, for example, foraging- and social behaviour (Butynski, 1990; Di Fiore and Rodman, 2001). Primates' activity budgets are largely controlled by food availability in their home ranges (Nakagawa, 1989; Kurup and Kumar, 1993; Ménard and Vallet, 1997; O'Brien and Kinnaird, 1997; Overdorff et al., 1997), which suggests that acquiring and ingesting food takes precedence over other activities, at least until daily nutrient requirements are met. Sacrificing time spent engaged in other activities may however have far-reaching consequences for a primate's survival and, ultimately, its fitness (Dunbar, 1991; Silk et al., 2003, 2009; Wittig et al., 2008; Sapolsky, 2009; Schülke et al., 2010). Primates might therefore be expected to exploit those foods which allow them to meet their daily nutrient-requirements in the shortest possible time.

Primate food choice and foraging ecology

Primate food choice and foraging ecology have received a great deal of attention in the literature, in both laboratory- and field-based studies (e.g. Ayres, 1989; Leighton, 1993; Krishnamani, 1994; Chapman et al., 2003; Hanya, 2003; Hill and Dunbar, 2003; Dew, 2005; Codron et al., 2006; Felton et al., 2009; Kool, 2011). Properties of foods that have been shown to affect primate food choice include protein content, fibre content, protein-to-fibre ratio and concentration of secondary metabolites that inhibit digestion (Oates et al., 1977; Milton, 1979; McKey, 1981; Glander, 1982; Calvert, 1985; Whiten et al., 1991; Barton and Whiten, 1994). These properties drive long-term patterns of food choice (Glander, 1982; Whiten et al., 1991; Barton and Whiten, 1994), but recent studies suggest that food choices on a given day are not made in isolation. Felton et al. (2009) found that spider monkeys (*Ateles chamek*) maintain a constant daily protein intake, while allowing total energy intake to vary. A study by Johnson et al. (2013) revealed that chacma baboons (*Papio ursinus*) on the other hand forage selectively to maintain a constant protein-to-non-protein energy ratio in their daily food intake. In contrast to both *A. chamek* and *P. ursinus*, mountain gorillas

(*Gorilla beringei*) over-ingest protein under certain circumstances in order to maintain a consistent daily non-protein energy intake (Rothman et al., 2011). These findings suggest that, with the exception of large, folivorous primates, primates adopt foraging strategies that allow them to maintain constant daily protein intake, be it an absolute amount or relative proportion of total daily caloric intake. Primate food choice might therefore vary at different times within a day, but the general pattern remains that small to medium-sized primates prefer protein-rich foods that contain little fibre and have low concentrations of tannins (Glander, 1982; Whiten et al., 1991; Chapman and Chapman, 2002).

Food availability in different habitats fluctuates through time however (Post, 1982; Chapman et al., 1999; Stone, 2007), and situations may arise in which preferred foods are in short supply or are entirely absent from a primate's home range (Tutin et al., 1997; Furuichi et al., 2001; Yiming, 2006). Studies have shown that primates alter their foraging behaviour in response to such shortages by switching to so-called 'fallback foods' (Altmann, 1998; Hanya, 2004a; Alberts et al., 2005; Grueter et al., 2009). These are foods that are readily available, but provide poorer nutritional rewards than preferred foods (Wrangham et al., 1998; Hanya, 2004a; Marshall and Wrangham, 2007), or provide rewards that are comparable to those provided by preferred foods, but which have higher processing costs in time and energy (Alberts et al., 2005; see Marshall et al., 2009 for a review). If a primate is to meet nutritional requirements by feeding only on fallback foods it must therefore dedicate a great deal of time to either ingesting large amounts of low-quality fallback food items, or processing and ingesting few high-quality fallback food items. Thus, as preferred food availability declines, so primates tend to increase the amount of time allocated to feeding-related activities (Dunbar, 1992; Gursky, 2000; Alberts et al., 2005; Stone, 2007). This is done at the expense of other activities (Dunbar, 1992; Gursky, 2000; Alberts et al., 2005), which, as mentioned above, may result in a drop in the animal's fitness.

A nutrient-stressed primate should be able to avoid this change in behaviour (and the concomitant drop in fitness), if it were able to exploit novel, nutrient-rich foods within its home range. Primates that might be more likely to do this would be those that exhibit neophilic behaviour and are able to feed on a wide variety of foods, such as baboons (*Papio* spp.; Altmann and Altmann, 1970; Whiten et al., 1991; Bergman and Kitchen, 2009).

Baboon dietary flexibility

Baboons are medium-sized, group-living primates that inhabit diverse habitats throughout much of sub-Saharan Africa (DeVore and Hall, 1965). They forage in terrestrial- and arboreal

habitats, and are therefore able to incorporate a wide variety of plant- and animal foods into their diet (Hall, 1962; Altmann and Altmann, 1970; Hamilton et al., 1978; Whiten et al., 1991). Although animal-derived foods (which are rich in protein) may be ingested on a regular basis, plant foods typically make up a much larger portion of baboon diet (Hamilton et al., 1978; Whiten et al., 1987). Baboons will however favour animal foods when these are readily available, and may even exclude plant foods from their diet entirely over short periods (Hamilton et al., 1978). This follows the abovementioned pattern of food preference found in other primates, and suggests that baboons favour plant foods simply because these are more abundant and more easily acquired, in most habitats (Hamilton et al., 1978).

In savannah-type habitats for example, items that are incorporated into baboon diets include fruits, flowers, leaves, tree gum, seeds and seed pods, underground storage organs, insects, and meat of various vertebrates (Altmann and Altmann, 1970; Post, 1982; Barton et al., 1993; Alberts et al., 2005). Preferred plant foods, such as fruits, flowers, seeds, and young leaves are abundant at certain times, but availability varies seasonally, and baboons are thus forced to switch to fallback foods at certain times of the year (Altmann, 1998). For the baboons of the Amboseli basin, Kenya, perhaps the most important fallback foods are corms of various grass species (Altmann, 1998; Alberts et al., 2005). Corms are comparable to preferred foods in terms of the nutritional rewards they provide (Altmann, 1998), but are only favoured when other plant foods are scarce (i.e. during the dry season), because they require substantial processing prior to ingestion (Alberts et al., 2005). Thus, in habitats such as this, high-quality plant foods with high associated foraging costs are considered to be the fallback foods of choice for baboons.

Animal foods make up a very small proportion of savannah baboons' diets (Altmann and Altmann, 1970; Altmann, 1998), despite offering a rich source of protein (Hamilton et al., 1978). It seems likely that the costs of finding, chasing and catching the highly mobile prey available in savannahs (e.g. grasshoppers, lizards and smaller primates) (Rhine et al., 1986), and the time required to chew raw vertebrate meat (Wrangham and Conklin-Brittain, 2003; Hardus et al., 2012), preclude the use of animal foods as a major component of their diet. This may not be the case for baboons that inhabit temperate coastal areas however, as marine intertidal zones in such regions are occupied by sedentary and slow-moving animals whose tissues are rich in protein and other macronutrients (Karakoltsidis et al., 1995; Fleurence, 1999; Norziah and Ching, 2000; Smith and Partridge, 2004). These marine foods might provide an important alternative to terrestrial fallback foods for local baboons. This is

however contingent on the abundance of these organisms, and the ease with which they can be exploited by terrestrial animals.

“Maritime mammals”

Coastal marine waters are among Earth’s most productive habitats (Lieth, 1978; Polis and Hurd, 1996). Under favourable conditions in coastal waters, marine algae exhibit extremely rapid growth (Mann, 1973; Pihl et al., 1996) and produce nutrient-rich tissues (Fleurence, 1999; Norziah and Ching, 2000; Wong and Cheung, 2000). These algae support diverse consumers, which may occur at extraordinary densities in the intertidal zone (Paine, 1974; Bustamante et al., 1995; Blanchette and Gaines, 2007). Biomass of both plants and animals therefore accumulates rapidly in these environments. In several regions, particularly where upwelling occurs, coastal marine systems are vastly more productive than neighbouring terrestrial habitats (Seely, 1978, 1984; Ware, 1992; Acha et al., 2004; Pennington et al., 2006; Warren-Rhodes et al., 2006; Iriarte et al., 2007; Davila et al., 2008).

Considering disparities in productivity between habitats across the coastal ecotone, it is unsurprising that a variety of terrestrial mammals supplement their diet with marine foods from the intertidal zone (Dalquest, 1948; Moore, 2002; Carlton and Hodder, 2003; Gaydos and Pearson, 2011). Carlton and Hodder (2003) refer to those “coastal mammalian predators that utilise living intertidal energy resources and transfer these resources to the land” as “maritime mammals”. It is important to note however, that these authors define “predation” as consumption of “living (not detrital) marine invertebrates, fish, algae, and seagrasses”, so reference to a “maritime mammal” does not imply that the animal in question is a carnivore. That said, more maritime mammals (22 out of 45 species) belong to the Carnivora than to any other order—Rodentia and Artiodactyla are the only other orders represented by more than just one or two species (Carlton and Hodder, 2003).

Examples of maritime mammals in the Carnivora include the raccoon (*Procyon lotor*; Tyson, 1950), badger (*Meles meles*; Sleeman et al., 2001), several species of fox (Murie, 1959; Huey, 1969; West, 1987), coyote (*Canis latrans*; Rose and Polis, 1998), black-backed jackal (*Canis mesomelas*; Nel et al., 1997) and two species of bear (Smith and Partridge, 2004; Gaydos and Pearson, 2011). The majority of these species exploit crustaceans (Hartman, 1990; Nel et al., 1997) and molluscs (Dalquest, 1948; Tyson, 1950; Smith and Partridge, 2004) obtained in the intertidal zone. Only two species, the arctic fox (*Alopex lagopus*) and *P. lotor* (Tyson, 1950; Nielsen, 1991), feed on live fish which are caught in the shallows. Interestingly, *A. lagopus* (Kapel, 1999), *C. latrans* (Rose and Polis, 1998) and the

American black bear (*Ursus americanus*; O'Clair and O'Clair, 1998) feed on algae as well as marine animal prey. These are the only species in the order that do so however (Carlton and Hodder, 2003), so for most maritime mammals in the Carnivora, the marine component of their diet is comprised entirely of marine animals.

The same is true of the majority (eight out of 12 species) of maritime rodents (Carlton and Hodder, 2003). Rodents such as the deer mouse (*Peromyscus maniculatus*; Osborne and Sheppe, 1971), Keen's mouse (*Peromyscus keeni*; Drever et al., 2000) and Townsend's vole (*Microtus townsendii cowani*; Drever et al., 2000) all feed on intertidal invertebrates only. Of the four rodent species that do not fall into this group, three feed on both marine plants and animals (Navarrete and Castilla, 1993; Carlton and Hodder, 2003). One of these, the Norway rat (*Rattus norvegicus*), has been particularly well-studied (Parisi and Gandolfi, 1974; Moors, 1985; Navarrete and Castilla, 1993; Drever and Harestad, 1998; Thompson et al., 2000) and is known to feed on an extraordinary variety of marine foods. At a single locality, *R. norvegicus* was observed feeding on 37 marine animal species (Navarrete and Castilla, 1993). This dietary breadth is in stark contrast to that of the Beechey ground squirrel (*Spermophilus beecheyi*), which feeds only on marine plants, and may in fact feed on just one marine species (Roest, 1993).

Most of the maritime mammals in the order Artiodactyla differ from those in the Carnivora and Rodentia (other than *S. beecheyi*), in that the marine components of their diets are comprised entirely of algae (Carlton and Hodder, 2003). The only maritime mammal in the Artiodactyla that feeds on both marine plants and animals is the feral pig, *Sus scrofa*; Chimera et al., 1995; Carlton and Hodder, 2003). Those that feed on marine plants only include the red deer (*Cervus elaphus*; Conradt, 2000), black-tailed deer (*Odocoileus hemionus*; Gaydos and Pearson, 2011), and feral goat (*Capra hircus*; Chimera et al., 1995) and sheep (*Ovis aries*; Hansen et al., 2003), which feed on a variety of benthic macrophytes.

Despite the clear benefits of exploiting marine foods (see above), it seems that this behaviour is extremely rare in primates (Carlton and Hodder, 2003). Feeding on aquatic organisms has been observed in primates belonging to just four genera, namely *Cebus* (Fernandes, 1991; Port-Carvalho et al., 2004), *Macaca* (Crockett and Wilson, 1980; Whitten and Whitten, 1982; Son, 2003; Malaivijitnond et al., 2007; Stewart et al., 2008), *Papio* (Hall, 1962; Davidge, 1978; Messeri, 1978; Hamilton and Tilson, 1985; Wrangham et al., 2009), and *Gorilla* (Fay et al., 1989; Nishihara, 1995). Of these, only *Macaca* (Crockett and Wilson, 1980; Son, 2003; Malaivijitnond et al., 2007) and *Papio* (Hall, 1962; Messeri, 1978) feed on marine organisms.

At several locations, *Macaca fascicularis* feeds on a variety of marine invertebrates in mangrove habitats (Crockett and Wilson, 1980; Son, 2003) and in the intertidal zone on rocky shores (Malaivijitnond et al., 2007). Two baboon species, the chacma baboon (*Papio ursinus*) and yellow baboon (*Papio cynocephalus*), feed on marine foods in different regions. On the south Somali coast, *P. cynocephalus* has been observed feeding on marine crabs on sandy beaches (Messeri, 1978) while *P. ursinus* at the south western tip of Africa feeds on a variety of marine organisms obtained largely from rocky shores (Hall, 1962, 1963; Davidge, 1978).

Intertidal organisms may represent abundant, nutrient-rich foods, but they are not always available to maritime mammals as the intertidal zone is periodically submerged (Branch et al., 1998). Animals that feed on these organisms therefore typically time their forays into the intertidal zone to coincide with low tide (Nielsen, 1991; Conradt, 2000). This behavioural adaptation allows them to access marine organisms, but time spent feeding on choice intertidal foods may still be limited by tidal cycles (Hansen et al., 2003).

Although live intertidal organisms are potentially important foods, they are not the only sources of marine nutrients available to terrestrial consumers. In some areas, large amounts of algal drift and high numbers of dead marine animals are washed ashore and left behind when the tide recedes (Polis and Hurd, 1995, 1996). Not surprisingly, many maritime mammals opportunistically exploit such resources (Dalquest, 1948; Murie, 1959; Huey, 1969; Hiscocks and Perrin, 1987; West, 1987; Rose and Polis, 1998; Conradt, 2000; Hansen et al., 2003; Kuhn et al., 2008; Watts et al., 2010), which in some cases, results in significant increases in the amount of marine foods that are consumed (Nel et al., 1997; Conradt, 2000). Irrespective of the source, the addition of non-trivial amounts of marine foods to an animal's diet can significantly enhance its daily food intake in terms of quantity (Rose and Polis, 1998) and quality (Smith and Partridge, 2004). Contributions of marine foods to the diets of terrestrial animals have been measured using direct observation (Hiscocks and Perrin, 1987), stomach content analysis (Navarrete and Castilla, 1993), scat analysis (Rose and Polis, 1998), and, in recent times, stable isotope analysis (Drever et al., 2000; Stapp, 2002; Chamberlain et al., 2005).

Direct observation, stomach content- and scat analyses may be useful in studies of animal diet, but they are not without limitations. Direct observation may be difficult, or even impossible, if animals do not habituate to human presence (Holechek et al., 1982; Karanth et al., 2010), or in habitats where visibility is limited (Smith and Shandruk, 1979; Sanders et al., 1980; Mills, 1996). Analysis of gut contents on the other hand only provides an indication of diet composition over relatively short periods (Stewart, 1967; Ward, 1970; Weaver, 1993),

and requires highly invasive sampling at best, so is therefore not used in the study of rare or endangered species (Holechek et al., 1982). Scat analysis does not require invasive sampling, but also only allows identification of foods ingested in the very recent past (Stewart, 1967; Weaver, 1993), and, as a result of differential digestion, may in fact provide biased estimates of diet composition (McInnis et al., 1983; Karanth et al., 2010). Thus, depending on the context and the research objectives, stable isotope analysis might be preferred over the above-mentioned methods for use in studies of animal diet and feeding ecology.

Stable isotope analysis

Analysis of naturally occurring stable isotopes has been used as a tool in studies of trophic and dietary ecology with increasing frequency over the last four decades (for reviews see Kelly, 2000; Newsome et al., 2010; Boecklen et al., 2011). The utility of stable isotope analysis in ecological research arises from variation in the ratios of light- to heavy isotopes in different pools of a given element (Garlick, 1978; Schwarz, 1978), and the fact that these ratios are either preserved (Guy et al., 1993), or change predictably (DeNiro and Epstein, 1978, 1981), through biochemical processes. Changes in isotope ratios are the result of isotopic discrimination or fractionation by chemical reactions (Peterson and Fry, 1987; Crawford et al., 2008), and have been quantified in diverse systems (Delwiche and Steyn, 1970; Zhang et al., 1995; Berner et al., 2000; McCutchan et al., 2003).

Researchers have used stable isotope analyses in ecological studies ranging in scale from animal movement patterns across continents (Kelly et al., 2002; Cryan et al., 2004; Hobson et al., 2012) to dietary ecology of animals at the level of the population (Darimont and Reimchen, 2002; Botha and Stock, 2005; Dalerum et al., 2009; Rutz et al., 2010), and even the individual (Yeakel et al., 2009; Newsome et al., 2010a; Blumenthal et al., 2012).

Stable isotopes in dietary studies

The isotope ratios that have been used most extensively in studies of dietary and trophic ecology in modern systems are those of carbon ($^{13}\text{C}/^{12}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$) (e.g., Ambrose and Deniro, 1986; Baugh et al., 2004; Ben-David et al., 2004; Louys et al., 2012; for a detailed review see Kelly, 2000), and, more recently, sulphur ($^{34}\text{S}/^{32}\text{S}$; Felicetti et al., 2003; Moreno et al., 2009; Salvarina et al., 2013).

The value of stable carbon and nitrogen isotope analysis as a tool in studies of trophic ecology is determined by natural variation in $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ ratios among consumers and their food sources (Peterson and Fry, 1987; Kelly, 2000). In terrestrial systems variation

in carbon isotope ratios arises at the level of primary producers, as plants that follow the C₃- and C₄ photosynthetic pathways exhibit disparate carbon isotope ratios (Bender, 1971; Sternberg and DeNiro, 1983). This is a result of processes underlying the different photosynthetic pathways discriminating against ¹³C to different degrees (O’Leary, 1988). Marine algae, which follow the C₃-photosynthetic pathway (Bell and Hemsley, 2000), display a remarkable range of carbon isotope ratios (Raven et al., 2002). There is some overlap between benthic algae and terrestrial C₄ plants in terms of carbon isotopes, but the δ¹³C values of the vast majority of benthic algae are intermediate between those of terrestrial C₃- and C₄ plants (O’Leary, 1988; France, 1995). Terrestrial C₃ plants are depleted in ¹³C relative to C₃-photosynthesising marine algae because the atmospheric carbon dioxide from which terrestrial plants take up carbon is depleted in ¹³C relative to the dissolved carbonates from which marine algae obtain carbon (Craig, 1953; Smith, 1972).

Differences in ¹⁵N/¹⁴N ratios on the other hand may arise at the base of the food chain (at a given location nitrogen-fixing plants differ from non-fixers in terms of ¹⁵N/¹⁴N ratios; Virginia and Delwiche, 1982), but this is not the only source of variation. So-called “trophic enrichment” in nitrogen isotopes results in isotopic differences between plants and animals at different trophic levels within a given system (DeNiro and Epstein, 1981; Minagawa and Wada, 1984; Kelly, 2000)—consumers are, on average, enriched in ¹⁵N by ~3.5‰ relative to their diets (Minagawa and Wada, 1984; Schoeninger and DeNiro, 1984). These patterns hold true within systems, but the isotope ratios of the same tissues from the same species, or species belonging to the same functional groups, may vary across systems as a result of differences in source isotope ratios and/or specific fractionation factors (Cerling et al., 2003; Sponheimer et al., 2003a; Swap et al., 2004).

In systems where foods are isotopically distinct, or can be sorted into biologically meaningful isotopically distinct groups, mathematical models can provide accurate estimates of the relative contributions of these sources to a consumer’s diet (Phillips, 2001; Phillips and Gregg, 2001; Phillips et al., 2005; Moore and Semmens, 2008; Yeakel et al., 2009; Rutz et al., 2010). Models used for this purpose range in complexity from simple linear models which incorporate ratios of just a single isotope from the consumer and two isotopically distinct sources, to much more complex Bayesian models which incorporate ratios of multiple isotopes from the consumer and multiple sources (Phillips, 2001, 2012; Parnell et al., 2010). The models developed by Parnell et al. (2008) in the Stable Isotope Analysis in R (SIAR) package, not only allow for incorporation of isotope ratios of a greater number of sources, but also error around the mean values for each source, the elemental concentrations

of the sources and different fractionation factors for different sources (Parnell et al., 2010). Irrespective of the type of model that is used, it is imperative that the appropriate input values be incorporated, be they fractionation factors or the isotope ratios themselves (Caut et al., 2008; Bond and Diamond, 2011; Phillips, 2012).

Isotope-based studies in which these models are used therefore typically involve isotopic analysis of foods known to be ingested by the animal in question, in addition to tissue samples taken from that animal (e.g., Hobson et al., 1999; Cerling et al., 2003; Codron et al., 2006). Tissues analysed thus include both biologically active tissues, such as bone, muscle and blood (Ambrose and Deniro, 1986; Fleming et al., 1993; Ben-David et al., 1997; Hobson et al., 1997), and biologically inert tissues, such as hair and feathers (Thompson and Furness, 1995; Mizukami et al., 2005a). The appropriate tissue for analysis is determined by the focus of the study, as tissues differ greatly in terms of rates of synthesis and turnover (Tieszen et al., 1983; Sponheimer et al., 2006b), and thus reflect dietary integration over vastly different time periods. Periods of dietary integration reflected in tissues range from less than a day in the case of hair (West et al., 2004), to years or even decades, in the case of bone (Chisholm et al., 1982). It is therefore possible to resolve dietary shifts through time by analysing samples of the same tissue collected at different times, by analysing tissues with different turnover rates collected simultaneously, or by comparing sections of inert tissues such as hair (see Dalerum and Angerbjörn, 2005).

Carbon and nitrogen isotopes have been used, either in isolation or in conjunction, in dietary studies of vertebrates including mammals (Angerbjörn et al., 1994; Cerling et al., 2006; Codron and Codron, 2009), birds (Minami and Ogi, 1997; Suryan and Fischer, 2010), and reptiles (Vidal and Sabat, 2010; Willson et al., 2010), and in both terrestrial (Struck et al., 2002; Urton and Hobson, 2005; Symes and Woodborne, 2009) and aquatic systems (Forero et al., 2002; Kurle and Worthy, 2002; Reich et al., 2007). Researchers have even used $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ ratios to successfully investigate the relative contributions of marine foods to the diets of terrestrial animals (e.g., Darimont and Reimchen, 2002; Stapp and Polis, 2003; Ben-David et al., 2004). Stable isotope analysis might therefore be used, either in isolation or as a source of complimentary data to direct behavioural observations in studies of marine foraging by primates. This technique would be particularly useful at study sites where direct observation of primate feeding behaviour is difficult (Sandberg et al., 2012). One such site is South Africa's Cape Peninsula, where large parts of the landscape are covered by dense evergreen shrubland (Rebelo et al., 2006).

Cape Peninsula baboons

The Peninsula is home to a population of approximately 500 chacma baboons (*Papio ursinus*) comprising 16 troops (Beamish unpublished data), that are geographically isolated from troops in neighbouring populations by urban sprawl (Hoffman and O’Riain, 2012a). The Peninsula baboons are currently excluded from relatively productive low-lying lands by human activities (Hoffman and O’Riain, 2012b), and are therefore restricted to oligotrophic high-lying habitats (Cowling et al., 1996). In light of this, wild-foraging Peninsula baboons are thought to be nutrient-stressed, particularly during the hot, dry summer months (Van Doorn et al., 2010). It is therefore not surprising that Peninsula baboons risk serious injury and even death in attempting to access anthropogenic food items on farms, in private residences and at waste disposal sites (Van Doorn et al., 2010; Kaplan et al., 2011). For troops that do not have access to such foods the nutrient-rich marine foods may provide succour during seasonal bottlenecks in food resources.

All of the 16 extant Peninsula troops have unobstructed access to coastal areas, but only seven occupy home ranges that extend to the coast (Hoffman and O’Riain, 2012), and are therefore likely to exploit marine resources. While foraging in the intertidal zone, Peninsula baboons are known to consume mussels (*Mytilus* sp.), limpets (*Patella* sp.), and the eggs of small shark species (likely either *Poroderma* sp. or *Haploblepharus pictus*) (Hall, 1962, 1963; Davidge, 1978; Peschak, 2005). In addition the remains of both crabs (*Cyclograpsus punctatus* and *Plagusia chabrus*), and sea lice (Isopoda) have been found in the faeces of these baboons (Hall, 1962, 1963).

Despite the novelty of marine foraging, and its potential impacts on the foraging ecology of Peninsula baboons, limited effort has been made to quantify the use of this novel food with most studies to date including only qualitative descriptions of feeding behaviour (Hall, 1962, 1963; DeVore and Hall, 1965). Hall (1963) stated that marine foraging occurred “almost daily when wind and tide allow... easy access to intertidal rock pools and to the sea verge” and that baboons on the shore “would rush away on the approach of a large wave.” Hall did not however quantify the behaviour, or the potential limiting effects of wind, tidal cycles or wave action on the frequency of this behaviour. The most detailed dietary study of a marine foraging troop conducted to date showed that the study troop spent little time feeding on marine foods during austral autumn and winter months (mean % feeding time during months from March–August = $1.8 \pm 1.5\%$), and even less time during spring and summer months (mean % feeding time during months from September–February = $0.8 \pm 1.5\%$; Davidge, 1978). Considering that marine foraging might be limited to periods either side of

low tide (Hall, 1962), it seems highly plausible that Davidge (1978) might have underestimated time spent marine foraging as her results were based on limited behavioural observations (range of observation time per month: 12–74 h).

Further research on this aspect of Peninsula baboons' dietary ecology is therefore needed to corroborate or refute Davidge's conclusions and to determine which environmental factors, if any, might be limiting the baboons' exploitation of marine resources. Limited visibility in the dense shrubland which dominates the Peninsula's untransformed habitats (Cowling et al., 1996; Rebelo et al., 2006), necessitates the use of an alternative data collection method complimentary to behavioural observation. The use of stable isotope analysis as a source of complimentary data might therefore enhance a behaviour-based study of marine foraging in Peninsula baboons (Sandberg et al., 2012).

Aims and objectives

The principal aim of this research is to provide a detailed account of marine foraging, and the abiotic and biotic factors that influence this behaviour, in Cape Peninsula chacma baboons. Due to the confounding effects that the ingestion of human foods have on baboon behaviour (Bronikowski and Altmann, 1996) and overall diet (Van Doorn et al., 2010), such research requires a free-ranging troop that marine forages but has no access to anthropogenic foods. At the outset of this study (and to the present day) only the Kanonkop troop, in the Cape of Good Hope section of the Table Mountain National Park, satisfied these criteria (Hoffman and O'Riain, 2012; O'Riain pers. comm.) thus limiting this study to a single free-ranging troop. Working within this limitation I attempt to address the following questions:

1. How do ranging patterns and activity budgets of a non-raiding, marine foraging troop of baboons vary seasonally and how do they compare with other baboon troops, both on the Peninsula and elsewhere?
2. How much time do natural-foraging Peninsula baboons allocate to exploiting marine foods, and does this vary seasonally?
3. Do stable isotope signals of hair and faeces reflect proportional contributions of terrestrial and marine foods to the diet of non-raiding Peninsula baboons?
4. If the extent of marine foraging is reflected in the isotope ratios of hair (see above), could isotope analysis of hair be used to determine whether or not an unknown baboon exploits marine foods?
5. How frequent are marine foraging bouts, and what environmental factors influence the frequency and intensity of exploitation?

Thesis outline

The thesis is divided into five chapters including this introductory chapter. Chapters 2 through 4 include short introductions that are specific to the subject matter therein. These introductions provide sufficient context to allow readers to comprehend the rationale and relevance of the chapters if these are read in isolation (without excessive overlap with the introductory chapter). In Chapter 2, I provide a detailed description of the activity budgets and ranging patterns of the study troop, as well as an account of the troop members' diet, and temporal and spatial variation in baboon food quality. In Chapter 3 I illustrate the utility of stable isotope analyses in the study of primates that exploit marine foods by comparing the results of isotope-based models of diet to the results obtained through behavioural observation. I then describe how baboons utilise marine food resources (in terms of frequency and intensity) and provide a numerical evaluation of environmental factors that affect the behaviour in Chapter 4. Finally, in Chapter 5, I synthesise the findings presented in Chapters 2 through 4, and comment on the broader significance of these findings.

Study site

Landscape and climate

The Cape Peninsula is a narrow strip of land that juts into the Atlantic Ocean on the south-western corner of South Africa (Fig. 1.1). The highest point on the Peninsula is Maclear's Beacon on Table Mountain (1086.7m above sea level), which is found near the northern end of the Peninsula Mountain Chain (Cowling et al., 1996). South of Table Mountain, a sandstone plateau and several smaller peaks and ridges complete the Chain, which runs in a roughly north-south orientation (Cowling et al., 1996). On the eastern and western margins, the edges of the plateau are marked by precipitous cliffs of bare rock, some of which are over 300m high (King, 1983). With the exception of a few smaller peaks (less than 700m above sea-level), the altitude of the Peninsula decreases steadily south of the main plateau. The topography of the southernmost reaches of the Peninsula is dominated by a second plateau approximately 150m above sea level (Cowling et al., 1996).

As is typical of sandstone-derived soils in the region, the soils of the Peninsula are generally shallow, sandy, acidic and extremely nutrient-poor (Kruger, 1979; Schloms et al., 1983). The exceptions to this rule are the soils of the Peninsula's colluvial slopes that are deeper, less acidic and rich in nutrients by comparison (Cowling et al., 1996). Soils on the

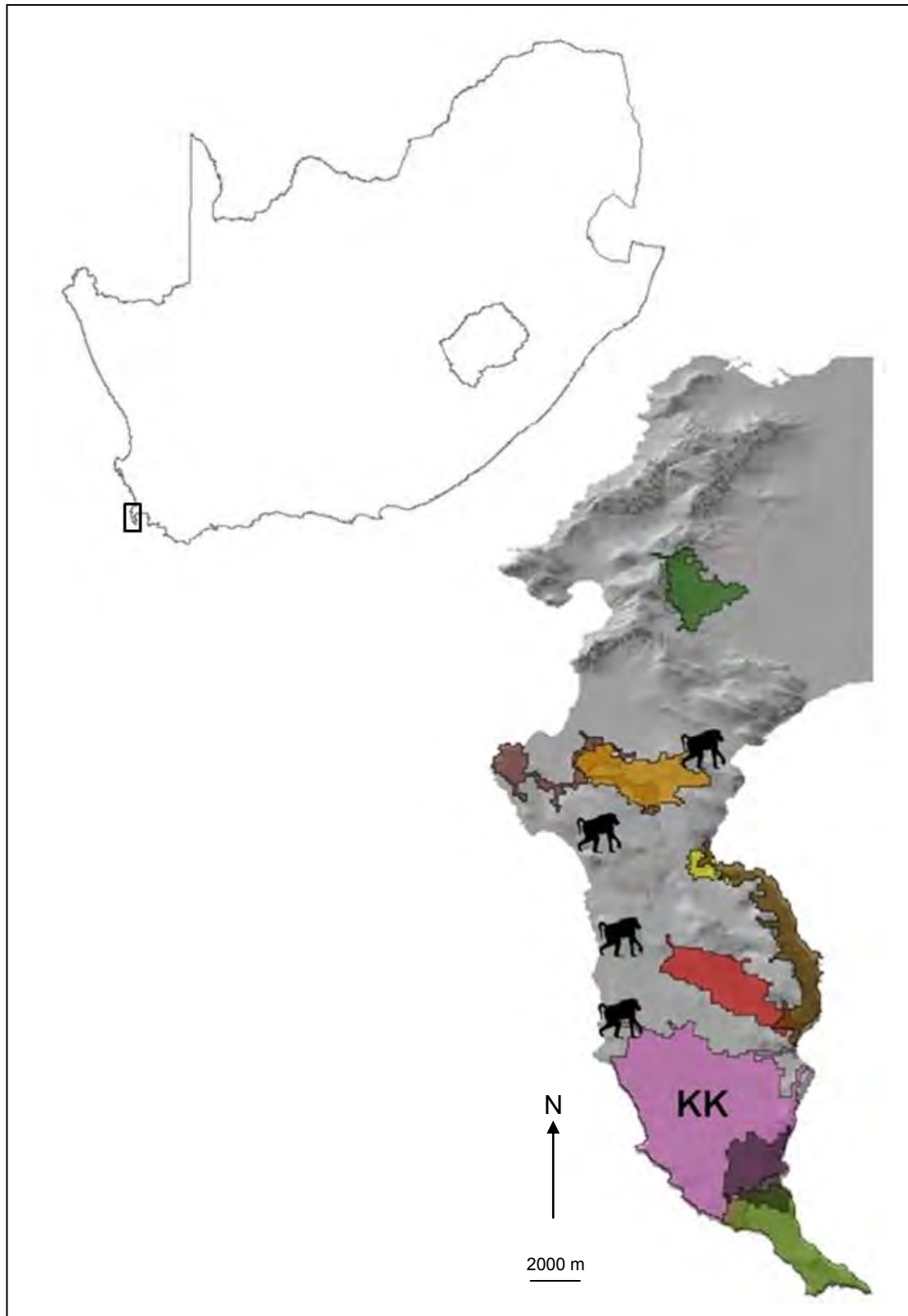


Fig. 1.1. Map of South Africa (inset) with the location of the Cape Peninsula indicated by the black rectangle. The main map shows the Cape Peninsula with locations of Peninsula baboon troops' home ranges marked either by a polygon (troops studied by Hoffman and O'Riain, 2012a) or a black baboon silhouette (troops for which home range size is currently unknown). The main map was adapted from Hoffman and O'Riain, (2012a) and was used with the first author's permission. KK = Kanonkop.

higher peaks and ridges are well-drained, but poor drainage on the plateaus results in saturation in these areas following heavy rains (Cowling et al., 1996).

The topography of the Peninsula has major effects on the distribution of rainfall in the area, as high-lying topographic features trap rain-bearing winds (Kruger, 1979; Cowling et al., 1996). The resultant orographic rain causes annual rainfall to exceed 2000 mm.y⁻¹ on parts of Table Mountain, while rainfall on the southern Peninsula may be as low as 400 mm.y⁻¹ (Cowling et al., 1996; South African Weather Service, unpublished data). Approximately 40% of annual rainfall occurs during the winter months (June – August), while just 10% occurs in summer (December – February; Kruger 1979). These seasonal differences in rainfall are linked to shifts in the prevailing winds, which buffet the Peninsula from the north-west in winter (often bearing rain) and from the southeast in the summer (Cowling et al., 1996). These winds frequently exceed gale force, with mean wind speeds exceeding 30 km.h⁻¹ and 40 km.h⁻¹ in winter and summer respectively at Cape Point (the windiest place on the Peninsula; Cowling et al. 1996).

Unlike rainfall and wind speed, air temperature does not exhibit marked spatial or temporal variation across the Peninsula (Cowling et al., 1996). During the five years preceding this study (2004 – 2008), mean monthly maximum and minimum temperatures measured at the Molteno Reservoir on Table Mountain averaged 22.5°C and 14.8°C respectively (South African Weather Service, unpublished data). Over the same period, mean monthly maxima and minima measured at Cape Point averaged 19.6°C and 13.4°C respectively (South African Weather Service, unpublished data). These mild temperatures, and the large percentage of annual rainfall that falls in winter, are the defining features of the Peninsula's temperate, Mediterranean-type climate.

Plant diversity and ecology

The dominant vegetation on the Cape Peninsula is an evergreen shrubland, known as fynbos (derived from the Dutch term for “fine bush”; Cowling et al., 1996; Rebelo et al., 2006). This vegetation type, is restricted to South Africa's Cape Floristic Region (CFR), and is known for its remarkable taxonomic diversity—there are 2250 plant species on the Cape Peninsula alone (Goldblatt and Manning, 2002). Many of these species belong to the three main plant groups which characterise fynbos, namely restios (Restionaceae), ericoid shrubs (belonging to several families including Ericaceae and Asteraceae) and proteoid shrubs (Proteaceae; Rebelo et al. 2006). Thus, fynbos exhibits high taxonomic diversity, but low structural and functional

diversity, as the majority of fynbos plants are either graminoid forms or shrubs (Kruger, 1979; Stock and Allsopp, 1992).

The dominance of small- to medium-sized plants in fynbos communities, such as those on the Peninsula, results in there being little above-ground standing phytomass ($< 4 \text{ kg.m}^{-2}$; Stock and Allsopp, 1992). This phytomass typically persists over multiple years between disturbances, but accumulates slowly, as net primary production rates in fynbos are low ($100 - 400 \text{ g.m}^{-1}.\text{y}^{-1}$; Kruger, 1977). The major limiting factor for primary production is nutrient availability in the region's sandstone-derived soils (Rebelo et al., 2006), which are generally extremely low in phosphorous and nitrogen (Kruger, 1979). Nutrient scarcity is therefore an important driver of ecological processes in these habitats.

Another major driver of ecological processes in fynbos is fire (Rebelo et al., 2006). Fires initiate successional changes in fynbos communities (Stock and Allsopp, 1992) and are followed by short-term nutrient flushes (Brown and Mitchell, 1986; Stock and Lewis, 1986; Musil and Midgley, 1990), and, consequently, periods during which primary production rates increase (Kruger, 1977). These events are relatively infrequent however, as inter-fire intervals range from 5 to 50 years (Rebelo et al., 2006). Thus, nutrient cycling in fynbos is slow, as the meagre nutrients in the soil that are taken up by plants typically remain trapped in persistent plant tissues (such as sclerophyllous leaves) for several decades (Stock and Allsopp, 1992).

Many fynbos species have adapted to take advantage of favourable post-fire conditions through traits such as serotiny (retention of seeds in protective structures and subsequent release following fire) and myrmecochory (dispersal of seeds by ants into underground nests; Le Maitre and Midgley, 1992). Plants that exhibit these traits produce structures that are energetically expensive, but require small amounts of soil-derived nutrients: fireproof seed heads in the case of the former, and elaiosomes (also known as ant-fruits), in the case of the latter (Le Maitre and Midgley, 1992; Rebelo et al., 2006). In both cases, nutrient-rich seeds are protected from predators while conditions remain unfavourable, and then germinate in a favourable post-fire environment (Rebelo et al., 2006).

Another trait which is common in fynbos plants is sclerophylly—the production of nutrient-poor fibre-rich leaves, often with high concentrations of phenolic compounds (Stock and Allsopp, 1992; Coetzee et al., 1997; Rebelo et al., 2006). Phenolic compounds, such as tannins, reduce digestibility of plant tissues (Waterman et al., 1980; Griffiths, 1986), so nutrient-uptake from tissues that are rich in these compounds is limited. The nutritive value of fynbos plants to generalist browsers and grazers is therefore extremely low (Campbell, 1986; Coetzee et al., 1997).

Fynbos covers the majority of the Peninsula, but there are also small patches of Peninsula Shale Renosterveld, Southern Afrotropical Forest, Cape Flats Dune Strandveld and Cape Seashore vegetation (for a detailed description see Mucina and Rutherford 2006). These communities grow on more nutrient-rich soils, and enhance the structural and functional diversity of the Peninsula's plant communities, as they are home to true grasses, low-growing succulents and trees (Mucina and Geldenhuys, 2006; Mucina et al., 2006; Rebelo et al., 2006). In terms of areas occupied by baboons, the most important of the above-mentioned communities is Cape Flats Dune Strandveld (Hoffman and O'Riain, 2012a). This community, which is typically found close to the coast, differs from neighbouring fynbos communities in a number of important ways: it is based on more nutrient-rich substrates than fynbos communities; fires are less frequent, and do not play the same important role in driving ecological processes; and different plant groups dominate—plants belonging to the Proteaceae are absent, Ericaceae is poorly represented and both true grasses and annual herbs are abundant (Rebelo et al., 2006).

Animal diversity and ecology

Historically, a variety of large mammalian herbivores and carnivores inhabited the Peninsula and surrounds (Skead, 1980). Resident carnivores included lion and leopard, but these were extirpated in the eighteenth and nineteenth centuries respectively (Skead, 1980). The largest terrestrial mammalian carnivore that is still found on the Peninsula is the caracal (*Caracal caracal*; Hey, 1994; Ward et al., 2010). Thus, there are presently no mammalian carnivores on the Peninsula which would be likely to predate on baboons (Cowlshaw, 1994).

Eland (*Taurotragus oryx*), Cape mountain zebra (*Equus zebra zebra*), and bontebok (*Damaliscus pygargus*) were reintroduced in the Cape of Good Hope (CoGH) section of the Table Mountain National Park (TMNP), and remain restricted to this part of the Peninsula (Davidge, 1976; Davison and Marshak, 2012). These large herbivores are able to survive in fynbos-type habitats, but tend to suffer from deficiencies of trace elements such as copper (Zumt and Heine, 1978). Resident medium-sized and small mammalian herbivores are grey rhebuck (*Pelea capreolus*), grysbok (*Raphicerus melanotis*), steenbok (*Raphicerus campestris*), klipspringer (*Oreotragus oreotragus*) and Cape hyrax (*Procavia capensis*; Hey, 1994; Cowling et al., 1996). These smaller herbivores typically feed selectively on nutrient-rich plant parts in order to fulfil their nutritional requirements (Campbell, 1986).

Rodent species that are found on the Peninsula include the Cape porcupine (*Hystrix africaeaustralis*), the Cape dune mole rat (*Bathyergus suillus*) and a variety of murids, three

of which are exotic (Davidge, 1976; Hey, 1994). Murids are known to play important ecological roles in fynbos habitats, as pollinators (Letten and Midgley, 2009) and seed predators (Bond, 1984), while bathyergids contribute to soil disturbance and turnover (biopedturbation; Davies and Jarvis, 1986) and feed extensively on underground storage organs of geophytes (Lovegrove and Jarvis, 1986).

There are 155 bird species that are known to breed regularly on the Peninsula (Picker and Samways, 1996). These species are not all found throughout the Peninsula however, as bird community composition varies with habitat type (across both natural and transformed habitats; Winterbottom, 1966; Cody, 1983; Fraser, 1990). In fynbos habitats, the bird communities are seasonally dominated by the Cape Sugarbird (*Promerops cafer*) and two sunbird species (Nectarinidae), all of which are nectarivores (Cowling et al., 1996). These birds are important pollinators for certain fynbos plant groups, including Proteaceae and Ericaceae (Rebelo, 1987). At the marine–terrestrial interface, bird communities include larger seabird species such gulls (*Larus* spp.), terns (*Sterna* spp.), and the African black oystercatcher (*Haematopus moquini*), as well as smaller migrant waders (Skead, 1966; Pringle and Cooper, 1977; Williams et al., 1990). The Cape kelp gull (*Larus vetula*) and *H. moquini* are both major predators of marine invertebrates including mussels and, in the case of *H. moquini*, limpets (Siegfried, 1977; Hockey and Underhill, 1984; Griffiths and Hockey, 1987).

With 48 resident species, including various snakes and lizards, and two terrestrial tortoise species, reptiles are well-represented in the Peninsula fauna (Wright, 1988; Hey, 1994; Branch, 1998). The 18 resident amphibian species, three of which are endemic to the south-western Cape, thus make up the smaller component of the Peninsula’s herpetological diversity (Baard, 1989; Picker and Samways, 1996; Channing, 2001). Both reptiles and amphibians occur in, but are not restricted to, the Peninsula’s fynbos habitats (Fraser and McMahan, 1994; Branch, 1998; Channing, 2001).

The invertebrate fauna of the Peninsula is diverse and certain groups display remarkably high endemism (Cowling et al., 1996; Picker and Samways, 1996; Sharratt et al., 2000). Indigenous invertebrates are found in both natural and transformed habitats, but invertebrate communities in natural habitats are generally more diverse (Ratsirarson et al., 2002; Pryke and Samways, 2009). In these habitats, resident insects play important ecological roles, pollinating flowers, and dispersing seeds, of a wide variety of indigenous plants (Johnson, 1992; Cowling et al., 1994; Johnson and Bond, 1994; Johnson and Steiner, 1997). Some of the above-mentioned invertebrates comprise part of a larger group of Peninsula

plants and animals, which are currently threatened with extinction, as a result of destruction or modification of natural habitats by humans (Baard, 1989; Cowling et al., 1996; Holmes et al., 2012). Habitats in low-lying areas (particularly in the north) have been transformed into residential gardens, agricultural land (mainly pine plantations and vineyards) and thickets dominated by invasive alien species such as *Acacia* spp. (Richardson et al., 1996; Rouget et al., 2003; Holmes et al., 2012). In 1998, in an attempt to restrict further degradation of Peninsula ecosystems, local government declared a little more than half of the Cape Peninsula (245 km²) part of the open-access Cape Peninsula National Park (Government Gazette, 1998), which would later become the TMNP. This means that indigenous flora and fauna in high-lying areas, and in some low-lying areas in the south, are accorded protection by the Protected Areas Act (2003).

CHAPTER 2

Ranging behaviour, activity budgets and diet
of a non-raiding troop of Cape Peninsula
chacma baboons (*Papio ursinus*)

ABSTRACT

The terrestrial habitats available to chacma baboons (*Parpjo ursinus*) on the Cape Peninsula, are, for the most part, oligotrophic in nature. The low nutrient levels, and widespread presence of chemical compounds that discourage herbivory in plant tissues, are thought to limit the ease with which resident medium-sized to large mammals fulfil their nutritional requirements. Peninsula baboons are however able to access nutrient-rich tissues of marine invertebrates in the intertidal zone. I investigated aspects of the behaviour and diet of the last remaining natural-foraging Peninsula troop. I tracked the troop using GPS technology, and recorded behavioural data using instantaneous scan sampling. I used these data to determine seasonal variation in: home range (HR) area and patterns of use (modelled using two different approaches), activity budgets, and diet. The troop used an area of $\sim 45 \text{ km}^2$ over the course of the study, and travelled a little more than 6 km per day on average. HR cell use was positively related to slope and habitat productivity, and negatively related to distance-to-coast, altitude and distance-to-fresh water (though this relationship was weak). A Bayesian spatial generalized linear mixed model (SGLMM) performed better than a generalized linear model (GLM) in terms of predicting frequency of cell use. Daily path length (DPL) and rate of travel were greater during the warm, dry summer than during the colder, wetter months. Feeding and walking were the dominant activities in all four seasons, but time spent engaged in these activities fluctuated seasonally. The diet of the troop was dominated by terrestrial foods of different types, with marine foods comprising only a small proportion of the diet across all seasons. All behavioural indicators suggest that this troop was nutrient-stressed relative to other Peninsula troops, and baboon troops elsewhere, but the severity of this stress varied through seasons.

INTRODUCTION

Primates have limited time available for allocation to different activities each day (Dunbar and Dunbar, 1988; Hill et al., 2003) and must therefore make behavioural choices when unable to engage in two activities simultaneously (McFarland, 1974). Over the medium- to long term, these choices manifest in an individual's activity budget, which is strongly influenced by food availability (Ménard and Vallet, 1997; Overdorff et al., 1997; Guo et al., 2007; Fan et al., 2008). When food is scarce or difficult to obtain, many primates increase time spent engaged in activities related to acquiring food (travelling or feeding) at the expense of resting or social activity (e.g. Isbell and Young, 1993; Doran, 1997; Agetsuma and Nakagawa, 1998; Hanya, 2004 a; Stone, 2007; Zhou et al., 2007; Sayers and Norconk, 2008). These behavioural changes are typically associated with a switch to so-called 'fallback foods' as important dietary items (Wrangham et al., 1998; Alberts et al., 2005; Grueter et al., 2009, 2013). Fallback foods are relatively nutrient-poor (Wrangham et al., 1998; Hanya, 2004a), or costly to consume (in terms of time or energy; Alberts et al., 2005; see Marshall et al., 2009 for a review), and dependence on these foods therefore forces primates to allocate greater amounts of time to foraging (*sensu* Bronikowski and Altmann, 1996).

Many primates experience temporal fluctuations in food availability within their home ranges, and shortages of preferred foods are commonplace (e.g. Kurup and Kumar, 1993; Ménard and Vallet, 1997; Gursky, 2000; Furuichi et al., 2001). These periods of food scarcity may occur annually, or semi-annually, and are typically related to seasonal processes such as rainfall, which affects plant phenology (Tutin et al., 1997; Wrangham et al., 1998; Furuichi et al., 2001). One solution to the temporal shortfalls of preferred food items is to increase dietary breadth. The general dietary adaptability and behavioural plasticity exhibited by many primates suggest that they have evolved to do just that (e.g. Poulsen et al., 2001; Matsumoto-Oda, 2002; Pavelka and Houston, 2004; Fan et al., 2008; Grueter et al., 2009, 2013; Masi et al., 2009; Morrogh-Bernard et al., 2009; Mekonnen et al., 2010; Chaves et al., 2011).

Baboons (*Papio* spp.) display extreme dietary flexibility (Altmann and Muruthi, 1988; Alberts and Altmann, 2006) and are able to "adapt to different habitats, taking advantage of whatever staple food items the local area may offer" (DeVore and Hall, 1965). This statement is supported by baboons' apparent ability to inhabit remarkably diverse habitats including semi-deserts (Hamilton et al., 1976; Cowlishaw, 1997), grasslands and savannahs (Stacey, 1986), forests (Rowell, 1966; Okecha and Newton-Fisher, 2006), and seasonal floodplains (Busse, 1980; Engh et al., 2006). Considering differences in plant- and animal communities

(and thus, food availability) across the above-mentioned habitats, it is unsurprising that baboons exhibit remarkable inter- and intra-population dietary variation (DeVore and Hall, 1965; Hamilton et al., 1978; Whiten et al., 1991; Byrne et al., 1993; Alberts et al., 2005). As might be expected (in light of the aforementioned links between diet and behaviour), baboons also exhibit variation in activity budgets and ranging behaviour across troops and populations (Post, 1981; Altmann and Muruthi, 1988; Dunbar, 1992).

When nutrient-stressed, baboons increase time spent feeding at the expense of time spent resting and, in extreme circumstances, time spent engaged in social activity (Dunbar and Dunbar, 1988; Alberts et al., 2005). Also, troops that are more nutrient-stressed travel further on a daily basis, and occupy larger home ranges, than less-stressed troops in the same region (Whiten et al., 1987). The profound effects of changes in food availability on baboon behaviour and ranging patterns are abundantly clear in populations where certain troops have access to nutrient-rich human foods (either through provisioning or raiding). At two different study sites in Kenya, members of semi-provisioned baboon troops spent less time feeding, and more time resting, than non-provisioned animals (Altmann and Muruthi, 1988; Strum, 2010). On the Cape Peninsula, South Africa, troops with access to human-derived foods occupied much smaller home ranges and, for the most part, travelled shorter distances on a daily basis, than those without (Hoffman and O’Riain, 2012a).

While exploitation of human foods is common in baboons (Altmann and Muruthi, 1988; Naughton-Treves et al., 1998; Hill, 2000; Strum, 2010), inclusion of marine foods in baboon diet has been documented in only two populations: the chacma baboons (*Papio ursinus*) of the Cape Peninsula (Hall, 1962, 1963; Davidge, 1978) and yellow baboons (*Papio ursinus*) of coastal, southern Somalia (Messeri, 1978). The tissues of intertidal marine organisms are typically rich in macronutrients (Karakoltsidis et al., 1995; Fleurence, 1999; Smith and Partridge, 2004), unlike the tissues of many plants in the Peninsula’s relatively unproductive terrestrial habitats (Kruger, 1977). Marine foods might therefore represent important alternatives to largely nutrient-poor terrestrial foods for Peninsula baboons. It has however been stated that tides, waves and wind affect the ease with which these foods may be exploited (Hall, 1963).

To date, no comprehensive study on the relative importance of terrestrial and marine foods to Peninsula baboons has been conducted. Given that nutritional rewards may vary annually in both marine- (Van Erkom Schurink and Griffiths, 1991), and terrestrial habitats (Pierce, 1984; Van Doorn et al., 2010) baboons are predicted to vary their use of these two

broad habitat types. Use of the two habitats types should also vary with conditions in the intertidal zone, which change over much shorter time scales (Palmer, 1995).

Aims and predictions

The main aim of this chapter is to provide a detailed account of the ranging patterns, activity budgets and diet, of the only troop of baboons on the Cape Peninsula that does not currently consume human-derived foods but has access to marine intertidal organisms. More specifically I aim to quantify the seasonal variation in home range (HR) size, daily path length (DPL), rate of travel, activity budgets and diet composition (in terms of broad food categories). The final aim is to determine which factors affect intensity of HR cell use, using two different approaches to modelling spatially-structured data. Based on trends observed elsewhere and fundamental theories of behavioural ecology I predict that:

1. HR size will be greatest, and DPL longest, during the season when food availability is lowest.
2. The study troop will favour those habitats that are most productive and offer the highest quality food items.
3. During the season(s) when the baboons experience food shortages, they will allocate greater amounts of time to foraging behaviour (*sensu* Bronikowski and Altmann, 1996).
4. The baboons of the study troop will favour foods that are richest in protein, and will adjust their seasonal diet composition in order to maximise intake of said foods.

METHODS

See Chapter 1 for a detailed description of the study site.

Study animals

The study troop for this research was the Kanonkop troop (KK), which is the only troop on the Peninsula that does not feed on either human foods or agricultural produce (Hoffman and O’Riain, 2012 a; this study). The troop’s documented home range encompasses approximately 37.7 km² in the northern part of the CoGH section of the TMNP, and allows them unlimited access to the Peninsula’s east and west coasts (Hoffman and O’Riain, 2012a). Due to the size of the troop and the large area over which they typically spread, the difficulty implicit in counting baboons in fynbos and the restrictions of my research permit, I was only

able to obtain two counts during the course of the study. In March 2010 (when I obtained a count that I believe included the entire troop), KK troop numbered 56 baboons, with an adult sex ratio (M:F) of 1:3.4.

Permit conditions

In light of KK troop's status as the last remaining non-raiding troop on the Peninsula, South African National Parks (SANParks) Scientific Services staff expressed concern regarding the potential effects of research on the behaviour of the troop. Ultimately, the permit was granted on condition that the research minimise human contact with the troop and hence the probability of habituation to tourists. Thus, it was stipulated that my assistants and I could spend only four months following the troop over the course of a year (one month in each season) to collect behavioural data, and that we were not allowed to habituate the troop to close (< 20m) human presence. I was later granted permission to collect data over a fifth short period in winter of a second year because minor technical difficulties had affected data collection during the first winter session. Due to the limitations on time spent with the troop, and stipulations regarding the minimum distance from which we could observe the animals (≥ 20 m), we were not able to compile identikits of individuals for the troop and hence collect focal data.

Data collection

With the help of volunteer field assistants (three per fieldwork session), I collected behavioural data on 136 days during five discrete fieldwork sessions spread across all four seasons between May 2009 and June 2010 (see Fig. 2.1; Kruger, 1979). During each of the first four fieldwork sessions (June and September 2009, and

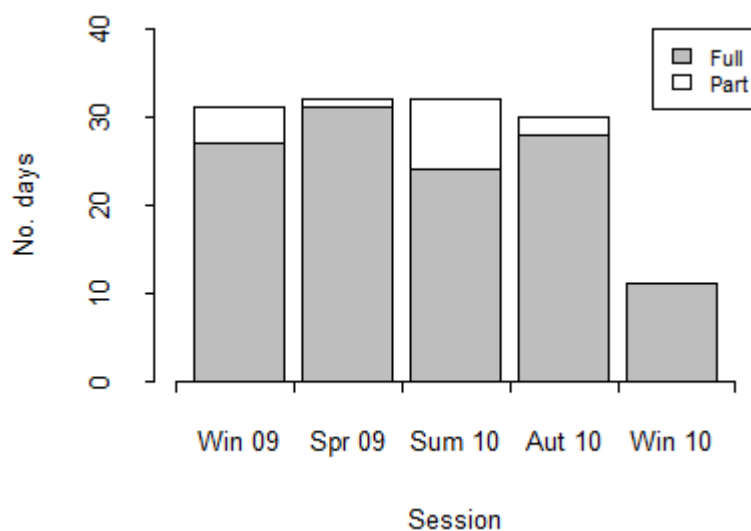


Fig. 2.1. Numbers of full- and part days (according to criteria used in analyses of ranging behaviour) on which data were collected during each fieldwork session. Win = winter, Spr = spring, Sum = summer, Aut = autumn, 09 = 2009, 10 = 2010.

January and March 2010) we attempted to collect data on 30 consecutive days within the calendar month (Fig. 2.1) in order to account for fluctuations in tide height through lunar cycles (Palmer, 1995). On each data collection day, we worked in pairs to improve our chances of maintaining contact with the troop, and to increase efficiency of data collection and reliability of data that were collected. A rotational roster was set up during each fieldwork session such that each observer spent equal time in the field with each other observer, and that I (M. Lewis) worked one shift with each assistant every four days. During each of these shifts I cross-checked the assistant's categorisation of habitat types and behaviour with my own as we conducted scans. These measures were taken to ensure continuity between myself and field assistants and hence to reduce the possible effects of observer bias.

We collected behavioural- and ranging data while following the troop on foot at a distance of 20 metres. This was possible because the troop had been habituated to human presence at this distance for a previous short-term spatial ecology study (Hoffman and O'Riain, 2012a). Whenever possible, we followed the troop from morning sleeping site to evening sleeping site. We were not able to follow the baboons from sunrise to sunset due to the Park's rules regarding use of roads (only during daylight hours). Time spent travelling to and from sleeping sites each morning and evening varied with site, and ranged from 10 to 40 minutes. We therefore strove to find the baboons before they left their sleeping site, and to follow them until they had arrived at their evening sleeping site, each day. On many occasions this was not possible however, either because the troop had left their sleeping site before we established visual contact (20.6% of days, $n = 136$), or because we had to leave the troop prior to arrival at a sleeping site (61.8% of days, $n = 136$). We were however able to determine (without doubt) which sleeping site the troop slept at on the majority of days (90.4% of days, $n = 136$). I considered the use of a sleeping site to be beyond doubt if we followed the troop to within 100 m of the sleeping site in the evening, or if we established visual contact while the troop was within 100 m of the sleeping site in the morning. I used 100 m as the threshold value because this was the average distance travelled during inter-scan intervals (rounded off to the nearest 10 m) during the study. If the troop split up into foraging groups during the course of follows we tracked the larger group (based on numbers of visible individuals) until the groups remerged. This was a relatively rare occurrence, and we were not biased to a particular group of animals, so it seems unlikely that we would have over- or under-sampled any particular subgroup of the troop.

Spatial data

For the analysis of ranging behaviour, we recorded the geographic coordinates of the estimated centre of the troop in degrees and minutes every ten minutes. When we could not move to the estimated centre of the troop at the appointed time without disturbing the baboons, we waited until they had moved away before walking to the appropriate location and recording the coordinates. We determined these coordinates using a Garmin® e-Trex hand-held GPS unit, and recorded them using a CyberTracker® Screen sequence uploaded to a Fujitsu Siemens® Pocket LOOX N500 pocket-PC. We only recorded the coordinates when the GPS unit registered accuracy of 10 m or less.

I added a number of coordinates retrospectively on days when we could not follow the troop from sleeping site to sleeping site, and the points could be inferred with a high degree of confidence. Thus, I added points when we encountered the troop near, but not at, a sleeping site and I could reliably infer which sleeping site had been used (in the mornings), or when we left the troop prior to sunset but identified which sleeping site would be used (in the evenings; see above). When this was the case, I assumed that the troop had taken the most direct route to or from the sleeping site in question and added one point in each grid cell along this route (see below).

For the purposes of analysing ranging patterns, it was necessary to define “full days” as opposed to “part days”. I defined full days as days on which we recorded, or were able to infer (see above), points that constituted the path from morning sleeping site to evening sleeping site. If we lost the troop during the course of the day, but re-established visual contact within 60 minutes, I still considered that day to be a full day. I defined part days as those on which we could not determine either the morning or evening sleeping site, or both, or we lost contact with the troop for longer than 60 minutes during the course of the day.

Ranging patterns

I converted the GPS coordinates from degrees and minutes to decimal degrees using the formula:

$$Dd = D + \frac{M}{60}$$

where Dd is latitude or longitude in decimal degrees, and D and M are the degrees and minutes for the same values. Because all of the coordinate points were situated south of the equator I multiplied the values obtained for latitude by -1 . I rounded off all values in decimal

degrees to nine decimal places, and then imported the points into Arcview 3.3 (ESRI 2002) and projected them in Transverse Mercator, spheroid WGS 84, central meridian 19.

I used the Repeating_shapes (repeat_shapes.avx) extension to Arcview 3.x (Jenness, 2005) to superimpose a grid of 0.0225 km² cells (150×150 m) on the points recorded (following Hoffman and O’Riain, 2011). The grid was clipped at the Peninsula’s east and west coasts such that the area covered did not extend into the sea. I then estimated seasonal home ranges (and the home range used over the entire year) based on the baboons’ use of cells within the abovementioned grid. For the purposes of home range estimation and home range use analysis, I included only a single point at each morning- and evening sleeping site on full days (i.e., the last point recorded prior to departure from the sleeping site in the morning, or the first point recorded following arrival at the sleeping site in the evening). I defined “used cells” as cells that contained at least one GPS point, or through which the baboons had travelled (based on paths between consecutive points). When estimating home ranges, I included used cells; cells that were bounded on any three sides, or on two opposite sides, by used cells; cells that were bounded on all sides by used cells and the coast; and cells in areas that were completely enclosed by the aforementioned cells. The cell accumulation curve for the home range estimated in this way reached a plateau after 19 weeks of data collection (no new cells were added to the home range beyond this point in time; Fig. 2.2).

I considered the grid cell accumulation method of home range estimation to be more appropriate than, for example, kernel density estimates or the local convex hull approach, for several reasons. As mentioned by Hoffman and O’Riain (2012a), this approach allows for analysis of the data at a scale that is appropriate, given spatial variation in habitats on the Peninsula, and the wide troop spread exhibited by Peninsula baboon troops (Hoffman and O’Riain, 2011). Also, implementation of this method allows for a straightforward comparison with the results reported by Hoffman and O’Riain (2011, 2012a).

I used Arcview 3.3 (ESRI 2002) to calculate the troop’s DPL and rates of travel. I calculated the distances between consecutive points using the Nearest_features (nearfeat.avx) extension in Arcview 3.x (Jenness, 2004), and then manipulated these as required. To determine DPL, I summed all distances travelled between consecutive points on a given day. I multiplied distances travelled during inter-scan intervals by six to calculate hourly rates of travel. For analysis of rates of travel I used only distances travelled during inter-scan intervals by six to calculate hourly rates of travel. For analysis of rates of travel I used only distances travelled between recorded points (as opposed to inferred points). Only data collected on full

days (according to the ranging criteria; $n = 121$) were used for analyses of DPL and rates of travel.

Behavioural data

While following the troop, we collected general behavioural data by means of instantaneous scans (Altmann, 1974), recorded every ten minutes, starting on the hour.

Whenever possible, one observer watched the baboons and called out

observations, and the other recorded these data using the same CyberTracker[®] Screen sequence that was used to record GPS coordinates. In this way, the caller could carry out the scan without losing visual contact with the troop and thus reduce his/her chances of including the same individual in the scan twice. We conducted scans from the estimated centre of the troop whenever possible. This was not possible when the baboons moved rapidly through dense vegetation. When this occurred we recorded observations from a position directly behind the estimated centre of the troop relative to the troop's direction of movement. For each scan we included all individuals that were visible within three minutes of the commencement of the scan. Using binoculars, we identified each baboon to sex and age-class where possible, and recorded its behaviour. If a baboon of a certain sex and age-class that had already been included in a given scan moved out of sight, animals of the same sex and age-class that later became visible (i.e. they were not visible at the beginning of the scan) were not included in the scan. This further reduced the probability of pseudoreplication within scans.

The four behavioural activities that we recorded were feeding, moving, socialising and resting (see Dunbar, 1992 for definitions), as these activities are known to constitute more than 95% of baboons' time budgets (Dunbar, 1992). Feeding was further divided into feeding while stationary and "walk-feeding". We included the latter category because the baboons of this troop often picked up and consumed small food items while walking. When this was done the food items were consumed whole and we were invariably not able to identify the items ingested. When baboons were feeding while stationary, we were more successful at identifying the food item being consumed and classified it as far as possible.

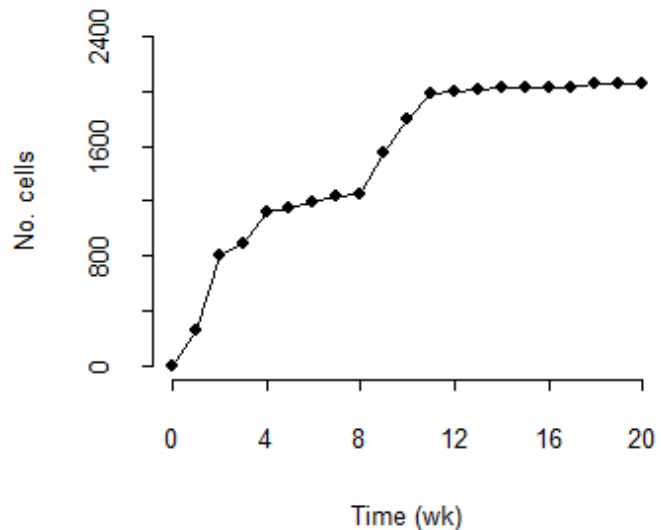


Fig. 2.2. Cumulative frequency of number of cells included in KK troop's estimated home range following each week (seven day period) of data collection.

Foods were classified as terrestrial or marine, then plant or animal, then (if terrestrial) subterranean or above-ground. Where possible, the anatomical structure (e.g. bulb, flower or stem) consumed by the baboons was determined, and the plant from which food was obtained was identified to genus-level.

Food samples

If we observed baboons feeding on a given food more than twice in any season, we collected three to five samples of this food item for macro-nutrient- and stable isotope analysis (see Chapter 3). We collected samples of the different foods from various parts of the troop's home range (i.e. marine foods were collected from both coasts) to avoid biasing our results to a single location. In the case of terrestrial foods, we collected only the structure(s) from which the baboons derived their food (e.g. flower, seed or leaf). Following collection we placed these samples in paper bags, and suspended them in a well-ventilated area in order to initiate air-drying of the samples, and to prevent rotting. We collected entire marine organisms that were known foods and placed them in zip-seal plastic bags, which we placed in a -20°C freezer on the day of collection. The marine food samples were stored in a -20°C freezer until they were processed as described below. All samples were collected over the course of a single day in the final week of the month during which behavioural data were collected.

In the laboratory, I processed both terrestrial and marine samples, such that only those tissues which were ingested by the baboons were included in the samples for analysis (following Rothman et al., 2008). Having removed extraneous tissue, I shredded desiccation-resistant plant tissues, such as *Leucodendron* spp. seeds and *Carpobrotus* sp. leaves, using a commercial blender (Waring®, Stamford, USA). I dried plant samples in a drying oven at 60°C and freeze-dried marine samples at -80°C , and then ground each sample to a homogeneous powder using a Wiley Mill Standard Model No. 3 (Arthur H. Thomas Co., Philadelphia, USA) and a custom-built hammer mill (United Scientific Pty. Ltd., Western Cape, South Africa). The samples prepared in this way were then analysed following methods recommended by Ortmann et al. (2006) to determine percentage nitrogen (using the Kjeldahl procedure) and percentage soluble protein (Biorad). The samples were also analysed to determine whether or not polyphenolics and alkaloids were present (following Bate-Smith, 1975 and Cromwell, 1955). Dragendorff's-, Mayer's- and Wagner's reagents (Cromwell, 1955) were used to test for the presence of alkaloids.

Statistical analyses

Home range use

I used the grid cells within the troop's home range as sampling units for investigation of factors affecting intensity of use of different parts of the home range. Not all cells were uniform in terms of area because cells along the coast were clipped (see above), and were therefore smaller than inland cells. To control for differences in cell size, and thus area available for use by the baboons, I adjusted the number of GPS points in each cell. I did so using the formula:

$$Adj_i = Obs_i / Area_i \times 0.0225$$

where Adj_i is the adjusted value for cell i (rounded to the nearest unit), Obs_i is the recorded number of GPS points in cell i and $Area_i$ is the area (in km²) of cell i .

Following Hoffman and O'Riain (2011, 2012 b) I quantified geographical and biological properties of each cell ($n = 2058$). I calculated average altitude (m) and average slope (°) in each cell in Arcview 3.3 (ESRI 2002) using a 10 m digital elevation model (DEM; City of Cape Town, 2008. CMA 10 m DEM, City Maps, City of Cape Town; Fig. 2.3A and B). I calculated the distances from each cell to the nearest perennial source of fresh surface water and to the nearer coast, in Arcview 3.3 (ESRI 2000) using the Nearest_features (nearfeat.avx) extension to Arcview (Jenness, 2004). The former was calculated using an edited version of a shapefile provided by SANParks (glcrveg; South African National Parks, unpublished data); I added two small water bodies (surface area < 0.001 km²), which I observed in the troop's home range (and which contained water during all four seasons), to the shapefile (Fig. 2.3D). Finally, I determined the dominant habitat type in each cell (by percentage area), using a shape file provided by Mucina and Rutherford (2006; Fig. 2.3 C). I used the number of GPS points (indicating the troop's location) in each cell as a measure of the intensity of use by the troop. This quantity was used as the response term in the models described below.

I tested for collinearity between predictor variables in each data set (the full data set and the sub-samples used for the non-spatial models) by performing Pearson correlations between all pairs of variables (Dormann et al., 2013). I considered two variables to be collinear if the absolute value of the Pearson correlation coefficient ($|r|$) exceeded 0.7 (as recommended by Dormann et al., 2013). Based on this criterion, no two pairs of variables within the dataset in question were collinear. I standardised all predictor variables prior to running the models (following Zuur et al., 2009), which meant that effect sizes were directly comparable.

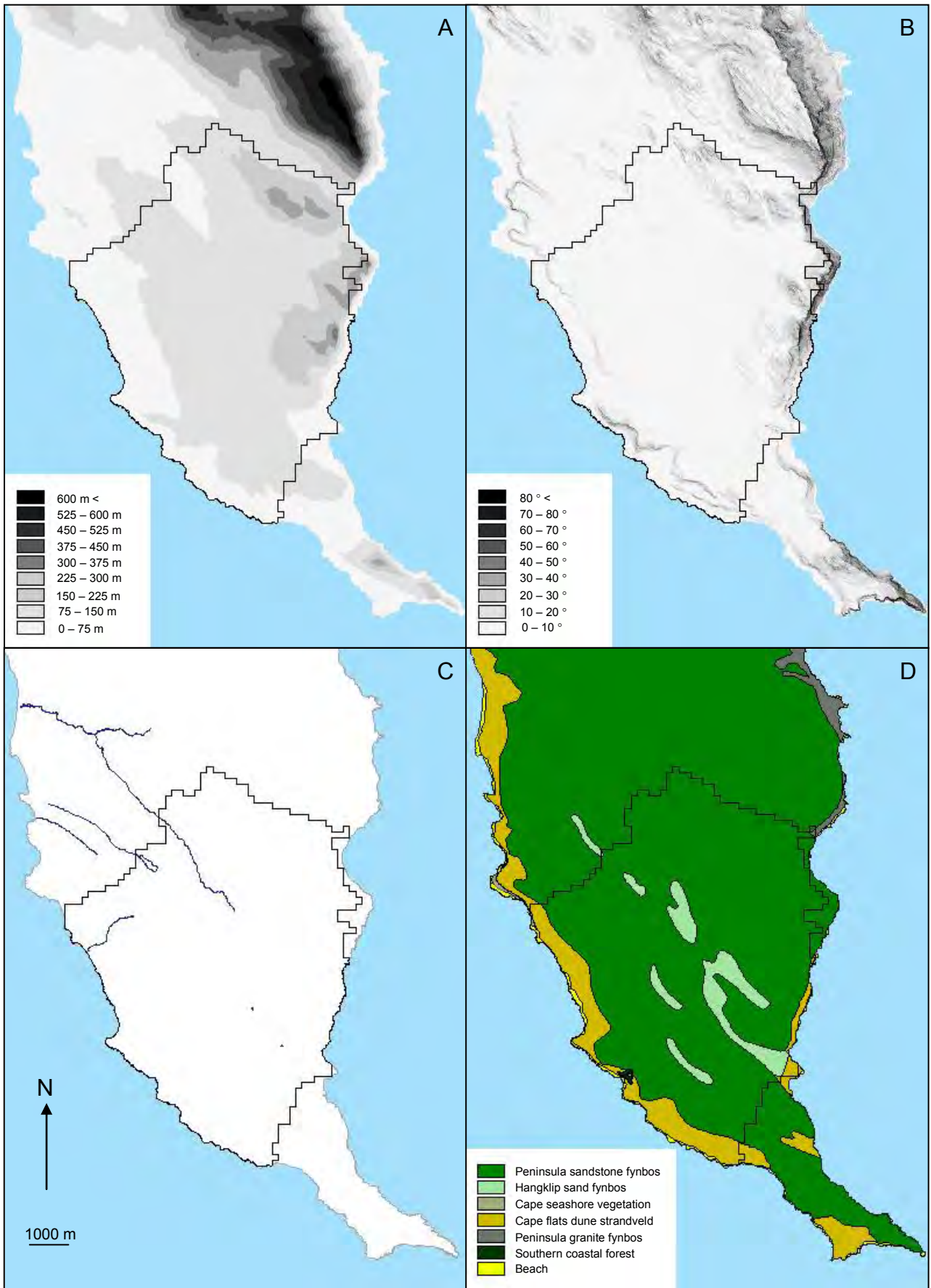


Fig. 2.3. Maps of the southern-most part of the Cape Peninsula showing altitude (A), slope (B), locations of permanent surface water (C; water is denoted by dark blue lines) and vegetation type (D). The black outline indicates the size and location of KK's home range.

Spatial autocorrelation

A common assumption implicit in most statistical tests is that of independence of observations (Hurlbert, 1984; Zar, 1999; Zuur et al., 2009, 2010). This assumption is frequently violated when ecological data are collected across geographic space, as many ecological phenomena exhibit spatial autocorrelation (SAC; e.g., Koenig, 1998; Badgley and Fox, 2000; Keitt et al., 2002; Diniz-Filho et al., 2003). SAC is defined as “the property of random variables taking values, at pairs of locations a certain distance apart, that are more similar (positive autocorrelation) or less similar (negative autocorrelation) than expected for randomly associated pairs of observations” (Legendre, 1993). Failure to address SAC in analyses of geographically-structured data may be problematic, as SAC inflates Type I errors (i.e., false positives) and non-spatial models might produce erroneous coefficient estimates in this context (Dormann, 2007; Dormann et al., 2007). Models that incorporate SAC may even generate coefficient estimates that differ in terms of sign from those generated by non-spatial models (Kühn, 2007). The incidence of spatial autocorrelation does not however necessarily mean that coefficients generated by non-spatial models should be disregarded (Hawkins et al., 2007).

SAC often arises as a result of distance-related processes such as dispersal and migration (Legendre, 1993; Dormann et al., 2007). Considering the spatial scale at which I analysed the KK troop’s home range use, and the temporal resolution of the GPS coordinate records, it seemed highly likely that the data might exhibit SAC (Aarts et al., 2008). Indeed, analysis of a similar data set in a previous study revealed significant SAC in model residuals (Hoffman and O’Riain, 2012b). I therefore assessed SAC in the residuals of the models described below with Moran’s *I* tests for SAC. Moran’s *I* is a spatially weighted measure of similarity across observations, that ranges from -1 to 1 in value, with zero indicating no SAC (Moran, 1950; Diniz-Filho et al., 2003; Dormann et al., 2007). In light of contrasting findings regarding the effects of SAC on model outcomes (Hawkins et al., 2007; Kühn, 2007), and differences in performance of different spatial models (i.e., models that account for or incorporate SAC; Dormann et al., 2007), I adopted two analytical approaches that differ in terms of how they deal with SAC and also in terms of the models used.

The first approach involved removing spatial dependence among observations prior to analysis and then using non-spatial statistical tests (Legendre, 1993). This may be accomplished by simply removing observations from the data set until SAC is no longer significant (Hawkins et al., 2007). This approach is easily implemented, and allows for the use of non-spatial models, but entails a net loss of information, and is contingent on relatively

large sample sizes (Legendre, 1993; Hawkins et al., 2007). The above-mentioned loss of information is seen as a major drawback of this approach (Legendre, 1993), but where sample size allows, it remains a viable option. This is the case in the model described below, as the sub-sample used to fit the model included almost twice as many observations as the largest dataset used in a recent assessment of the effects of sample size on model performance (Wisz et al., 2008).

The second approach that I adopted involved the use of models that incorporate, or at least account for, SAC (Legendre, 1993; Dormann et al., 2007). There are a variety of models in both Bayesian and frequentist frameworks, that have been designed for, or modified for, use in analyses of spatial data of this type (Kühn, 2007; Hughes and Haran, 2013; for a review of frequentist models see Dormann et al., 2007). In light of the fact that the spatial model accounts for SAC (Hughes and Haran, 2013), I used data from all cells within the troop's home range as the input for this model.

Models

I used Generalized Linear Models (GLM; Nelder and Wedderburn, 1972) and sparse spatial Generalized Linear Mixed Models (SGLMM; Hughes and Haran, 2013) to examine the relationships between frequency of use of cells within the troop's home range and predictor variables (environmental and topographic factors). GLMs are not spatial models, and were used in the first approach described above. Sparse SGLMMs alleviate spatial confounding by incorporating the spatial structure in the data into the model (Hughes and Haran, 2013), and were therefore used in the second approach described above.

GLMs are extensions of classical linear models that allow for modelling of response variables that follow non-normal distributions (Nelder and Wedderburn, 1972; Guisan et al., 2002). Response variables might follow, for example, the binomial or Poisson distributions (Nelder and Wedderburn, 1972; McCullagh and Nelder, 1989), which are appropriate for modelling of 0–1 (presence–absence) and count-type response variables (under certain conditions), respectively (Vincent and Haworth, 1983; McCullagh and Nelder, 1989; Manel et al., 1999; Brotons et al., 2004; Dobson and Barnett, 2008).

Prior to running the GLMs, I tested for over-dispersion by first calculating the variance-to-mean ratio of the response variable in each of the models. The variance-to-mean ratio of frequency of cell use was 31.6, which indicates that the data are over-dispersed relative to a standard Poisson distributions (Potts and Elith, 2006). I then used the “fitdist” and “gofstat” functions in the fitdistrplus package (Delignette-Muller et al., 2014) in R (R

Core Team, 2014) to determine whether or not a negative binomial distribution (Ver Hoef and Boveng, 2007) provides a better fit for the data better than a Poisson distribution or a zero-inflated Poisson (ZIP) distribution (used specifically where overdispersion has arisen as a result of zero-inflation; Gurmu and Trivedi, 1996; Maunder and Punt, 2004). The plots generated by the “fitdist” function suggest that the observed data are not zero-inflated relative to the negative binomial distribution (Fig. 2.4). Akaike’s Information Criterion (AIC) values indicate that the negative binomial distribution fits the observed data better than either a Poisson or ZIP distribution ($AIC_{\text{neg. bin}} = 10\,414.9$, $AIC_{\text{Poisson}} = 27\,126.5$, $AIC_{\text{ZIP}} = 23\,610.5$). I therefore ran the GLMs assuming a negative binomial distribution (Potts and Elith, 2006; Hilbe, 2011). I included predictor variables that have previously been shown to affect baboon ranging patterns and intensity of home range use in the full model (DeVore and Hall, 1965; Altmann and Altmann, 1970; Hoffman and O’Riain, 2011, 2012b). Thus, the full GLM used to examine the relationships between cell use and environmental predictor variables is described by the equation:

$$\log(f) = \beta_0 + \text{Altitude} + \text{Slope} + \text{Dist. coast} + \text{Dist. water} + \text{Vegetation type}$$

where \log denotes the negative binomial link function, and f is the frequency of cell use (i.e., the number of GPS points in the cell).

GLMMs are extensions of GLMs that allow for correlation between observations through inclusion of random effects (Zuur et al., 2009). The sparse SGLMM, proposed by Hughes and Haran (2013) is a new parameterization of the GLMM for areal data (i.e., data observed at the vertices of a graph; Hughes, 2014), first proposed, and applied in a Bayesian setting by Besag et al. (1991). Although the model proposed by Besag et al. (1991) was formulated for analysis of spatial data, it has since been shown that this model is in fact spatially confounded (Clayton et al., 1993; Reich et al., 2006). The sparse SGLMM alleviates spatial confounding through inclusion of random effects that incorporate patterns corresponding to spatial autocorrelation (Hughes and Haran, 2013). The random effects take the form of eigenvectors (of the Moran operator; Moran, 1950), which represent potential patterns of spatial dependence in the data (Hughes and Haran, 2013). The model is computationally efficient because it permits inclusion of only positive eigenvalues (i.e., positive spatial dependence is assumed; Hughes, 2014). I ran this model assuming a Poisson distribution, because this is the best available approximation of the distribution of the data (the package does not yet allow for assumption of a negative binomial distribution). I included the same predictors as in the GLM described above. Thus, the first stage of the

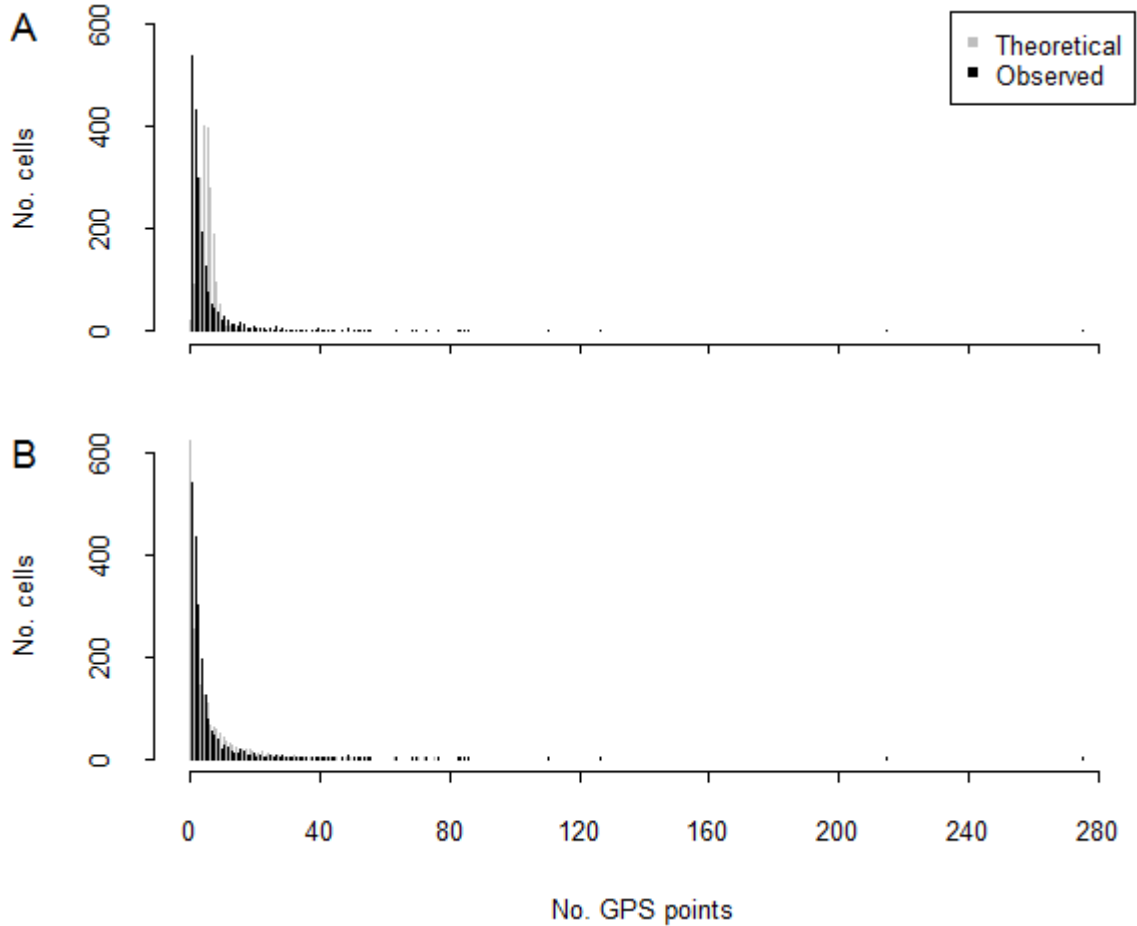


Fig. 2.4. Histograms of observed values and theoretical Poisson (A) and negative binomial (B) distributions with parameter values obtained using the “fitdist” function in R.

SGLMM used to investigate the relationships between home range cell use and environmental predictor variables is described by the equation (in vectorised form):

$$g(\mu) = X\beta + M\gamma$$

where X is the design matrix (i.e., fixed effects of altitude, slope, distance-to-coast, distance-to-water, and vegetation type). The second stage, that is the prior for γ , is described by the equation:

$$p(\gamma | \tau_s) \text{ proportional to } \tau_s^{(q/2)} \exp(-\tau_s/2 \gamma' M' Q M \gamma')$$

where τ_s is a smoothing parameter and Q is the graph Laplacian. As the response variable follows a Poisson distribution, β and γ are updated using Metropolis-Hastings random walks with normal proposals.

Model building

I included data from all home range cells in the initial run of the GLM described above. Having run this model, I tested for SAC in the model residuals with a Moran’s I test (run

using the `spdep` package; (Bivand, 2014). This test indicated that there was significant SAC in the model residuals (Moran's $I = 0.367$, $p < 0001$) and the estimated x-intercept of a Moran's I correlogram was 1521 (i.e., I dropped to 0 at 1521 m). I therefore took a random sub-sample of 203 cells and ran the model again including data from sub-sampled cells only. Sub-sampling to this extent did not eliminate SAC in the residuals of this model however (Moran's $I = 0.398$, $p < 0.05$), so I repeated these steps (reducing the size of the sub-sample by one each time) and tested for SAC in the residuals of resultant models. A Moran's I test indicated that a sub-sample of 197 cells was sufficiently small to eliminate significant SAC from the residuals of the model (Moran's $I = 0.109$, $p = 0.189$). I therefore used the model based on this sub-sample of cells in further analyses.

In order to find the optimal GLM, I used the “`drop1`” command in the `stats` package (R Core Team, 2014) to run analysis of deviance tests on candidate models (the full model with each predictor variable removed in turn; Zuur et al., 2009). Where these tests indicated that a variable (or variables) did not contribute a significant amount of the deviance explained by the model, I removed the variable(s) in question and ran the model without said variable(s). I then assessed the models with and without said variable(s) using second-order Akaike's information criterion (AIC_c), to determine which model was more parsimonious. I used AIC_c rather than AIC because n/K (where n = number of observations and K = number of parameters) was slightly smaller than 40 (Burnham and Anderson, 2004). Based on the above-mentioned criteria, I excluded distance-to-water from the final model, as this variable did not contribute significantly to the deviance explained by the model, and the AIC_c of the model with only four predictor variables (altitude, slope, distance-to-coast and vegetation type) was lower than that of the full model.

I included data from all home range cells in the sparse SGLMM. I used the default priors and default value for the number of Moran eigenvectors ($q = 50$) in the initial run of this model (Hughes, 2014). As in the GLM, I tested for SAC in the residuals of this model using a Moran's I test, which showed that there was significant SAC in the residuals of the model (Moran's $I = 0.211$, $p < 0.001$). I therefore increased the number of eigenvectors (q) in the model by 25 and ran the model again. I repeated this step until the resultant model yielded residuals that did not exhibit significant SAC—this was true of the model with $q = 200$ (Moran's $I = 0.043$, $p = 0.068$). Values of all estimate-to-Monte Carlo standard error ratios for different predictors were indicative of convergence of the Markov chain (Jones et al., 2006). I did not investigate the effects of removing predictor variables from the model (on the deviance information criterion; DIC) because none of the highest posterior density (HPD)

intervals generated by the model included 0. I therefore used the model with all proposed predictor variables as the final sparse SGLMM, and considered the coefficient estimates generated by this model in further analysis and discussion.

I evaluated the final GLM and sparse SGLMM using the parameters recommended by Potts and Elith (2006). Thus, I determined Pearson's- and Spearman's rank correlation coefficients (r and ρ respectively) of observed and fitted values. These values provide an indication of the degree of relative agreement (Pearson's), and similarity of ranks (Spearman's), between observed and fitted values. I assessed model calibration (i.e., bias and spread of predicted values; Potts and Elith, 2006) by fitting a simple linear regression to observed- and fitted values. I did not compare the root mean square errors (RMSE) of the models because this quantity is dependent on sample size (Potts and Elith, 2006). The difference in sample size between the models therefore renders such a comparison of little meaning in the context of assessing model performance.

I fitted the GLMs using the stats package (R Core Team, 2014), and the sparse SGLMM using the ngspatial package (Hughes and Cui, 2013), in the statistical platform R (R Core Team, 2014).

Ranging behaviour

I took random sub-samples of 24 daily paths from winter, spring and autumn, thereby obtaining equal sample sizes across seasons, for the purposes of statistical analysis. These samples were close to normally distributed and variances were homogeneous across seasons (Levene's test: $F_{3, 92} = 1.917$, $p = 0.132$), so I used a parametric analysis of variance (ANOVA) to test for differences between daily path lengths in different seasons. The ANOVA revealed significant differences in DPL across seasons, so I performed a Tukey's Honest Significant Difference (HSD) test to determine which seasons differed in terms of DPL.

For the purposes of investigating seasonal differences in ranging rates, I obtained equal sample sizes of ranging rates by taking random sub-samples of 1798 values from each of winter, spring and summer. The resultant data were highly skewed, and violated the assumption of homogeneity of variances across seasons (Levene's test: $F_{3, 7188} = 30.447$, $p < 0.001$). I therefore conducted a Kruskal-Wallis rank sum test to determine whether or not there were seasonal variations in the troop's rate of movement. This test indicated that there were significant differences in KK troop's ranging rates across seasons, so I used Wilcoxon's

rank sum tests (with a Holm correction applied to the p-values; Holm, 1979) to determine which seasons differed in terms of ranging rates.

Activity budgets and diet

In order to control for the effects of seasonal fluctuations in day length on time allocated to different activities (Hill et al., 2003, 2004), I converted behavioural scan data to time spent engaged in different activities on each day. I did so by first calculating the proportion of scan observations comprised of different activities within discrete time periods during each day. This was necessary because the numbers of scans during different periods were not equal (Hanya, 2004b). I then multiplied the proportions determined in this way by the duration (in minutes) of each period to calculate the number of minutes allocated to different activities during that period. A new period commenced at sunrise and then at the turn of each hour through the rest of the day until sunset. Having calculated the number of minutes allocated to different activities during each period, I summed these values through each day in order to obtain daily values for the respective activities. For analysis of activity budgets and behavioural patterns, I used data collected on full days only. These were defined using the same criteria as those used for analysis of ranging behaviour, but I used scans as the defining characteristic of time spent with the troop. The numbers of full days in different seasons differed (and were small, particularly during summer) and the values for all four behaviours were not normally distributed during each season. I therefore used Kruskal-Wallis rank sum tests (with Holm corrections applied to the p-values; Holm, 1979) to determine whether or not the amount of time allocated to each activity differed across seasons. Where time spent in a given behaviour varied significantly, I performed Wilcoxon's rank sum tests (with a Holm correction applied to the p-values; Holm, 1979) to determine which seasons differed in this respect.

Calculating time (in hours or minutes) allocated to different activities is important in areas where day length varies seasonally (Hill et al., 2003, 2004), but percentage or proportion time activity budgets may also be informative in studies of seasonal variation in behaviour (Van Doorn et al., 2010). I therefore calculated proportion time activity budgets for each season as well, by dividing the values calculated as described above by the number of hours in the day in question. I arcsine transformed these data prior to further analysis because these values were proportions (Quinn and Keough, 2003). The transformed data were not normally distributed, and the proportions of time spent walking violated the assumption of homogeneity of variances across seasons (Levene's test: $F_{3,67} = 3.912$, $p < 0.05$). I therefore

used Kruskal-Wallis rank sum tests (with Holm corrections applied to the p-values; Holm, 1979) to determine whether or not the percentage of time allocated to each activity differed across seasons. Where the percentage of time spent in a given behaviour varied significantly, I performed Wilcoxon's rank sum tests (with a Holm correction applied to the p-values; Holm, 1979) to determine which seasons differed in this respect. I present seasonal changes in amounts of time (Hill et al., 2003, 2004), and proportions of daylight hours (Van Doorn et al., 2010), allocated to different activities for comparative purposes.

I inferred the proportions of the troop's diet comprised of foods belonging to different categories (above-ground plant-, subterranean plant- and animal foods) by determining the proportions of scan observations during which baboons fed on different foods. For the purposes of analyses of dietary composition, I used data from full days (based on the definition for calculation of activity budgets) only and arcsine transformed the data. These data were not normally distributed and the proportions comprised of subterranean foods differed across seasons in terms of standard deviations (Levene's test: $F_{3, 67} = 3.278$, $p < 0.05$). I therefore used Kruskal-Wallis rank sum tests (with Holm corrections applied to the p-values; Holm, 1979) to determine whether there was significant variation in percentages of time spent feeding on different foods across seasons. If there was significant variation in percentages of a food type consumed across seasons, I used Wilcoxon's rank sum tests (with a Holm correction applied to the p-values; Holm, 1979) to determine which seasons differed in terms of the baboons' consumption of that food type.

I calculated median values and inter-quartile ranges (IQR; where possible) of soluble protein content for foods belonging to each of the above-mentioned categories (with samples lumped according to genus). Due to small sample sizes, the only category in which I could conduct a statistical test (a Kruskal-Wallis rank sum test) for seasonal differences in soluble protein content was above-ground terrestrial plant foods. I used mass:length ratio of marine food items as a measure of the reward per unit foraging effort offered by marine prey items during different seasons. I performed Kruskal-Wallis rank sum tests to test for differences in the mass:length ratios of *Cymbula* sp. and *Mytilus* sp. collected during different seasons.

RESULTS

Ranging

Home range use

The home range used by the troop over the entire study period covered an area of 45.262 km² and extended to the coast on both the east- and west sides of the Peninsula (Fig. 2.5). Thus, the per capita area (PCA) of KK troop was 0.81 km².baboon⁻¹. The home range included 2058 cells, 108 of which were clipped (along the coast) and therefore did not cover a full 0.0225 km². There was considerable variation in the frequency of cell use (0 to 140 GPS

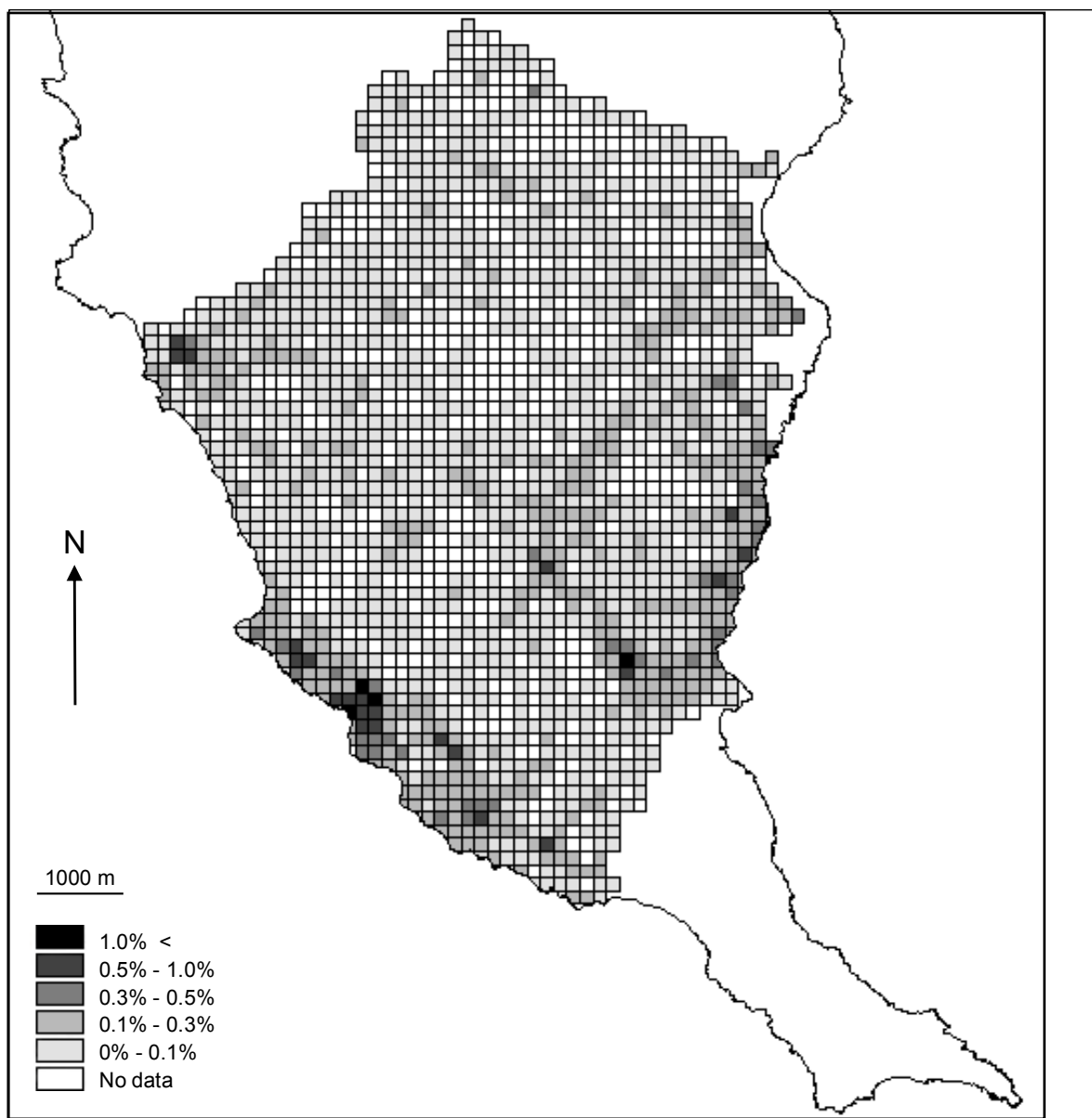


Fig. 2.5. The home range occupied by the troop throughout the study period. The shade of the cell indicates frequency of use as denoted in the legend.

points) within the troop's home range. The vast majority of cells (89.1%, $n = 2058$) contained fewer than 10 GPS points however, and 540 cells contained zero GPS points (Fig. 2.5).

There was marked variation in the size of areas of the home range used by the troop during different seasons. The largest and smallest areas used during a season, were those used during the austral summer (41.531 km^2) and winter (32.126 km^2), respectively (Fig. 2.6). The corresponding PCA values were $0.74 \text{ km}^2 \cdot \text{baboons}^{-1}$ and $0.57 \text{ km}^2 \cdot \text{baboons}^{-1}$ in summer and winter respectively. The PCA values of areas used in spring and autumn were intermediate

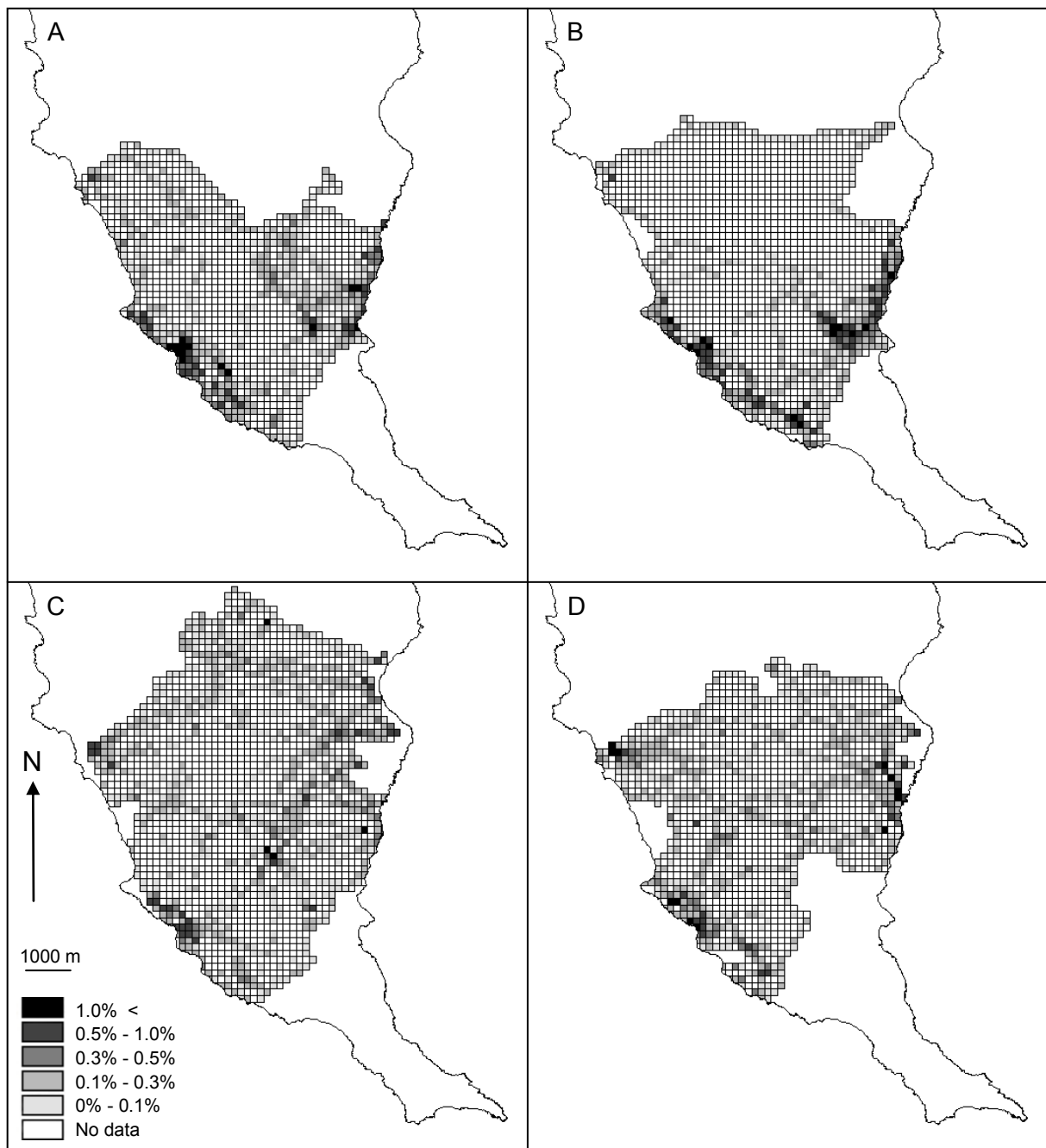


Fig. 2.6. The home range areas occupied by the troop throughout winter (A), spring (B), summer (C) and autumn (D). The shade of each cell indicates frequency of use as denoted in the legend.

between those of summer and winter. The areas used during all four seasons extended to the coast on both sides of the Peninsula, and included stretches of rocky shore on both coasts.

The outputs of the final GLM and sparse SGLMM were similar in certain respects, but there were several important differences between the two. The GLM and SGLMM differed in terms of the number of predictor variables included in the models (distance-to-water was removed from the GLM through the model-building process). Both analyses indicated that the predictor variables that were included in both models were significant predictors of frequency of cell use by the troop (Table 2.1). The signs of the estimates of the three numerical predictors that were included in both models (altitude, slope and distance-to-coast) were the same in the GLM and SGLMM. Both models indicated that frequency of cell use decreased with increasing altitude and distance-to-coast, and increased with increasing slope. The magnitudes of the numerical predictors' effects differed between models however, with the GLM indicating greater change per unit altitude and slope than the SGLMM, and the SGLMM indicating a greater change per unit of distance to the coast than the GLM. Both models however showed that the effect of distance-to-coast on frequency of cell use was greater in magnitude than those of altitude or slope. The SGLMM indicated that the magnitude of the effect of distance-to-water on frequency of cell use was small relative to those of altitude, distance-to-coast and slope.

The GLM and SGLMM both indicated that vegetation type is a significant predictor of frequency of cell use, but the signs and the sizes of the estimates differed between the two models in two out of three cases. The GLM indicated that frequency of cell use was significantly higher in cells dominated by Hangklip Sand Fynbos than in cells dominated by beach-type habitats. The output of the same model showed no significant difference between frequency of cell use in cells dominated by Cape Flats Dune Strandveld and Peninsula Sandstone Fynbos, and those dominated by beach-type habitats. The SGLMM on the other hand indicated that frequency of use was highest in cells dominated by beach-type habitats. Relative to these cells, the cells dominated by Peninsula Sandstone Fynbos were used least frequently by the troop. The higher r - and ρ -values of the correlations (Pearson's and Spearman's correlations respectively) between observed- and fitted values from the SGLMM (Table 2.2) indicate that this model performed better than the GLM (fitted values from the SGLMM were more similar to the observed values, and the ranks of these values were more similar to those of the observed values; Potts and Elith, 2006). The intercept terms from the regressions of observed values against fitted values from the two models indicate that the levels of bias in the fitted values from the SGLMM were lower than in those from the GLM.

Table 2.1. Results of the GLM and SGLMM fitted to area-corrected frequency of use of cells within the KK troop's home range¹

Predictor	GLM				SGLMM			
	Estimate	SEM	z	p(> z)	Estimate	H.P.D. interval limits		MCSE
						Lower	Upper	
Altitude	-0.339	0.115	-2.940	< 0.01	-0.133	-0.170	-0.093	0.0006
Slope	0.268	0.100	2.673	< 0.01	0.205	0.176	0.232	0.0004
Dist. Coast	-0.407	0.117	-3.486	< 0.001	-0.507	-0.562	-0.454	0.0006
Dist. Water	–	–	–	–	-0.048	-0.091	-0.007	0.0006
C.F.D. Strandveld	0.720	0.589	1.224	0.221	-0.629	-0.735	-0.532	0.0013
H.S. Fynbos	1.512	0.615	2.457	< 0.05	-0.324	-0.515	-0.145	0.0032
P. S. Fynbos	-0.166	0.543	-0.305	0.760	-0.759	-0.875	-0.651	0.0016

¹H.P.D. = highest probability density; SEM = standard error of the mean; MCSE = Monte Carlo standard error; Dist. = distance to; C.F.D = Cape Flats Dune; H.S. = Hangklip Sand; P.S. = Peninsula Sandstone.

The slope terms from the same regressions indicate that the bias in the fitted values of the SGLMM (what little there was) was more consistent than that in those of the GLM. In light of the SGLMM's superior performance and lower levels of bias, the results of this model only will be considered in the discussion.

Table 2.2. Results of evaluation and calibration of non-spatial and spatial models¹

Model	<i>n</i>	Correlation		Calibration	
		<i>r</i>	ρ	<i>b</i>	<i>m</i>
GLM	197	0.536	0.401	0.689	0.864
SGLMM	2058	0.712	0.612	-0.131	1.028

¹*n* = number of cells included in model; *r* = Pearson's correlation coefficient; ρ = Spearman's rank correlation coefficient; *b* = intercept of line generated by linear regression; *m* = gradient of line generated by linear regression.

Ranging behaviour

The troop's mean (\pm SE) daily path length (DPL) throughout the study period (based on 24 randomly selected paths from each season) was 6.044 (\pm 0.179) km. There were significant seasonal differences in the troop's DPL ($F_{3, 92} = 12.14$, $p < 0.001$; Fig. 2.7). The troop travelled further on summer days (mean \pm SE = 7.600 \pm 0.331 km) than on days in winter ($p < 0.001$), spring ($p < 0.001$) or autumn ($p < 0.01$).

The troop's mean (\pm SE) rate of travel throughout the study period was 0.556 (\pm 0.006) km.hr⁻¹. There were significant differences in travel rates across seasons ($\chi^2 = 22.037$, $df = 3$, $p < 0.001$; Fig. 2.8), with the troop's travel rates being significantly higher during summer (median = 0.489 km.hr⁻¹, IQR: 0.185 – 0.872 km.hr⁻¹) than during winter ($p < 0.05$), spring ($p < 0.001$) or autumn ($p < 0.05$). The troop

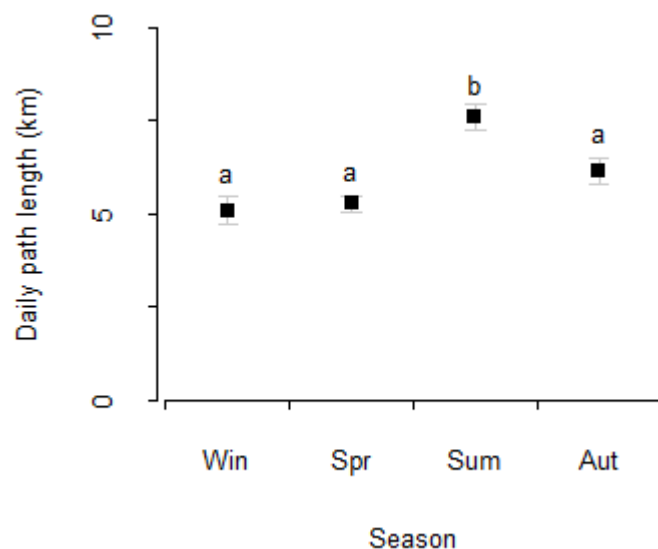


Fig. 2.7. Daily path lengths (DPL) of the Kanonkop troop during different austral seasons. Points and error bars indicate mean values and standard errors respectively. Win = winter, Spr = spring, Sum = summer, Aut = autumn.

travelled slowest during spring (median = 0.420 km.hr⁻¹, IQR: 0.143 – 0.757 km.hr⁻¹), but spring travel rates were not significantly slower than those recorded in either winter or autumn.

General behaviour and diet

Activity budgets and activity patterns

During all four seasons, the two activities that the baboons allocated the most time to were feeding and walking (Fig. 2.9). There was some variation in the medians of time spent feeding in different seasons (range: 249.0 – 281.1 min.day⁻¹), but there were no significant seasonal differences in time allocated to this activity ($\chi^2 = 2.327$, df = 3, p = 0.507). Time spent walking varied to a much greater extent across seasons (range of median values: 161.1 – 277.2 min.day⁻¹) and the seasonal differences were statistically significant ($\chi^2 = 37.492$, df = 3, p < 0.001). The troop spent more time walking in summer and autumn than in winter or spring (p < 0.001 in all cases; Fig. 2.9A). Neither differences in time spent walking in winter and spring, nor differences in time spent walking in summer and autumn, were significant. In winter and spring the troop spent more time feeding than walking, while in summer and autumn the reverse was true (Fig. 2.9A).

Within a given season, the amounts of time that the troop spent resting and socialising were markedly shorter than those spent walking and feeding (Fig. 2.9A). There were no significant differences in time spent engaged in social behaviour across seasons, but there

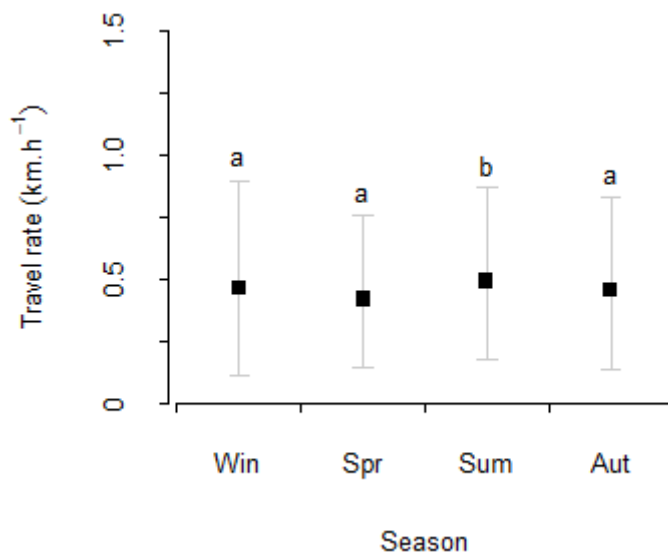


Fig. 2.8. Travel rates of the Kanonkop troop during different seasons. Points and bars indicate median values and inter-quartile ranges respectively. Win = winter, Spr = spring, Sum = summer, Aut = autumn.

were significant differences in time spent resting across seasons ($\chi^2 = 27.620$, df = 3, p < 0.001). The troop spent more time resting in summer than during any other season (p < 0.001 in all cases), and less time resting in winter than in spring (p < 0.01).

The proportion time activity budgets displayed a similar pattern to time spent engaged in activities, in that the larger proportions of the troop's

time in each of the seasons were comprised of time spent feeding and walking (Fig. 2.9B). The ranges of median proportions of time allocated to feeding and walking, in different seasons, were 0.34 – 0.44, and 0.29 – 0.39, respectively. The significant differences across seasons, for given behaviours, were not the same however. The proportion of time allocated to feeding differed significantly across seasons ($\chi^2 = 21.392$, $df = 3$, $p < 0.001$), with the proportion of time spent feeding in winter being greater than proportions spent feeding in summer and autumn ($p < 0.001$ in both cases). There were also significant differences in the proportion of time spent resting in different seasons ($\chi^2 = 16.998$, $df = 3$, $p < 0.001$). The

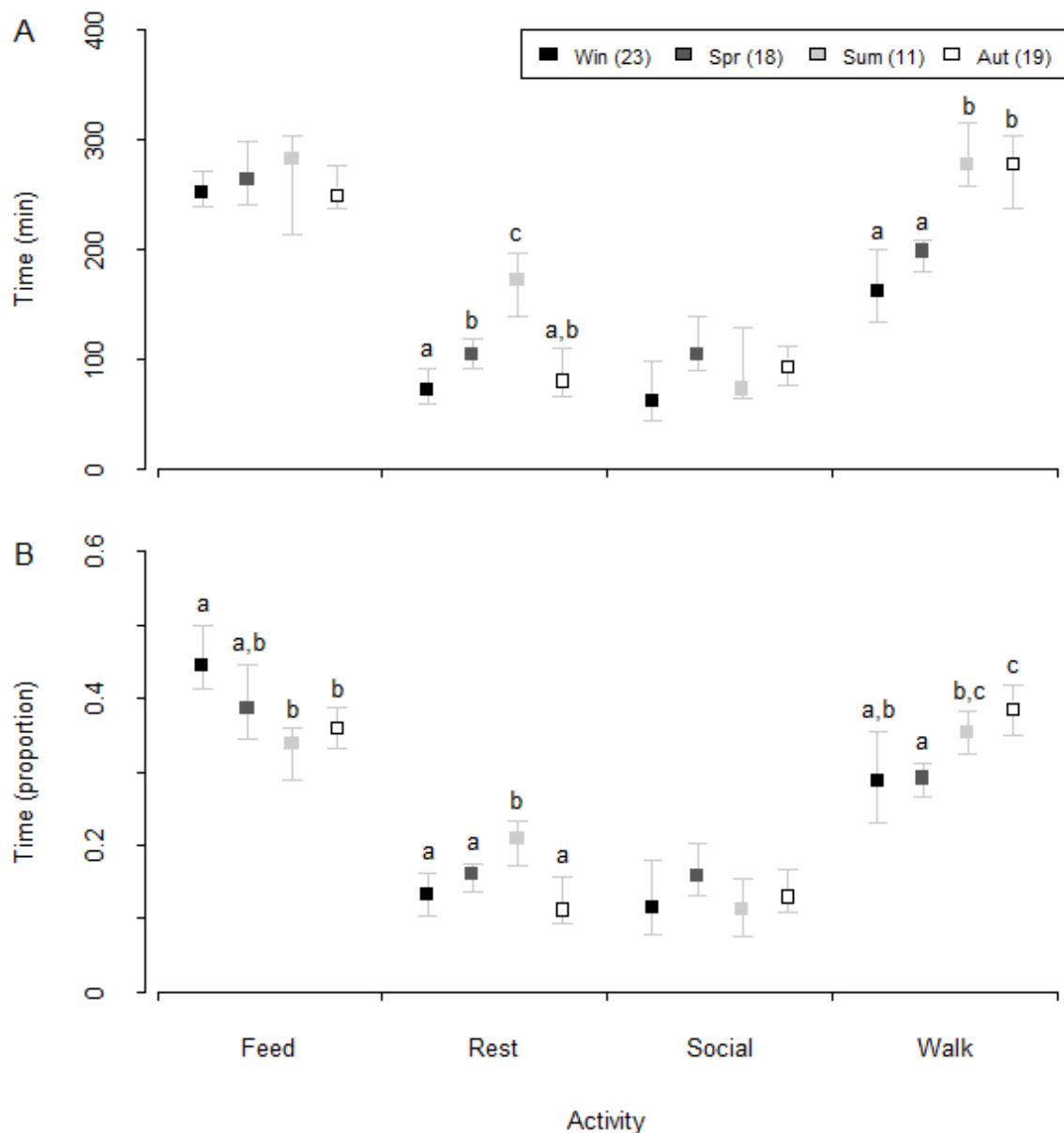


Fig. 2.9. Activity budgets divided into times (in minutes) allocated to different activities (A), and proportions of daylight hours allocated to different activities (B). Win = winter, Spr = spring, Sum = summer, Aut = autumn; values in parentheses in the legend indicate numbers of full days per season; error bars indicate interquartile ranges; lower case letters in plots indicate significant differences (values that share letters are not significantly different).

troop allocated a larger proportion of time available to time spent resting in summer, than in any other season (comparison with spring: $p < 0.05$; comparison with autumn and winter: $p < 0.01$). Finally, the proportion of time spent walking differed across seasons ($\chi^2 = 18.456$, $df = 3$, $p < 0.001$). The baboons allocated a larger proportion of their time to walking in autumn

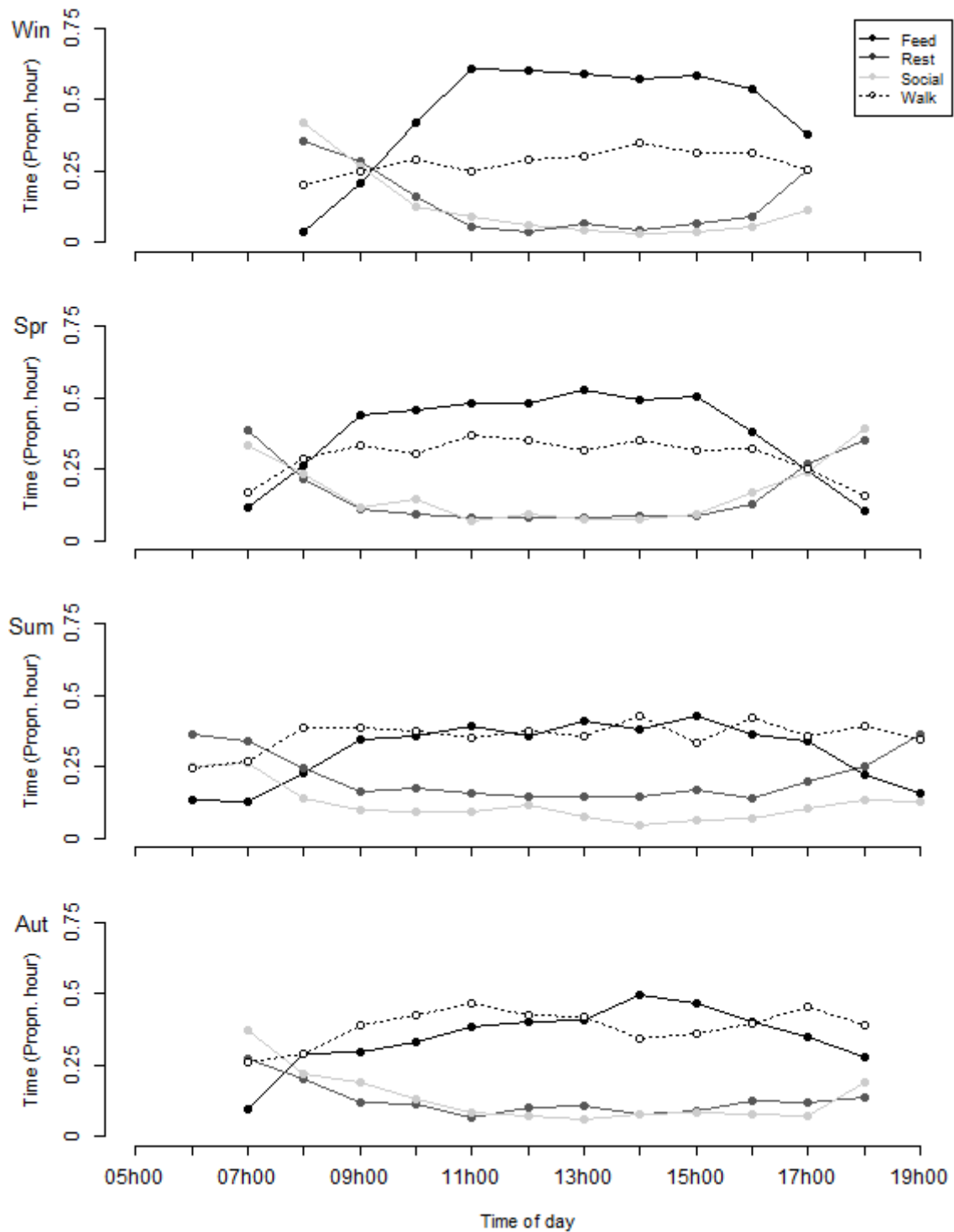


Fig. 2.10. Activity patterns (proportions each hour allocated to different behaviours) through daylight hours in different seasons. Win = winter, Spr = spring, Sum = summer, Aut = autumn.

than in winter or spring ($p < 0.01$ in both cases). Also, the proportion of time allocated to walking in summer was greater than the proportion allocated in spring ($p < 0.05$).

In all four seasons, there were changes in the predominant activities at different times of day (Fig 2.10). These differences in proportions of time allocated to different activities were more pronounced in winter and spring, than in summer and autumn. In winter and spring, the early hours of the morning were dominated by resting and social behaviour. Through mornings in these seasons, the proportions of hours allocated to feeding increased, to the extent that feeding was the dominant activity from four hours after sunrise (in both seasons) until sunset (in winter), and three hours before sunset (in spring). In winter, proportions of hours spent resting and engaging in social activity increased slightly towards sunset. This trend was more pronounced in spring when resting and socialising were the dominant activities during the hour immediately preceding sunset. The patterns were similar in summer and autumn, with time spent feeding increasing through the morning and decreasing in the latter part of the afternoon. In all four seasons, proportions of hours spent walking were relatively stable, with slight increases in the early part of the morning (within four hours of sunrise) and decreases during the latter part of the afternoon (two to three hours before sunset).

Diet and nutrient analyses

The KK troop's diet was dominated by above-ground terrestrial plant tissues during all four seasons (range of median values: 0.56 – 0.84; Fig. 2.11). There were however significant differences in the proportion of the terrestrial foods consumed across seasons ($\chi^2 = 13.057$, $df = 3$, $p < 0.05$). The proportion of the troop's diet comprised of above-ground foods was greater in spring than in summer ($p < 0.05$) and autumn ($p < 0.01$). The dietary proportion comprised of subterranean foods varied across seasons, but differences across seasons were not significant. The proportion of the troop's diet comprised of marine animal foods was small in all four seasons (range of median values: 0 – 0.03), and there were no significant differences in proportions of marine animal foods across seasons.

There were pronounced differences in the median soluble protein contents of foods belonging to different groups (Fig. 2.12). The vast majority of above-ground terrestrial plant foods (range of median values: 3.56 – 6.24) and subterranean plant foods (range of median values: 2.91 – 5.48) were much poorer in soluble protein, than marine foods (range of median values: 26.39 – 29.43). The exception was the seed of the *Leucodendron* spp. plants (range: 43.64 – 51.06), which was richer in soluble protein than marine foods during all four seasons.

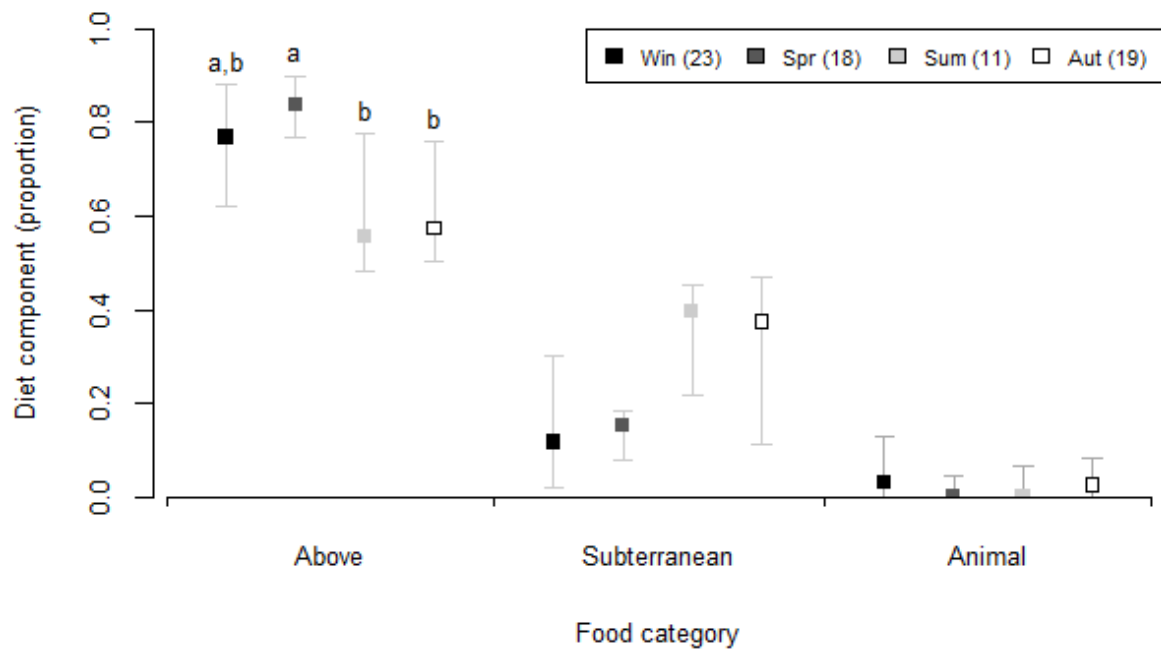


Fig. 2.11. Proportions of the troop's diet comprised of food items belonging to different categories (based on time spent consuming foods) during different seasons. Points indicate median values, and error bars denote inter-quartile ranges. Letters above error bars indicate significant differences among seasons. Win = winter, Spr = spring, Sum = summer, Aut = autumn.

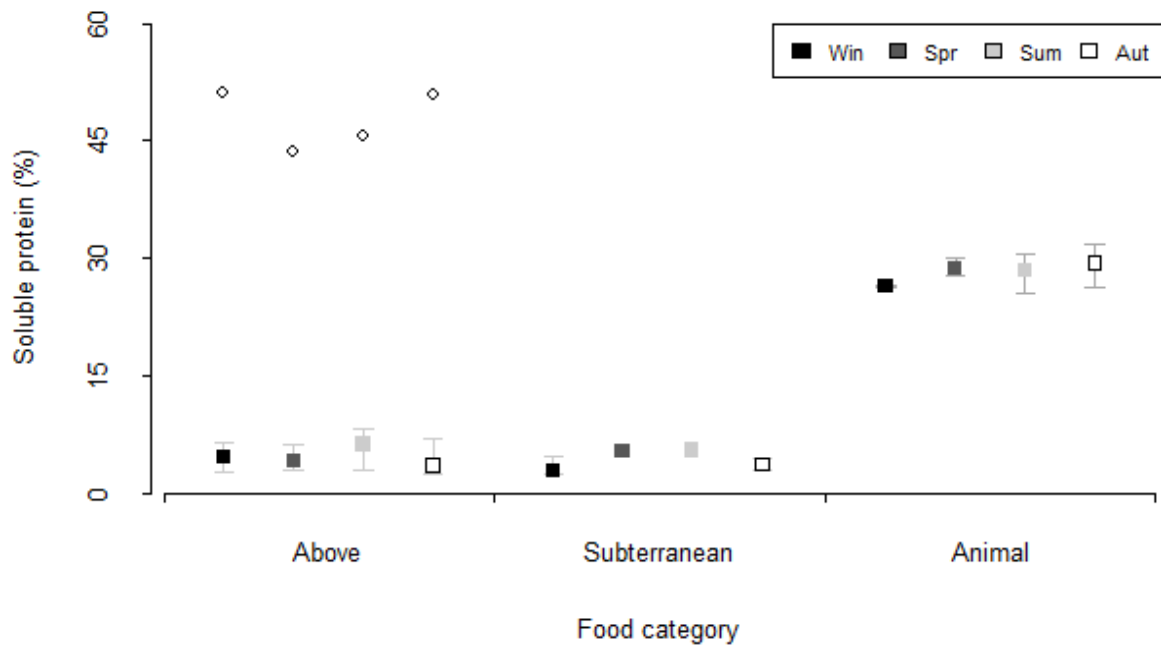


Fig. 2.12. Soluble protein contents of foods consumed by KK troop during different seasons. Squares indicate median values of all foods in the respective categories, error bars denote inter-quartile ranges of said foods, and hollow circles denote values for *Leucodendron* seeds during respective seasons. Win = winter, Spr = spring, Sum = summer, Aut = autumn.

A Kruskal-Wallis rank sum test indicated that the small seasonal differences in soluble protein contents of above-ground foods were not significant. Small sample sizes did not allow for a statistical comparison of protein in either subterranean or animal foods. All marine animals that were sampled tested positive for alkaloids (with all three reagents), and contained low levels of polyphenols (see Appendix A).

The mass:length ratios of the marine invertebrates that were analysed (*Mytilus* sp. and *Cymbula* sp.) showed some variation (Fig. 2.13), but Kruskal-Wallis rank sum tests indicated that seasonal differences in this quantity were not significant.

DISCUSSION

Home range size

The home range used by the KK troop during the course of this study was larger than that occupied by any other Peninsula troop studied to date (Hall, 1962; Davidge, 1978; Hoffman and O’Riain, 2012a). The home range used over the course of this study was in fact larger than that occupied by the same troop during Hoffman and O’Riain’s (2012 a) study. There are two plausible (non-mutually exclusive) explanations for this difference. The first is that Hoffman and O’Riain (2012 a) underestimated the size of the troop’s home range in their study. This is likely, because the cell accumulation curve for the home range estimated by Hoffman and O’Riain did not reach a plateau (Hoffman, 2011). The cell accumulation curve

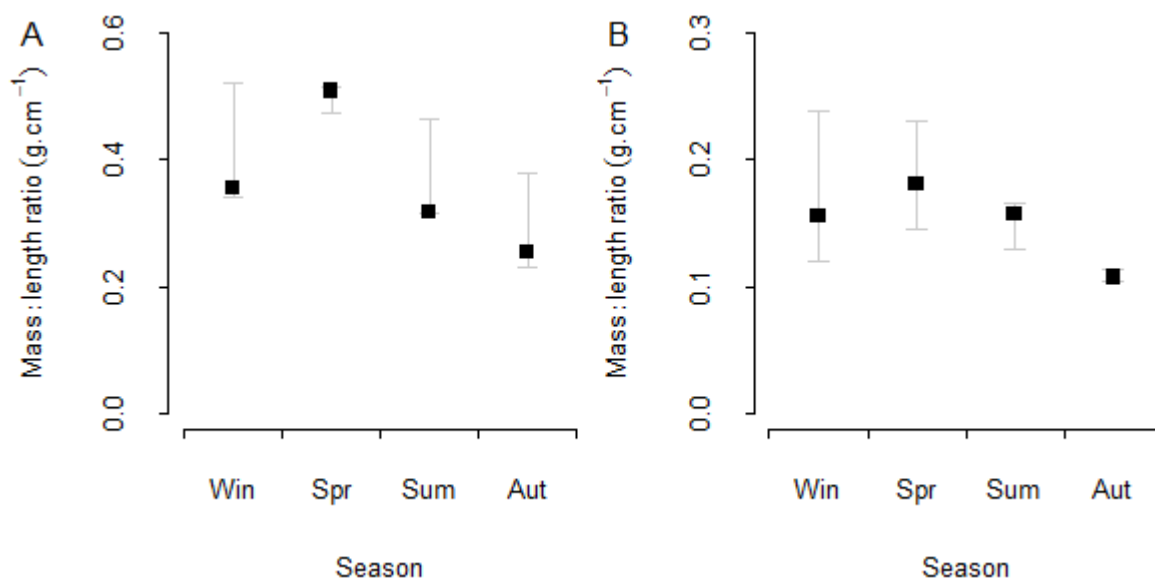


Fig. 2.13. Soft tissue mass-to-shell length ratio of *Cymbula* sp. (A) and *Mytilus* sp. (B) collected from the intertidal zone within the KK troop’s home range during different seasons. Win = winter, Spr = spring, Sum = summer, Aut = autumn.

generated in this study on the other hand did reach a plateau prior to the conclusion of data collection (Fig. 2.2). This qualitative difference is unsurprising as data were collected for this study on a greater number of days than for the study mentioned above (136 days as opposed to 91). Also, Hoffman and O’Riain (2012 a) collected data on a relatively small number of days in summer—the season during this study in which the troop used the largest area (Fig. 2.6).

The second plausible explanation is that the difference in the size of the troop’s home range was a consequence of troop growth over the period between the two studies. It has been well-documented that for groups of a given primate species, in habitats which are similarly productive (see below), home range size is positively correlated with the number of animals in the group (Iwamoto and Dunbar, 1983; Barton et al., 1992; Gillespie and Chapman, 2001; Dias and Strier, 2003; Ganas and Robbins, 2005; Hoffman and O’Riain, 2012a). It is for this reason that PCA has been used as a measure of range size for comparison across groups of the same species (Riley, 2008). The KK troop grew from 49 to 55 animals between the previous study and the culmination of this study, which meant that PCA values were very similar across the two studies (0.77 vs 0.81 km².baboon⁻¹). This suggests that if Hoffman and O’Riain (2012 a) did underestimate the size of the troop’s home range, they did so only to a very small extent. Thus, although there were slight quantitative differences between the results of this study and those reported by Hoffman and O’Riain (2012 a), the results presented here support the inference based on their data that the PCA of KK troop is higher than that of any other Peninsula troop (see Table 2.3).

The high PCA of KK troop suggests that the availability of food resources in this troop’s home range is lower than in those of all other extant Peninsula troops. Previous studies have shown that within a given primate species, PCA is negatively correlated with food availability within a group’s home range (Hanya et al., 2005; Riley, 2008) and may change with time as food availability fluctuates (Di Bitetti, 2001). KK is the only Peninsula troop that does not feed on human-derived foods, including agricultural produce (Hoffman and O’Riain, 2012 a) or the nutrient-rich tissues of alien-invasive plants (Davidge, 1978). The abundance, low processing costs and (in some cases) nutrient-richness of human-derived foods result in primates with access to these foods being released from the ecological constraints of foraging on natural foods (Forthman Quick, 1986; Altmann and Muruthi, 1988; Van Doorn, 2009; Van Doorn et al., 2010; Kaplan et al., 2011).

Table 2.3. Troop sizes, home range sizes, per-capita areas, and densities of baboon (*Papio* spp.) troops with similar social structures to KK¹

Species	Troop size	Home range (km ²)	PCA (km ² .individual ⁻¹)	Density (individuals.km ⁻²)	Locality	Reference
<i>Papio ursinus</i>	20	9.1	0.45	2.2	Cape Peninsula, R.S.A.	DeVore and Hall, 1965
	35	14.8	0.42	2.4	Cape Peninsula, R.S.A.	DeVore and Hall, 1965
	80	33.7	0.42	2.4	Cape Peninsula, R.S.A.	DeVore and Hall, 1965
	115	9.5	0.08	12.1	Cape Peninsula, R.S.A.	Hoffman and O’Riain, 2012a
	49	37.7	0.77	1.3	Cape Peninsula, R.S.A.	Hoffman and O’Riain, 2012a
	36	9.1	0.25	4.0	Cape Peninsula, R.S.A.	Hoffman and O’Riain, 2012a
	35	10.6	0.30	3.3	Cape Peninsula, R.S.A.	Hoffman and O’Riain, 2012a
	26	9.3	0.36	2.8	Cape Peninsula, R.S.A.	Hoffman and O’Riain, 2012a
	24	8.3	0.35	2.9	Cape Peninsula, R.S.A.	Hoffman and O’Riain, 2012a
	22	7.5	0.34	2.9	Cape Peninsula, R.S.A.	Hoffman and O’Riain, 2012a
	16	1.5	0.10	10.4	Cape Peninsula, R.S.A.	Hoffman and O’Riain, 2012a
	16	5.6	0.35	2.8	Cape Peninsula, R.S.A.	Hoffman and O’Riain, 2012a
	9	18.9	2.10	0.5	Drakensberg, R.S.A.	Whiten et al., 1987
	14	10.0	0.71	1.4	Drakensberg, R.S.A.	Whiten et al., 1987
	60	23.3	0.39	2.6	N. Limpopo Province, R.S.A.	Stoltz and Saayman, 1970
	77	13.0	0.17	5.9	N. Limpopo Province, R.S.A.	Stoltz and Saayman, 1970
	40	15.5	0.39	2.6	N. Limpopo Province, R.S.A.	Stoltz and Saayman, 1970
	33	9.4	0.29	3.5	Namib Desert, Namibia	Hamilton et al., 1976
	28	4.0	0.14	7.0	Namib Desert, Namibia	Hamilton et al., 1976
	108	4.7	0.04	23.0	Okavango, Botswana	Hamilton et al., 1976

	109	6.5	0.06	16.8	Okavango, Botswana	Hamilton et al., 1976
	39	2.1	0.05	18.6	Okavango, Botswana	Hamilton et al., 1976
	71	4.8	0.07	14.8	Okavango, Botswana	Hamilton et al., 1976
	88	28.3	0.32	3.1	Suikerbosrand, R.S.A.	Anderson 1981
	74	24.9	0.34	3.0	Suikerbosrand, R.S.A.	Anderson 1981
	82	24.8	0.30	3.3	Suikerbosrand, R.S.A.	Anderson 1981
	68	20.5	0.30	3.3	Suikerbosrand, R.S.A.	Anderson 1981
<i>P. anubis</i>	50	19.7	0.39	2.5	Gilgil, Kenya	Harding, 1976
	100	43.8	0.44	2.3	Laikipia Plateau, Kenya	Barton et al., 1992
	12	5.2	0.43	2.3	Nairobi, Kenya	DeVore and Hall, 1965
	17	23.8	1.40	0.7	Nairobi, Kenya	DeVore and Hall, 1965
	24	18.1	0.76	1.3	Nairobi, Kenya	DeVore and Hall, 1965
	28	7.8	0.28	3.6	Nairobi, Kenya	DeVore and Hall, 1965
	28	40.1	1.43	0.7	Nairobi, Kenya	DeVore and Hall, 1965
	40	24.9	0.62	1.6	Nairobi, Kenya	DeVore and Hall, 1965
	77	30.3	0.39	2.5	Nairobi, Kenya	DeVore and Hall, 1965
	87	35.8	0.41	2.4	Nairobi, Kenya	DeVore and Hall, 1965
	58	3.9	0.07	14.9	Queen Elizabeth N.P., Uganda	Rowell, 1966
	32	5.4	0.17	5.9	Queen Elizabeth N.P., Uganda	Rowell, 1966
<i>P. cynocephalus</i>	42	24.1	0.57	1.7	Amboseli, Kenya	Altmann and Altmann, 1970
	106	16.7	0.16	6.3	Amboseli, Kenya	Altmann and Altmann, 1970
	130	43.0	0.33	3.0	Mikumi N.P., Tanzania	Rasmussen, 1979

¹N.P. = National Park; R.S.A. = Republic of South Africa.

The PCA of KK troop is towards the upper extreme of the range of values observed in troops of congeneric- and conspecific animals across the genus's distribution (see Table 2.3; DeVore and Hall, 1965; Rowell, 1966; Altmann and Altmann, 1970; Stoltz and Saayman, 1970; Hamilton et al., 1976; Harding, 1976; Rasmussen, 1979; Anderson, 1981; Whiten et al., 1987; Barton et al., 1992). The only troop of chacma baboons that exhibited higher PCA than KK troop was a troop that inhabited a high-altitude home range in the Drakensberg mountains characterised by severe thermal and nutrient-stress (Whiten et al., 1987; Henzi et al., 1992). The PCA observed elsewhere that was most similar to that of KK troop was that of Whiten et al.'s (1987) Low troop. Although conditions in Low troop's home range were less severe than those in the home range of the above-mentioned authors' other study troop, the baboons of this troop were still considered to be highly stressed. KK troop's PCA reported here was more than double that of troops studied in habitats defined as the most extreme in South Africa based on climatic variables and altitude (Anderson, 1982). These comparisons suggest that, despite the temperate climate, the presence of moderate standing plant biomass (relative to baboon habitats elsewhere) and marine invertebrates within their home range (Stock and Allsopp, 1992; Cowling et al., 1996), KK troop is among the most nutrient-stressed baboon troops for which data of this type are available in the literature.

The variation in the size of areas used by the troop across seasons suggests that the severity of nutrient-stress experienced by KK baboons changes on an annual basis. This is likely related to seasonal changes in plant phenology (Pierce, 1984; Stock et al., 1987) and perhaps changes in the nutritional reward offered by marine foods (Branch, 1974; Van Erkom Schurink and Griffiths, 1991; Hodgson, 2010) per unit foraging effort. The troop's use of a relatively large area in summer, and a relatively small area in winter, indicate that the upper and lower extremes of nutrient stress are experienced during these two seasons respectively.

Home range use

As is typical in primates (e.g., Whiten et al., 1987; Wallace, 2006; Grueter et al., 2008; Willems et al., 2009), the KK troop did not use all parts of their home range evenly (Fig. 2.5). In a predator-free environment it can be assumed that primates' preference for land with particular attributes is related to one or more of their principle ecological needs, namely food (Clutton-Brock, 1975; Harding, 1976; Henzi et al., 1992; Kirkpatrick et al., 1998; Di Bitetti, 2001), water (Altmann and Altmann, 1970; Stoltz and Saayman, 1970; Chapman, 1988; Scholz and Kappeler, 2004) and sleeping sites (Rasmussen, 1979; Zinner et al., 2001; Liu and Zhao, 2004). The results of the sparse SGLMM indicated that KK troop made preferential use

of parts of their home range at lower altitudes, parts with steeper slopes, parts that were close to the coast and parts that were close to sources of fresh surface water.

In a recent population-level study, Hoffman and O’Riain (2012 b) reported similar preferences for land at lower altitudes and with steeper slopes across nine Peninsula troops. The above-mentioned authors attribute Peninsula baboon’s partiality to low-lying land to a preference for relatively more productive areas (within the terrestrial context; Hoffman, 2011) and land which is home to greater standing biomass (Hoffman and O’Riain, 2012b). They also refer to the availability of marine foods at the coast as a possible factor explaining the Peninsula baboons’ preference for low-lying land. This is presumably based on the assumption that cells at lower altitude allow easier (or at least quicker) access to the coast. This may be true across the Peninsula as a whole but, as demonstrated here, there is not a significant correlation between distance-to-coast and altitude within the KK troop’s home range. The results of the model presented here do however indicate that both altitude and distance-to-coast are significant predictors of baboons’ use of different parts of their home range. This finding therefore corroborates Hoffman and O’Riain’s (2012 b) assertion that ease of access to the coast is a factor that explains (at least in part) the Peninsula baboons’ (particularly those without access to human foods) home range use patterns. As there is no other ecologically important resource available right at the coast, it is plausible that this pattern arises from the baboons’ desire to obtain the foods that are available in the intertidal zone.

The results of the sparse SGLMM reported here, like those reported by Hoffman and O’Riain (2012 b), indicated that habitat type also had a significant effect on baboon area use. The habitat categories used in the two models were markedly different however, as Hoffman and O’Riain (2012 b) investigated baboons’ preference for transformed habitats of different types over natural habitats (which they lumped into one category). Hoffman and O’Riain (2012 b) attributed baboons’ preference for human-modified habitats to augmented food availability in these habitats. It seems highly likely that the patterns observed here might also be driven largely by differences in food availability between habitat types. KK troop preferred cells dominated by beach-type habitats to those dominated by any of the terrestrial vegetation-type habitats. Considering the absence of either water or sleeping sites (both of which are considered to be critical resources for baboons; Henzi et al., 1992) on the coast, this finding suggests that KK baboons use this habitat because of the availability of marine food rewards.

The magnitudes of the effects of terrestrial habitats on baboon cell use varied considerably, and are likely linked primarily to differences in food availability between vegetation types. The largest negative effect on cell use, relative to that of beach-type habitats, was that associated with Peninsula Sandstone Fynbos, which is the least productive terrestrial vegetation type in the KK troop's home range (Zhao and Running, 2010). This indicates that, as was predicted, the baboons opted to spend greater amounts of time in more productive habitats. The pattern does not however hold true across the two more productive vegetation types in the KK troop's home range, namely Hangklip Sand Fynbos and Cape Flats Dune Strandveld. Relative to beach-type habitats, Cape Flats Dune Strandveld had a greater negative effect on cell use than Hangklip Sand Fynbos. This pattern is surprising as Hangklip Sand Fynbos is the less productive of the two habitats (Zhao and Running, 2010), and sclerophylly is less common in plants that make up Cape Flats Dune Strandveld communities (Rebello et al., 2006), so nutrients should be more accessible in these communities. The apparent preference for Hangklip Sand Fynbos (over Cape Flats Dune Strandveld) is therefore unlikely to be driven by nutritional needs, and might in fact be a result of the baboons' use of a particular sleeping site. Hangklip Sand Fynbos-dominated cells in which high numbers of GPS points were recorded, were those in the southern part of KK troop's home range, 600 – 1500 m inland from the east coast. These cells surrounded (and included, in the case of one cell) one of the KK troop's frequently-used sleeping sites. It is therefore plausible that the troop made extensive use of these cells both because they offered valuable food resources, but also because they were along paths to the sleeping site in question. This inference is given further credence by findings of previous studies on baboons, which have shown that sleeping site location may have profound effects on ranging patterns (Rasmussen, 1979; Henzi et al., 1992).

KK troop's preferential use of cells characterised by steep slopes was not unexpected considering the findings of Hoffman and O'Riain (2012 b). These authors attributed Peninsula baboons' preference for steeply sloped land to their need for sleeping sites that are located on cliffs. This is a plausible explanation for the preference shown by KK troop as all but one of the troop's 16 sleeping sites were located on cliffs and steeply-sloped rocky outcrops within their home range.

Thus, the results of this study and those reported by Hoffman and O'Riain (2012 b), are in direct contradiction in only one respect, namely the effect of distance to fresh surface water on baboon land use. The above-mentioned authors found that probability of baboon occurrence increased with distance-to-water, while abundance (i.e. number of GPS points

within cells) was not affected by distance-to-water. Based on these results, Hoffman and O’Riain (2012 b) concluded that the Peninsula is not a water-stressed environment. The negative effect of distance-to-water reported here suggests that this is not the case for all Peninsula troops, as it shows that KK troop prefers land that is in close proximity to fresh water sources. This is likely a result of there being fewer perennial sources of fresh water on the southern-most part of the Peninsula (South African National Parks, unpublished data), which might result in access to water being a more important driver of baboon ranging patterns on this part of the Peninsula. That said, the magnitude of the effect was small compared to those of altitude and slope, and was an order of magnitude smaller than that of distance-to-coast. Thus, despite the contradiction, it seems that the results of this study and those reported by Hoffman and O’Riain (2012 b) lead to the same inference: the presence of surface water is not a key driver of land use patterns of baboons in the Cape Peninsula.

Daily paths and rates of travel

The troop’s DPLs observed over the entirety of this study were longer (on average) than those observed in the same troop by Hoffman and O’Riain (2012 a) and Hall (1962) (Hall’s C troop is assumed to be the same troop based on home range location). In the case of the former, the difference might be due, at least in part, to variation in data collection protocols between the studies. The distribution of DPLs reported here was more even across seasons than was the case in Hoffman and O’Riain’s (2012 a) study—more DPLs were recorded in summer and autumn for this study (see Fig. 2.1). There is however an alternative explanation for the differences between the results reported here and those reported by Hoffman and O’Riain (2012 a), that is related to the troop’s biology. Seasonal bias in sampling can be ruled out as a cause of the difference between the results reported and those reported by Hall (1962), as Hall’s sample sizes in different seasons were very similar. It is however worth noting that he recorded fewer DPLs overall than were reported either in this study, or by Hoffman and O’Riain (2012 a). Interestingly, the differences between the results reported here, and those presented in each of the above-mentioned studies are likely caused by different biological factors.

As is the case in other primates (Doran, 1997; Goldsmith, 1999; Steenbeek and Van Schaik, 2001; Ganas and Robbins, 2005), baboon troops’ DPLs are affected by group size and food availability—DPL increases with troop size (Hoffman and O’Riain, 2012a) and with decreasing food availability (Barton et al., 1992; Henzi et al., 1992). It seems likely that the former might be the cause of the difference between the results reported here and those

reported by Hoffman and O’Riain (2012 a), as troop size increased by seven over the period between the studies. The difference between the troop’s ranging patterns during Hall’s (1962) study and this study on the other hand, was probably caused by changes in food availability (troop size varied very little across the two studies). At the time when Hall was collecting data, there were large, dense stands of alien plants (mostly *Acacia* spp.) within the Park (Hall, 1963). These plants produce nutrient-rich seeds, which were an important food source for baboons in the area (Hall, 1962; Davidge, 1976, 1978). It stands to reason therefore that removal of these plants as part of an alien clearing project (prior to the period during which data were collected for this study), would have resulted in a marked decline in food availability within the troop’s home range. This decline could have driven the troop to travel further in search of food on a daily basis.

Relative to most other troops studied by Hoffman and O’Riain (2012 a), KK troop travelled further on a daily basis. This is perhaps unsurprising, as this troop is larger than all but one of the above-mentioned authors’ study troops. It was, however, not the largest of the Peninsula troops that travelled further than KK troop (that troop’s average DPL was in fact less than half of that reported here). In this case (where the larger troop travels the shorter distance), it is clear that food availability is much lower in KK troop’s home range than in that of the other troop. The reason for this is that the larger troop occupies a home range which is dominated by agricultural land which includes both grapes and barley (Hoffman and O’Riain, 2012a). A comparison between KK troop and the other troops studied by Hoffman and O’Riain (2012 a) is more difficult to interpret, as the effects of troop size and food availability are difficult to tease apart. The same is true of a comparison between KK troop and “O troop” studied by Davidge (1978).

Despite the mean value reported here being almost half-a-kilometre longer than that reported by Hoffman and O’Riain (2012 a), it would not rank higher or lower than said value when compared to mean DPLs of other Peninsula troops reported by the above-mentioned authors. Thus, the results of this study corroborate Hoffman and O’Riain’s finding that KK troop travels further on a daily basis than four other non-monitored Peninsula troops, and further than all other Peninsula troops studied by the above-mentioned authors, bar one.

The troop most similar to KK troop (in terms of number of individuals) for which DPL data are available was that studied by Harding (1976) at Gilgil, Kenya. This troop, which inhabited land dominated by grassland with occasional patches of scrub, numbered 50 baboons and travelled roughly a kilometre less than KK troop on a daily basis. This suggests

that KK troop is more nutrient-stressed than baboons living in the above-mentioned habitat matrix.

Perhaps the most telling comparison that may be drawn between KK troop and other troops includes troops at Suikerbosrand (Anderson, 1981, 1982). The baboons at this site must endure adverse environmental conditions (due to high altitude and extreme climate) and are therefore stressed as thermoregulation is energetically costly (Anderson, 1982). All of the Suikerbosrand troops studied by Anderson (1981, 1982) were larger than the KK troop (two of the four troops numbered more than 80 individuals), but travelled shorter distances on a daily basis. This suggests that thermally stressed Suikerbosrand baboons fulfil their nutrient- and energetic requirements more easily than KK baboons. Considering the Peninsula's temperate climate, it might be inferred that foods are in short supply in KK troop's home range, or that the quality of foods that are available is poor.

The seasonal fluctuation in DPL does however suggest that either the baboons' requirements, or the availability of higher quality foods (or both), varied through the year. KK baboons needed to travel further in summer than during other seasons, in order to find sufficient food to fulfil their nutrient- and energy requirements. Interestingly, this was not merely a result of increased day length (allowing the troop more time to travel), as the increased DPL in summer was mirrored by a higher rate of travel during the same season. KK troop's rates of travel during spring were comparable to those of baboons at Gilgil, Kenya (Harding, 1976), but were longer during other seasons and over the study period as a whole. This provides further evidence for the inference that KK baboons are nutrient-stressed relative to troops elsewhere, and that this stress is most severe during the warm, dry summer months.

Time allocation and behavioural patterns

In terms of both time spent (in minutes), and percentage, of activity budgets, feeding and walking were the dominant activities throughout all four seasons. This is typical of baboons (Post, 1981; Whiten et al., 1987; Hill et al., 2003; Alberts et al., 2005), except where troops have access to abundant human-derived foods (Forthman Quick, 1986; Altmann and Muruthi, 1988; Bronikowski and Altmann, 1996; Hoffman and O'Riain, 2011). The effect of exploitation of human-derived foods is indicative of a broader trend in baboon behavioural ecology. That is, like other primates (Agetsuma and Nakagawa, 1998; Hanya, 2004b; Riley, 2007; Harris et al., 2009; Chaves et al., 2011), baboons typically allocate more time to activities involved in the acquisition of food when food availability decreases (Post, 1981;

Alberts et al., 2005) or when their nutrient requirements increase (Dunbar and Dunbar, 1988). Due to the role of locomotion in food acquisition, certain authors have defined “foraging time” as the sum of time spent feeding and walking (Bronikowski and Altmann, 1996; Alberts et al., 2005). This is a more suitable proxy for nutrient stress than feeding time only, because certain primates respond to declines in the availability of preferred foods by spending more time travelling (in order to reach widely dispersed foods), either instead of, or in addition to, increasing feeding time (Overdorff et al., 1997; Gursky, 2000; Clarke et al., 2002).

Most studies of baboon time allocation to date have reported percentage time activity budget (PTAB) data rather than time (in minutes or hours) allocated to different activities (e.g., Forthman Quick, 1986; Whiten et al., 1987; Altmann and Muruthi, 1988; Alberts et al., 2005; Dunbar et al., 2009; Hoffman, 2011). Thus, there are more PTAB data available for the purposes of comparing KK troop’s time allocation to that of other troops. As a percentage of the KK troop’s PTAB, foraging time (*sensu* Bronikowski and Altmann, 1996) was lower than that of troops of congenics that regularly feed on human foods both elsewhere (Forthman Quick, 1986; Altmann and Muruthi, 1988; Bronikowski and Altmann, 1996) and on the Peninsula (Van Doorn et al., 2010; Hoffman, 2011); was comparable to that of natural-foraging troops in Amboseli, Kenya (Post, 1981; Bronikowski and Altmann, 1996); and was lower than that of natural-foraging, thermal- and nutrient-stressed troops in the Drakensberg (Whiten et al., 1987). This suggests that KK baboons are more nutrient-stressed than baboons with access to human foods, but not markedly more stressed than savannah baboons, over the course of the year.

There was however significant seasonal variation in the percentages of KK troop’s time allocated to feeding and walking, with the result that in winter and summer (when foraging time comprised greater proportions of KK troop’s PTAB), KK troop allocated similar amounts of time to foraging as did the lower of the study troops in the Drakensberg (Whiten et al., 1987). This may be indicative of higher nutrient-stress in these two seasons (than in either spring or autumn). Although interesting, and useful for purposes of comparison with other troops, PTAB data comparisons across seasons should be carried out with caution where study sites are located far from the equator. The reason for this is that PTAB data fail to account for the (potentially substantial) seasonal changes in time available for allocation to different activities that result from variation in day length (Hill et al., 2003, 2004).

Foraging time (in minutes) did vary with season, but this was entirely due to seasonal variation in time spent walking, as time spent feeding varied little across seasons. KK troop spent significantly more time walking during the warm, dry summer and autumn months than during winter or spring. A similar seasonal pattern was observed in the time allocation of baboons at De Hoop (a fynbos habitat at a similar latitude to the east of the Cape Peninsula; Hill et al., 2003) and even a semi-provisioned Peninsula troop (Van Doorn et al., 2010). The amount of time that KK troop allocated to foraging was greater than that allocated by Hill et al.'s (2003) study troop in De Hoop (similar habitat to the Peninsula), and much greater than that allocated by Van Doorn et al.'s (2009; 2010) study troops on the Peninsula. These comparisons suggest that KK troop is indeed nutrient-stressed (certainly more so than nearby troops with access to human foods), and that the troop adjusts to the relative harshness of the Peninsula's warm, dry summers by increasing time spent walking and foraging at the same time.

The other activity which exhibited seasonal variation in time allocation was resting—KK troop spent less time resting in winter or spring than in summer. As has been reported elsewhere (Dunbar and Dunbar, 1988), the amount of time allocated to social activity was held almost constant through the four seasons. This corroborates Dunbar and Dunbar's (1988) statement that resting time is somewhat more plastic, and will be sacrificed before time spent engaged in social activity where baboons are nutrient-stressed. The percentage of their time that KK troop allocated to social activity was similar to that reported for other troops in several regions, including the Cape Peninsula (Altmann and Muruthi, 1988; Alberts et al., 2005; Hoffman, 2011), and the amounts of time spent grooming in different seasons were similar to, but more constrained than, those observed in De Hoop baboons (Hill et al., 2003).

The behavioural patterns exhibited by KK troop on days during the study were not unlike those observed in other troops. Baboons at Amboseli (Altmann and Altmann, 1970), and elsewhere on the Peninsula (Hall, 1962; Davidge, 1978) have also been shown to concentrate resting and social activity in the early hours of the morning and latter part of the afternoon and into the evening. Conversely, feeding and walking comprise smaller percentages of hours in the early morning and late afternoon, but are the dominant activities in the hours in between. Like other Peninsula troops studied previously (Hall, 1962; Davidge, 1978), and unlike certain other primates (Huang et al., 2003), KK troop did not exhibit two feedings peaks during the day.

Diet and nutritional rewards

KK troop's diet was dominated by plant material, with marine animal foods comprising only very small percentages during all four seasons. This high plant-to-animal food ratio is typical of baboons as has been demonstrated through both direct observation (Altmann and Altmann, 1970; Harding, 1976; Post, 1982; Whiten et al., 1987, 1991; Okecha and Newton-Fisher, 2006), and stable isotope analysis (Codron et al., 2006). There have however been cases where baboon diets have been comprised largely of animal tissues over short periods (up to a few days), but these are exceptions rather than the norm. Where baboons have fed extensively on animal foods, the change in diet composition has occurred in response to extraordinarily high abundance of animal foods, typically for only brief periods (Hamilton et al., 1978). In light of the abundance, and sessile nature, of marine intertidal foods consumed by baboons, it seems likely that there is some other factor limiting the extent to which the baboons exploit these organisms.

The plant component of KK troop's diet was in turn dominated by above-ground plant foods. Subterranean foods are generally not thought to be preferred foods due to the high processing costs associated with exploitation (Altmann, 1998; Alberts et al., 2005; Wrangham et al., 2009). It is for this reason that the size of the subterranean component of baboons' diets is seen as an indicator of food availability (or, conversely, nutrient stress) in baboon troops' home ranges. Baboons in harsh environments tend to feed on more subterranean foods than their counterparts in more favourable habitats (Whiten et al., 1987) and the degree of exploitation of subterranean foods increases during periods of food scarcity (Alberts et al., 2005). As a percentage of the total diet, the subterranean component of KK troop's diet is similar to that observed in another Peninsula troop (Davidge, 1978), and markedly smaller than that observed in two troops in the Drakensberg (Whiten et al., 1987). Although not statistically significant, there was some seasonal variation in the percentage of KK troop's diet comprised of subterranean foods. This has been shown to be the case in two other Peninsula troops (Davidge, 1978; Van Doorn et al., 2010), but the pattern reported here differs from those reported by the above-mentioned authors; KK troop fed on subterranean foods more during the warm, dry months of summer and autumn. This difference is likely a result of the changes in nutrient availability within a troops' home range brought about by the presence of human-derived foods (in the case of the troop studied by Van Doorn et al., 2010) and abundant, nutrient-rich foods derived from alien tree species (in the case of the troop studied by Davidge, 1978).

The seasonal differences in diet composition suggest that, for KK baboons, fulfilling nutrient- and energetic requirements is more difficult in summer and autumn than in winter or spring. This could be related to seasonal variation in availability of different foods, or to fluctuation in quality of foods that are available and consumed. In light of baboons' preference for foods with relatively high protein contents (Whiten et al., 1991; Barton and Whiten, 1994), and their tendency to forage selectively to maintain constant proportional daily intake of protein (Johnson et al., 2013), I investigated how the protein content varied in foods consumed by the KK troop in each season. The one plant food that was much richer in protein than all other plants foods, and also richer in protein than marine animals, was *Leucodendron* spp. seeds. There was however marked seasonal variation in the protein content of the seeds. In light of this, I determined the proportions of the troop's diet comprised of *Leucodendron* spp. seeds during each season and found that the ranks (relative to other seasons) of dietary proportions comprised of these seeds matched the variation in their protein contents very closely.

Like lumped terrestrial foods, marine animals did not exhibit seasonal variation in protein content per unit mass. This does not necessarily mean that the nutritional rewards offered by these foods would not vary. In fact, it is highly likely that the nutrient yield per unit time and energy expended processing marine animals should vary with season due to changes in condition related to spawning (Branch, 1974; Van Erkom Schurink and Griffiths, 1991; Hodgson, 2010). Seasonal changes in the ratio of the soft tissue mass-to-length were evident in marine invertebrates consumed by the baboons, but differences were not significant. It seems highly likely that this is a result of small sample sizes. Ideally, such a comparison should be done with larger sample sizes from both coasts (sampled separately) as the timing of spawning may vary markedly over short distances (Van Erkom Schurink and Griffiths, 1991).

Although tissues of marine invertebrates are richer in protein than most of the baboons' terrestrial foods, these foods might not represent a suitable food for extensive exploitation (availability aside). Like various fynbos and strandveld plants (Glyphis and Puttick, 1988; Coetzee et al., 1997), certain marine invertebrates produce (or accumulate) chemical compounds that act to discourage ingestion of these organisms by consumers (Bryan et al., 1997; Gray et al., 1998; Kvittek and Bretz, 2005; Sotka et al., 2009). In some cases, the compounds in question are alkaloids (Pathirana and Andersen, 1986; McClintock and Baker, 1997; Zimmer and Ferrer, 2007), which may have profound effects on consumers. The nature and severity of the effects are however dependent on the alkaloid in question

(McClintock and Baker, 1997; Assmann et al., 2000; Kem and Soti, 2001; Kem et al., 2006), and the amount consumed (Koleva et al., 2012). Thus, the presence of alkaloids in the tissues of the marine invertebrates consumed by the baboons could limit their exploitation of these foods to some extent. This is not necessarily the case however, as the alkaloids in question could be among the less harmful compounds belonging to this group.

Conclusion

All behavioural indicators suggest that baboons of KK troop face significant challenges in fulfilling their nutritional- and energetic requirements relative to other Peninsula troops and troops in other parts of southern Africa, and that the severity of nutrient stress varies seasonally. This implies that, unlike exploitation of human foods for example, inclusion of marine foods in baboons' diets does not release them from the ecological constraints of feeding on relatively nutrient-poor foods. It is plausible that this is a result of how seldom KK baboons consume marine foods, which in turn begs the question of whether there is some factor, or suite of factors, that is limiting exploitation of marine foods by natural-foraging Peninsula baboons.

CHAPTER 3

Stable carbon and nitrogen isotope ratios of
faeces and hair of Cape Peninsula baboons

ABSTRACT

Despite the novelty of the behaviour, exploitation of marine foods by Cape Peninsula chacma baboons has not previously been studied in detail. Behavioural data presented in Chapter 2 indicate that marine food comprises only a small proportion of natural-foraging Peninsula baboons' diet. These data were however collected through only four months of observation, and were recorded at the level of the troop rather than the individual due to permit restrictions. In this chapter, I present estimates of KK troop's diet composition based on stable carbon- and nitrogen isotope ratios of faeces from unknown individuals, and hair from seven different sub-adults and adults of each sex. I compared these isotope ratios to those of hair from other Peninsula troops to assess the efficacy of this method in differentiating animals and their diets within the same population. Faecal $\delta^{13}\text{C}$ - and $\delta^{15}\text{N}$ values of animals from the non-raiding troop ranged from -29.3‰ to -25.6‰, and from 0.9‰ to 6.3‰, respectively. Faecal $\delta^{15}\text{N}$ values were positively correlated with a composite measure of marine foraging calculated for the dietary integration period. Mean (\pm SD) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for hair from the non-raiding troop were -21.7 (\pm 0.2)‰ and 4.5 (\pm 0.6)‰ respectively. Output from SIAR models based on isotope ratios of hair and faeces indicated that the diet of these baboons is dominated by C_3 -terrestrial plants, and that marine foods comprise only a small percentage ($< 10\%$). These results are in accordance with estimates based on behavioural observation. Adult individuals of the same sex from different troops differed in terms of carbon- and nitrogen isotope values—animals with access to human foods were enriched in ^{13}C and ^{15}N relative to non-raiding animals. This indicates that human foods are typically enriched in ^{13}C and ^{15}N relative to natural plant foods. Results presented therefore suggest that stable isotope analysis represents a viable method for quantifying marine food use by Peninsula baboons, but only in non-raiding animals.

INTRODUCTION

The method most commonly used in studies of baboon diet, and which might be used in a survey of marine food exploitation by baboons and other primates, is direct behavioural observation (e.g. Davidge, 1978; Post, 1982; Byrne et al., 1993; Bronikowski and Altmann, 1996; Okecha and Newton-Fisher, 2006; Van Doorn et al., 2010; Johnson et al., 2013). This method requires considerable time and effort to implement however and, depending on the sampling protocol, may be contingent on habituation of the animals to close human presence (e.g. Wrangham and Waterman, 1981; Cords, 1986; Krishnamani, 1994; Fairgrieve and Muhumuza, 2003; Dew, 2005; Yiming, 2006). In certain contexts, habituating primates to close human presence and spending large amounts of time with them is difficult, impossible, or ill-advised, either because environmental factors preclude such protocols, or due to ethical considerations (Jack et al., 2008; Williamson and Feistner, 2011; Gruen et al., 2013). The latter may be seen as just cause for rejection of research permit applications, or restriction of research-related activities, by local conservation authorities (as was the case here). Restrictions imposed by local conservation authorities meant that data for Chapter 2 were collected over relatively short, discrete periods, at the level of the troop rather than the individual. In studies where this is the case, data collected through alternative approaches may prove hugely informative (Deblauwe and Janssens, 2008; McGrew et al., 2009). One such approach, which has been used in dietary studies of terrestrial animals that consume marine foods elsewhere, is stable isotope analysis (Hobson and Sealy, 1991; Stapp and Polis, 2003; Balasse et al., 2005).

Stable isotope analysis is useful in dietary studies because isotope ratios of animal tissues reflect those of their diets (DeNiro and Epstein, 1978, 1981). This is not to say that diet- and tissue isotope ratios are always the same, but rather that isotopic enrichment of a given tissue (or lack thereof) is consistent across conspecific individuals on the same diet (DeNiro and Epstein, 1978, 1981; Hobson et al., 1996; McCutchan et al., 2003; Sponheimer et al., 2003b; c). Provided the appropriate fractionation factor is known, proportional contributions of different foods to an animal's diet may be inferred from isotope ratios of those foods and a tissue sample collected from the animal in question (Caut et al., 2008; Bond and Diamond, 2011; Phillips, 2012).

The isotope ratios most commonly analysed in dietary studies are those of carbon (^{13}C and ^{12}C) and nitrogen (^{15}N and ^{14}N), which are often used in concert in such studies (e.g. Minami et al., 1995; Hilderbrand et al., 1996; Abend and Smith, 1997; Polischuk et al., 2001;

Kurle and Worthy, 2002; Estrada et al., 2005; Sare et al., 2005; Dalerum et al., 2009). These same isotopes have been used to determine the extent of marine food exploitation in a variety of terrestrial consumers (Hobson et al., 1999; Szepanski et al., 1999; Stapp and Polis, 2003; Ben-David et al., 2004), but not primates.

Both biologically active- and inert tissues have been used in isotopic studies of primate diet (for reviews see Crowley, 2012; Sandberg et al., 2012). When dead specimens cannot be obtained, hair and faeces are favoured as materials for analysis (Schoeninger et al., 1997; Codron et al., 2006, 2008; Sponheimer et al., 2006a; O'Regan et al., 2008; Oelze et al., 2011) because they can be harvested non-destructively. This is an important consideration in light of ethical concerns implicit in primate studies, and the uncertain conservation status of many primates (Mittermeier et al., 2005). As in other animals, stable isotope ratios of primate hair (Loudon et al., 2007; Nakashita et al., 2013) and faeces (Blumenthal et al., 2012) have been shown to reliably reflect dietary isotopic composition.

Hair (which is a biologically inert tissue; Martínez del Rio et al., 2009), reflects isotope ratios of animal diet at the time of production (Sponheimer et al., 2003b; c), and provides remarkable temporal resolution in dietary reconstruction (Ayliffe et al., 2004; West et al., 2004). This property has facilitated the use of serial analysis of hair segments to investigate dietary switches through time in primates (Oelze et al., 2011). This approach may be hugely informative, but the reliability of conclusions drawn from serial analyses is contingent on a good understanding of hair growth patterns and growth rates in the study-animal, and the classification of hairs according to growth phase (Schwertl et al., 2003). Another hair isotope-based approach to diet reconstruction (which may be used when the above-mentioned criteria are not met) involves inference of diet composition from isotope ratios of homogenised hair samples (Schoeninger et al., 1997, 1999; Sponheimer et al., 2006a; O'Regan et al., 2008). This approach does not provide the same temporal resolution as serial analysis of hair segments, but allows for inference of diet integrated over longer periods (the duration of which is determined by hair growth rate and length; O'Connell and Hedges, 1999).

An alternative to serial analysis in studies of dietary shifts in animals is analysis of samples of the same material collected at different points in time (Dalerum and Angerbjörn, 2005). This is however only possible with material that can be collected non-destructively, such as hair (Mizukami et al., 2005b), blood (Hobson and Stirling, 1997) and faeces (Djagoun et al., 2013). Collection of faecal samples is not only non-destructive, but may also be carried out non-invasively (Codron et al., 2006), and, therefore, with relative ease

(Sponheimer et al., 2009). Importantly, the period of integration reflected in faeces is determined by gut throughput time, and is short (up to several days in medium-sized to large primates) (Clemens and Phillips, 1980; Lambert, 1998; Sponheimer et al., 2009). Analysis of faecal samples collected during different months has therefore been used to investigate seasonal shifts in proportional composition of primate diets (Codron et al., 2006, 2008). Stable isotope analysis could therefore be used to investigate exploitation of marine foods by primates, but the results would only prove truly informative if the marine signal in hair or faecal matter is fairly strong (i.e., the animals consume a substantial amount of marine food), and if there is considerable isotopic variation among the baboons' marine and terrestrial foods (Phillips and Gregg, 2001; Phillips, 2012). The latter condition is expected to be met in the system at the marine–terrestrial interface, as terrestrial plants and marine organisms in many regions are known to differ in terms of either $^{13}\text{C}/^{12}\text{C}$ ratios or $^{15}\text{N}/^{14}\text{N}$ ratios, or both (Sealy et al., 1986, 1987). The same is not necessarily true of the former however, as behavioural studies suggest that marine foods comprise only small percentages of Peninsula baboons' diets (Davidge, 1978; Chapter 2 of this thesis).

In light of the above discussion, the efficacy of isotopic analyses of faeces and hair of baboons, for determining whether or not baboons in coastal areas exploit marine foods, should be assessed. Should this prove to be the case, this method could potentially be used to determine the extent of marine food exploitation, and both annual and seasonal variation at the individual, troop and population level. Stable isotope analysis could therefore possibly be used to investigate differences between the sexes. Such differences warrant investigation, as males of various other primate genera consume more meat than their female counterparts (Fedigan, 1990; Watts and Mitani, 2002). Research to date has shown that baboons do not display consistent, marked inter-sex differences in animal-tissue consumption, but where there are differences males consume more animal tissue than females (Harding, 1973; Strum, 1975; Hausfater, 1976; Rhine et al., 1986).

Aims and predictions

The main aim of this study is to determine whether or not stable isotope analysis provides a viable alternative, or complimentary, source of data to behavioural observation in studies of marine food exploitation in primates. This will be done by estimating the extent of marine food exploitation by natural-foraging Peninsula baboons using stable isotope analysis, and then comparing the resultant estimates to those derived from behavioural observations. The secondary aim of the study is to investigate how documented dietary differences between

Cape Peninsula baboon troops are manifested in hair isotope ratios, if at all. In light of findings reported elsewhere (see above), I predict that:

1. Stable isotope ratios of baboon hair and/or faeces will reflect exploitation of marine foods by a natural-foraging Peninsula troop.
2. The ranges of values for seasonal marine food intake estimated from stable isotope ratios will include estimates of proportional intake based on behavioural observations.
3. Stable isotope ratios of Peninsula baboon hair will reflect documented differences in dietary ecology of Peninsula troops, and between sexes within troops.

METHODS

See Chapter 1 for a detailed description of the study site.

Study animals

The main study troop for this research was the Kanonkop (KK) troop (see Chapter 2 for a detailed description of KK troop). With the help of field assistants, I obtained hair- and faecal samples from this troop, and collected samples of foods consumed by this troop from within the troop's home range.

I also obtained hair samples from the Buffels Bay (BB), Da Gama (DG) and Main Tokai 1 (MT1) troops, either directly through the method described below, or indirectly from autopsies performed by other members of the University of Cape Town Baboon Research Unit. The above-mentioned troops inhabit home ranges spread across much of the Peninsula (see Fig. 3.1; the baboons that comprise MT1 troop were members of TK troop prior to a fission event), and each one differs from the others in terms of the amount of time that they spend in human-modified habitats (Hoffman and O'Riain, 2012a).

BB inhabits a 5.6 km² home range on the eastern side of the CoGH section of the TMNP, which overlaps with KK troop's home range to some extent. The vast majority of their home range is covered by untransformed habitat, but BB does make extensive use of the human-modified habitat within its home range (Hoffman and O'Riain, 2012a). Like KK, the BB troop is known to marine forage, but unlike KK, BB obtain human foods on an almost daily basis (Lewis unpublished data). They do this by raiding picnics or stationary vehicles, which routinely visit the tourist facilities within their home range (Hoffman, 2011).

DG's home range covers an area of 10.6 km², approximately 15 km NNW of KK troop's home range (see Fig. 3.1). This troop spends almost half of its time in human-modified habitats and is known to aggressively raid human dwellings on a regular basis (Hoffman and O'Riain, 2012a; Kaplan, 2013). The troop's current home range does not

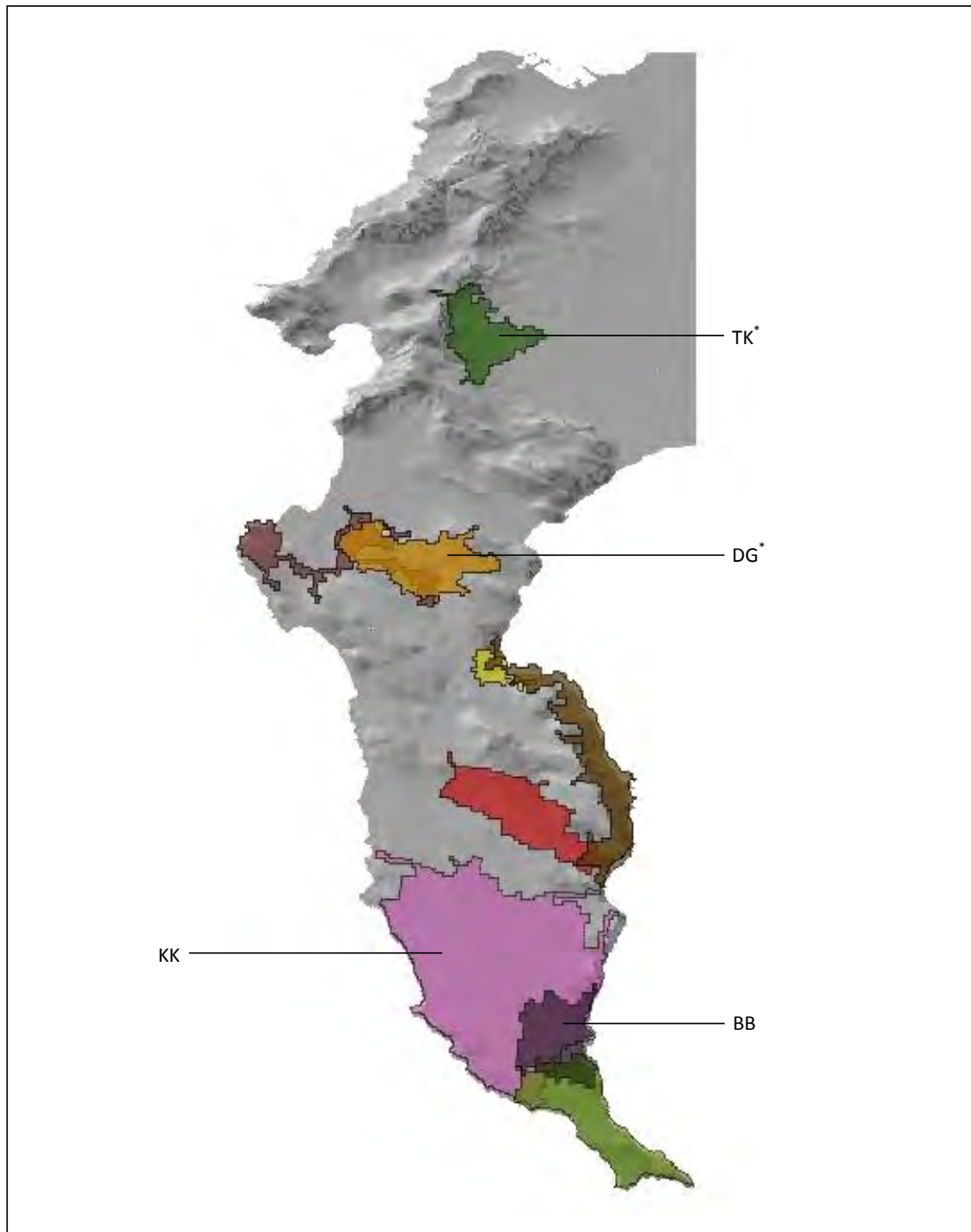


Fig. 3.1. Three-dimensional map of the Cape Peninsula showing home ranges of troops studied by Hoffman & O'Riain (2012 a; used with the first author's permission). Home ranges belonging to troop's mentioned in the text are labelled; asterisks denote troops that were herded by "baboon monitors"; BB = Buffels Bay, DG = Da Gama Park, KK = Kanonkop, TK = Main Tokai.

extend to the coast, but there is no physical barrier (e.g. hard development) that would impede the troop's movement to the intertidal zone to the west of their home range.

MT1 troop occupies a 9.5 km² home range in the Tokai area, approximately 25 km N of KK troop's home range (in the northernmost area on the Peninsula still occupied by baboons; see Fig. 3.1). These baboons, which are geographically isolated from the other study troops, spend the vast majority of their time in agricultural land at the urban edge and are known to raid on a regular basis (Hoffman and O'Riain, 2012a). Like DG troop, MT1 is not prevented from accessing coastal land by any physical barriers.

Sample collection and preparation

Faeces

With the help of field assistants, I collected faecal samples from the Kanonkop troop during five discrete periods across all four seasons between June 2009 and June 2010 (behavioural data were collected simultaneously for a companion study). We collected faecal samples from unknown individuals at various sleeping sites in each season. Only scats which had been voided on the morning of sampling were collected. We froze scats within two hours of collection and stored them at -20°C until preparation for analysis.

Dietary items

We collected three to five samples of all identifiable marine and terrestrial foods which the Kanonkop baboons ingested on more than two occasions during each season. We collected foods from as wide a variety of locations as possible within the troop's home range in order to provide some measure of the variation in isotopic signatures of the baboons' main food items through space. In each case, we collected only the structure from which the baboons derived their food (e.g. flower or cone). Following collection we placed the terrestrial plant samples in paper bags, and suspended these in a well-ventilated area in order to prevent rotting, and to partially air-dry the samples at the field site. We placed marine invertebrate samples in sealed plastic bags in a -20°C freezer on the day of collection.

In the laboratory, I processed both terrestrial and marine samples, such that only those tissues which were ingested by the baboons were included in the samples for analysis (following Rothman et al., 2008). I shredded desiccation-resistant plant tissues, such as *Leucodendron* sp. seeds and *Carpobrotus* sp. leaves, using a commercial blender (Waring®, Stamford, USA). I dried plant- and faecal samples in a drying oven at 60°C (following Codron et al., 2006) and freeze-dried marine samples at -80°C, and then ground each sample

to a homogeneous powder using a Wiley Mill Standard Model No. 3 (Arthur H. Thomas Co., Philadelphia, USA) and a custom-built hammer mill (United Scientific Pty. Ltd., Western Cape, South Africa).

Hair sampling

I collected hair samples from adult and sub-adult baboons of three Cape Peninsula troops (Buffels Bay, Kanonkop and Main Tokai 1) between 2 November 2011 and 20 March 2012 (after all behavioural data had been collected). I collected samples from at least five females in all three troops, and from at least five males in the Kanonkop and Main Tokai 1 troops. As the Buffels Bay troop was a single-male troop at the time, I collected only a single sample from a male in this troop. In order to avoid pseudoreplication within the KK, MT1 and BB (female) samples, I collected samples from animals of both sexes (and from females in the case of BB) with the most distinctive features (e.g., scars and ear notches) that allowed for swift identification without the need for close observation. Also, I only moved to within shooting distance immediately prior to launching the dart, and the target animal (and the whole troop on most occasions) moved away from me after the dart had struck an animal. This approach minimised the possibility of further habituating the KK troop and may even have made them more cautious of close human presence.

I collected hair samples by launching blunt wooden darts smeared with glue from a simple blow-pipe (1.5 m piece of 15 mm-diameter copper pipe) into the target animal's pelage from a distance of 10–15 m (following Améndola-Pimenta et al., 2009). Although I followed Améndola-Pimenta et al.'s (2009) methods, I made two important modifications to the dart design recommended by these authors. Firstly, instead of coiling thread around the front end of the dart, I affixed a 12 mm metal “washer” to the dart 20 mm from the tip using Super Glue (Glue Devil, Johannesburg; see Fig. 3.2). This allowed for a greater area to be

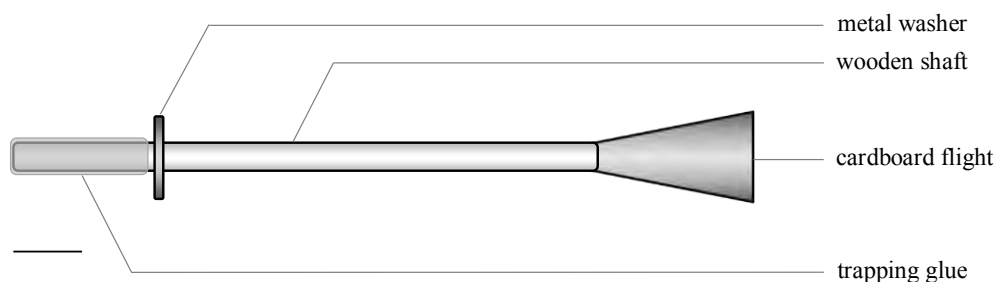


Fig. 3.2. Diagram of dart used to collect hairs from baboons on the Cape Peninsula, South Africa. Scale bar = 1 cm.

smearred with glue, without hampering the movement of the dart through the blow-pipe. Secondly, I replaced the wool stabilisers at the rear of the dart with a small cardboard cone, which I attached using Scotch® tape (3M South Africa Pty Ltd.). This cardboard “flight” caused less drag in the blow-pipe, thus allowing the dart to be launched with greater velocity, whilst still stabilising the dart in flight.

As recommended by Améndola-Pimenta et al. (2009), I used glue from a rodent trap (Trapper^{RT} Ltd., Bell Laboratories, Inc. Madison, USA) to coat the front end of the darts. While in the field, I stored the rodent trap in a rigid plastic cooler box with a plastic “ice brick” which had been in a -20°C freezer for at least 12 h beforehand. I did this because the viscosity of the glue, and thus its efficacy in retaining hairs, decreased, when it was exposed to relatively high ambient temperatures (> ~20°C). For this reason, I launched the dart as soon as possible after coating the front end with glue.

Upon being struck by a dart, the target baboon typically ran a short distance (10–20 m), before pausing to remove the dart using its hands or feet and then dropping the dart to the ground. Upon seeing the baboon drop the dart, I went and retrieved the dart, and with it, the hair sample. The number of hairs retained by a single dart ranged from 1 to 40 (mean = 11.8, SD = 10.3, n = 33). I placed each dart, with attached hairs, in a zip-seal plastic bag, which I then placed in a freezer on the day of collection. I stored samples at -20°C until preparation for analysis.

In the laboratory, I removed hairs from each dart by pouring a small amount of mineral turpentine onto the end of the dart and then gently pulling the hairs from the glue using forceps. I performed a simple experiment which showed that $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of hairs which had been treated with glue and mineral turpentine, and control hairs, were not significantly different (see Appendix B). Where more than 10 hairs had been collected from a given individual, I took a random sub-sample of 10 hairs from that individual for stable isotope analysis. I wiped down each hair multiple times with 95% ethanol and allowed it to dry (following Macko et al., 1999; West et al., 2004). I examined all hairs under a microscope to ensure that all surface debris had been removed, and then cut hairs into 2–3 mm sections with surgical scissors (Moritz et al., 2012) and pooled sections from the same individual. Thus, I obtained a homogenised hair sample for each individual for analysis.

Stable isotope analysis

I weighed out sub-samples of the requisite mass of baboon hair (~0.5 mg), faeces (~2.0 mg) and foods (~2.9 mg for most plants and ~0.5 mg for marine invertebrates) into tin cups, to an

accuracy of 1 microgram on a Sartorius micro balance. I then squashed the cups using forceps to enclose the sample and to reduce the amount of air that was included in the analysis. The samples were then combusted in a Flash EA 1112 series elemental analyser (Thermo Finnigan, Italy) and the resultant gases passed to a Delta Plus XP IRMS (isotope ratio mass spectrometer) (Thermo electron, Germany), via a Conflo III gas control unit (Thermo Finnigan, Germany), for stable isotope analysis. Appropriate in-house standards, all of which have been calibrated against IAEA (International Atomic Energy Agency) standards, were used to determine precision of the analyses. Repeated analyses of chocolate, valine and sucrose standards (for analyses of baboon hair and faeces, and marine food samples) and lentil, Merck gel and sucrose standards (for analyses of terrestrial plant samples) yielded mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values with standard deviations less than 0.25 ‰ in all cases.

I present $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ ratios in standard delta (δ) notation in parts per thousand (i.e., per mil, ‰), relative to the PeeDee Belemnite (PDB) standard for carbon and atmospheric N_2 for nitrogen. The δ values are derived from the expression:

$$\delta^H X = \left(\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right) \times 1,000 ,$$

where H is the atomic mass of the heavier stable isotope of element X , and R represents either the $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ ratio of the material indicated. Stable isotope ratio mass spectrometry was thus used to determine $\delta^{13}\text{C}_{\text{PDB}}$ and $\delta^{15}\text{N}_{\text{AIR}}$ values (hereafter referred to “ $\delta^{13}\text{C}$ ” and “ $\delta^{15}\text{N}$ ” respectively), and also yielded %C and %N values for both foods and faeces.

Statistical analyses

I used a parametric analysis of variance to test for significant differences between $\delta^{13}\text{C}$ values of faeces collected from Kanonkop baboons in different seasons. The standard deviations of $\delta^{15}\text{N}$ and %N values of faeces collected in different seasons were significantly different ($\delta^{15}\text{N}$: $F_{3,140} = 8.6$, $p < 0.01$; %N: $F_{3,140} = 7.5$, $p < 0.001$), so I used Kruskal-Wallis rank sum tests to test for differences in faecal $\delta^{15}\text{N}$ and %N values between seasons. In both cases, these tests indicated that there were significant differences between faeces collected in different seasons, so I performed Wilcoxon’s rank sum tests (with a holm correction applied to the p-values) to determine which seasons’ faeces differed.

In order to determine whether or not foods collected in different years could be combined in order to increase sample sizes, I performed Wilcoxon rank sum tests on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of samples of *Arctotheca calendula* and *Pterocelastrus tricuspidatus* (both terrestrial plants) and *Mytilus galloprovincialis* (a marine mussel) collected during

corresponding seasons in different years. I used Wilcoxon- (where samples were collected during two seasons) and Kruskal-Wallis rank sum tests (where samples were collected during more than two seasons) to test for significant isotopic differences between tissues of all species that were collected during more than one season ($n = 10$). I also performed Wilcoxon rank sum tests for paired samples to determine whether or not different tissues of *Mimetes cycullatus* (flowers and seeds) and *Pterocelastrus tricuspidatus* (flowers and leaves) collected during the same season in the same year differed in terms of carbon or nitrogen isotope ratios. Where these tests indicated that isotopic differences across years and seasons, and between tissues were not statistically significant I lumped samples accordingly. Following this, I grouped species by habitat and then by photosynthetic pathway (i.e., terrestrial C_3 , terrestrial C_4 or marine) for further analysis.

I investigated relationships between marine foraging and $\delta^{13}C$, $\delta^{15}N$ and %N values in order to determine whether or not marine food input had a discernible effect on faecal isotope ratios. Due to the sporadic nature of marine foraging (see Chapters 2 and 4), these analyses require a reliable estimate of the period of dietary integration for faeces. In the absence of data from an isotope-based controlled feeding study, the best proxy for this is gut throughput time, which is 26.8–96.8 h in baboons (Clemens and Phillips, 1980). Thus, I determined the average number of animals per marine foraging count, and the total duration of marine foraging bouts, during the period 26.8–96.8 h prior to the median time of faecal sample collection on a given day. I then multiplied these two values to determine a marine foraging index (MFI_f) for each faecal sample. I used Spearman rank correlations to test for relationships between MFI_f and mean $\delta^{13}C$, mean $\delta^{15}N$, and mean %N of faecal samples with the same MFI_f across all four seasons, and during spring, summer and autumn only. The results for the winter samples could not be analysed in this manner due to the small number of samples for which the full complement of behavioural data were available. If only a single sample with a given MFI_f value was collected during a season, I excluded that sample from the analyses.

I used the Stable Isotope Analysis in R package (SIAR v. 4.2) to run models which provided estimates of the proportional contributions of different food groups to the diet of KK baboons. The initial set of models incorporated isotope ratios of faeces and mean isotope ratios of different food groups (corrected for trophic enrichment), collected in different seasons. I included only the isotope ratios of food plant and animal species that were consumed in a given season in the model input, grouped as described above. Hence, foods derived from C_4 plants were excluded from the models of spring and summer diet as the

baboons were not observed eating these foods. I verified that these groups were in fact significantly different using a K nearest-neighbour randomisation test (Rosing et al., 1998). Due to the uncertainty regarding the appropriate trophic enrichment factor (TEF) value for use in the model, I ran four versions of the model with four different TEF values (three different, plausible TEF values from the literature, and an average of these values). The values from the literature were those determined for large mammalian herbivores (Sponheimer et al., 2003b; d), pigs (Hare et al., 1991), and gorillas (Blumenthal et al., 2012). In this way, I was able to test for effects of TEF variation on estimated dietary proportions.

To test for differences between hair isotope values of KK males and females, I ran Wilcoxon rank sum tests for independent samples on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of hairs from animals of the two sexes. I then used Stable Isotope Analysis in R package (SIAR v. 4.2) to run a set of models which provided estimates of the proportional contributions of different food groups to the diet of males and females. This set of models incorporated isotope ratios of hair samples (divided by sex) and foods consumed by the baboons throughout the year. As with the faeces-based models, I ran four versions of the model, each of which incorporated a different set of TEF values for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. The values that I incorporated into the models were those determined for large mammalian herbivores (Sponheimer et al., 2003b; c), pigs (Nardoto et al., 2006) and macaques (Nakashita et al., 2013) in hair-based models. Having run models which did not incorporate prior information regarding dietary proportions, I ran a second set of models which included prior information based on behavioural observations as parameters.

Finally, I investigated variation in hair isotope values of females and males from different Peninsula troops. I used Kruskal-Wallis rank sum tests to test for inter-troop differences in hair $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ value of female baboons. Females differed in terms of both isotopes, so I then performed pair-wise comparisons using Wilcoxon's rank sum tests (with a Holm correction applied to the p-values) to determine which troops differed from each other. As I was able to obtain sufficient samples for statistical analysis from males of only two troops, I used Wilcoxon rank test for independent samples to test for inter-troop differences in hair $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of male baboons. I then also used Wilcoxon rank sum tests for independent samples to test for differences between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of males and females from MT1 troop.

RESULTS

Stable isotopes of Kanonkop foods

There was some inter-annual and inter-seasonal variation in isotope ratios of both marine and terrestrial baboon foods, but none of the differences between foods of the same type were significant (Table 3.1). The mean $\delta^{13}\text{C}$ value of *P. tricuspidatus* flowers was 3.3‰ greater than that of leaves, and this difference was statistically significant ($V = 21$, $n_{\text{leaves}} = 6$, $n_{\text{flowers}} = 6$, $p < 0.05$). The flowers and leaves of *P. tricuspidatus* did not differ in terms of $\delta^{15}\text{N}$ however, and neither did *Mimetes cycullatus* flowers and seeds, in terms of either $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values. Food groups based on habitat and photosynthetic pathway were isotopically distinct across all four seasons and also within all seasons (K nearest neighbour randomisation $p < 0.05$ in all cases).

Table 3.1. $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and %N values of baboon foods collected during different seasons in the Cape of Good Hope section of the Table Mountain National Park¹

Season	Food group	n	$\delta^{13}\text{C}$ (‰)		$\delta^{15}\text{N}$ (‰)		%N	
			Mean	SD	Mean	SD	Mean	SD
All	C ₃	293	-27.1	1.7	1.1	3.3	1.8	2.3
	C ₄	14	-13.6	0.6	0.3	1.6	1.0	0.5
	Marine	55	-13.8	2.2	8.3	1.2	9.2	1.5
Winter	C ₃	214	-27.3	1.7	1.2	3.6	2.0	2.6
	C ₄	14	-13.6	0.6	0.3	1.6	1.0	0.5
	Marine	49	-14.0	2.3	8.2	1.1	9.1	1.5
Spring	C ₃	175	-27.3	1.7	1.6	2.9	2.2	2.8
	Marine	49	-14.0	2.3	8.2	1.1	9.1	1.5
Summer	C ₃	162	-27.0	1.7	1.2	2.9	2.1	2.9
	Marine	55	-13.8	2.2	8.3	1.2	9.2	1.5
Autumn	C ₃	151	-27.0	1.7	0.8	3.0	2.2	3.0
	C ₄	10	-13.9	0.5	-0.5	1.1	0.7	0.3
	Marine	55	-13.8	2.2	8.3	1.2	9.2	1.5

¹n = number of samples included in food group; SD = standard deviation around the mean.

Kanonkop faecal isotopes

The range of $\delta^{13}\text{C}$ values for faeces across all four seasons was -29.3‰ to -25.6‰ (faeces with minimum and maximum values were collected in spring and summer respectively). There were significant differences between $\delta^{13}\text{C}$ values of faeces collected during different seasons ($F_{3, 140} = 35.0, p < 0.001$). The $\delta^{13}\text{C}$ values of faeces collected in autumn and summer were similar (mean \pm SD = $-27.0 \pm 0.5\%$ and $-27.1 \pm 0.4\%$ respectively), and were higher than those of faeces collected in winter ($p < 0.01$ in both cases) and spring ($p < 0.0001$ in both cases). Faeces collected in winter were enriched in ^{13}C relative to those collected in spring by 0.6‰ ($p < 0.0001$). The largest difference in mean $\delta^{13}\text{C}$ values of faeces collected during different seasons was 1.1‰—the difference between autumn faeces and spring faeces (Table 3.2).

Table 3.2. Mean $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and %N values of baboon faeces collected during different seasons from a natural foraging troop in the Cape of Good Hope section of the Table Mountain National Park¹

Season	n	$\delta^{13}\text{C}$ (‰)		$\delta^{15}\text{N}$ (‰)		%N	
		Mean	SE	Mean	SE	Mean	SE
Winter	32	-27.52	0.07	4.07	0.31	3.36	0.04
Spring	38	-28.06	0.09	3.08	0.13	1.86	0.09
Summer	38	-27.13	0.07	2.46	0.13	3.12	0.09
Autumn	36	-26.98	0.09	3.53	0.14	3.62	0.09

¹n = number of faecal samples collected during each season; SE= standard error around the mean.

Faecal $\delta^{15}\text{N}$ values ranged from 0.9‰ to 6.3‰ across all four seasons (samples with minimum and maximum values were both collected in winter). Faeces collected in different seasons differed in terms of $\delta^{15}\text{N}$ ($\chi^2_3 = 32.27, p < 0.001$). Faeces collected in winter (mean $\delta^{15}\text{N} = 4.1 \pm 1.8\%$) were enriched in ^{15}N relative to those collected in spring ($p < 0.01$), summer ($p < 0.001$) and autumn ($p < 0.05$), by 1.0‰, 1.6‰ and 0.6‰ respectively (Table 3.2). The $\delta^{15}\text{N}$ values of faeces collected in autumn were significantly higher than those of faeces collected during spring ($p < 0.05$) and summer ($p < 0.001$), and the values of faeces collected in spring were higher than those of faeces collected in summer ($p < 0.01$).

Faecal samples collected during different seasons differed in terms of nitrogen content (%N; $\chi^2_3 = 84.01, p < 0.0001$). The nitrogen content of faeces collected in spring (mean %N = $1.9 \pm 0.6\%$) was significantly lower than that of faeces collected in any other season ($p < 0.0001$ in all three cases). Nitrogen comprised more than 3% of faeces collected in winter, summer and autumn, on average (Table 3.2). Winter faeces did not differ from summer or

autumn faeces in terms of %N, but autumn faeces were richer in nitrogen than summer faeces ($p < 0.01$).

There were strong positive correlations between $\delta^{15}\text{N}$ and MFI_f of faeces collected in all four seasons ($r = 0.81$, $n = 25$, $p < 0.001$), and faeces collected in spring ($r = 0.74$, $n = 8$, $p < 0.05$), and autumn ($r = 0.86$, $n = 7$, $p < 0.05$; Table 3.3). Nitrogen content (%N) and MFI_f were positively correlated in faeces collected in all four seasons ($r = 0.51$, $n = 25$, $p < 0.01$), and strongly positively correlated in summer faeces ($r = 0.95$, $n = 7$, $p < 0.001$; Fig. 3.3).

Table 3.3. Spearman's rank correlation coefficients for correlations between $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and %N of baboon faeces, and MFI_f (a composite measure of marine foraging) between 18.9 and 96.8 hours prior to faecal sample collection¹

Season	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	%N
All seasons	25	0.32	0.81**	0.51**
Spring	8	-0.33	0.74*	0.31
Summer	7	0.7	0.49	0.95**
Autumn	7	0.75	0.86*	-0.46

¹n = number of points included in correlation; MF = marine foraging; * indicates significance at the 5% significance level; ** indicates significance at the 1% significance level.

Baboon faecal sample $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were markedly lower than those of marine foods, corrected for trophic enrichment, in all four seasons (Fig. 3.4). On average, the $\delta^{13}\text{C}$ values of baboon faeces collected in different seasons were 12.9 – 13.8‰ lower than corrected values of marine foods, while faecal $\delta^{15}\text{N}_{\text{AIR}}$ values were 5.7 – 7.5‰ lower than those of marine food samples. Faeces were also depleted in ^{13}C relative to C_4 plant-derived foods—faecal samples collected in autumn and winter were depleted in ^{13}C by 12.8‰ and 13.6‰ respectively, relative to C_4 plant-samples. Winter and autumn faeces were enriched in ^{15}N relative to C_4 plants, on average, but only by 2.2‰ and 2.4‰ respectively. The patterns of enrichment and depletion of faeces relative to C_3 plants were less consistent than those mentioned above. Relative to C_3 plants, faecal samples collected in winter were enriched in ^{13}C by less than 0.1‰, whereas autumn faeces were enriched by 0.3‰. Faeces collected in winter and autumn were enriched in ^{15}N by 1.3‰ and 1.2‰ respectively, relative to C_3 foods. Summer faeces were enriched in ^{13}C by just 0.1‰, and depleted in ^{15}N by 0.3‰, relative to C_3 plants. Spring faeces were slightly depleted in both ^{13}C ($\delta^{13}\text{C}_{\text{faeces}} - \delta^{13}\text{C}_{\text{C}_3} = -0.4‰$) and ^{15}N ($\delta^{15}\text{N}_{\text{faeces}} - \delta^{15}\text{N}_{\text{C}_3} = -0.1‰$), relative to C_3 foods.

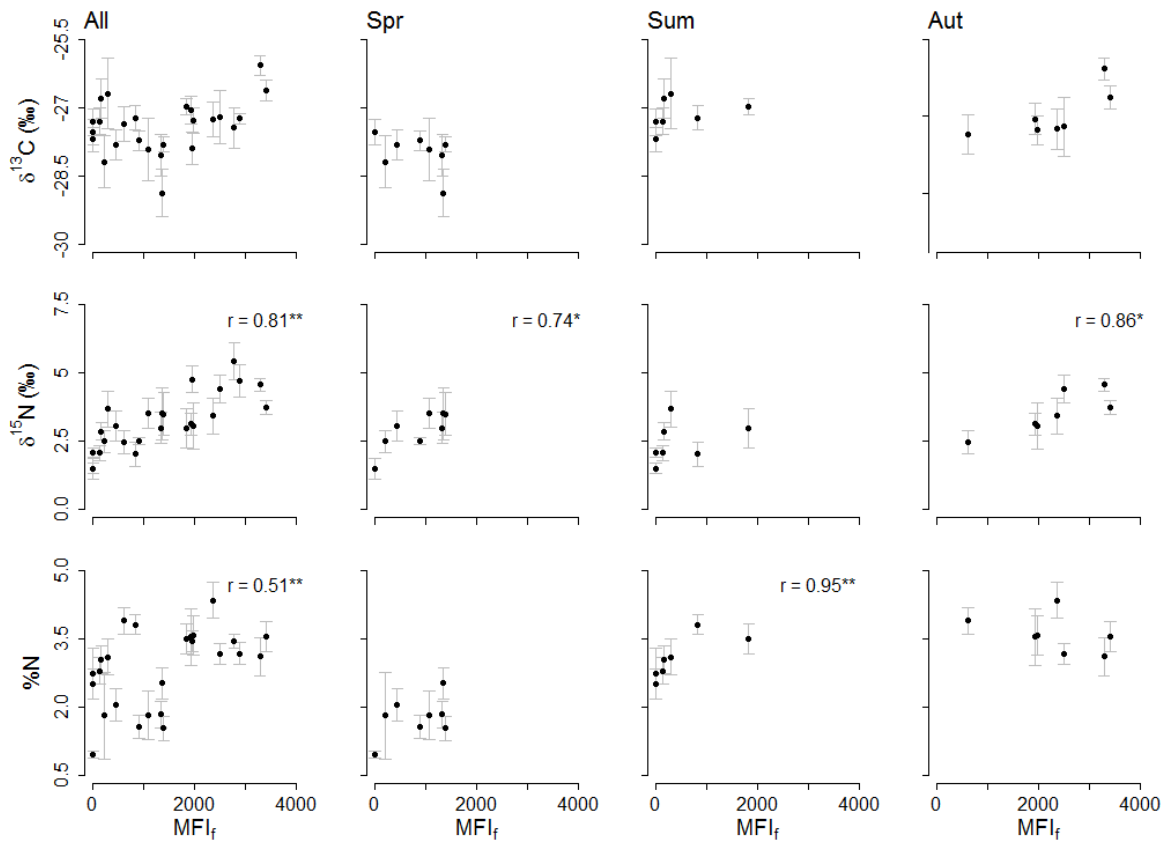


Fig. 3.3. Values of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and %N values, and MFI_f (see Methods) of faecal samples collected from a natural foraging troop of chacma baboons on the Cape Peninsula, South Africa during different seasons. Values on the vertical axis are mean values \pm SD for faeces collected on different days. Significant Spearman rank correlation coefficients are displayed; All = all seasons, Sp = spring, Su = Summer, A = Autumn; * indicates significance at the 5% significance level; ** indicates significance at the 1% significance level.

Diet based on faecal isotopes

Models based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of baboon faecal samples indicate that across all four seasons, C_3 plant-derived foods comprised the vast majority (88 – 100%) of KK baboons' diets. C_4 plant-derived foods (when eaten), and foods obtained in the marine intertidal zone, made up only small percentages (0 – 10% and 0 – 11% respectively; Fig. 3.5). Models that incorporated different TEF values showed the same patterns, but differed in terms of the estimated percentages of each food type in the diet. The maximum difference between upper extremes of 95% credibility intervals from models run using different TEF values was 8% (between estimated C_4 dietary contributions in autumn), and the maximum difference between lower extremes was 6% (between estimated C_3 dietary contributions in summer). Due to the uncertainty regarding appropriate TEF values for use in models of baboon diet, further results in text will refer to the models which incorporated the averages of the TEF

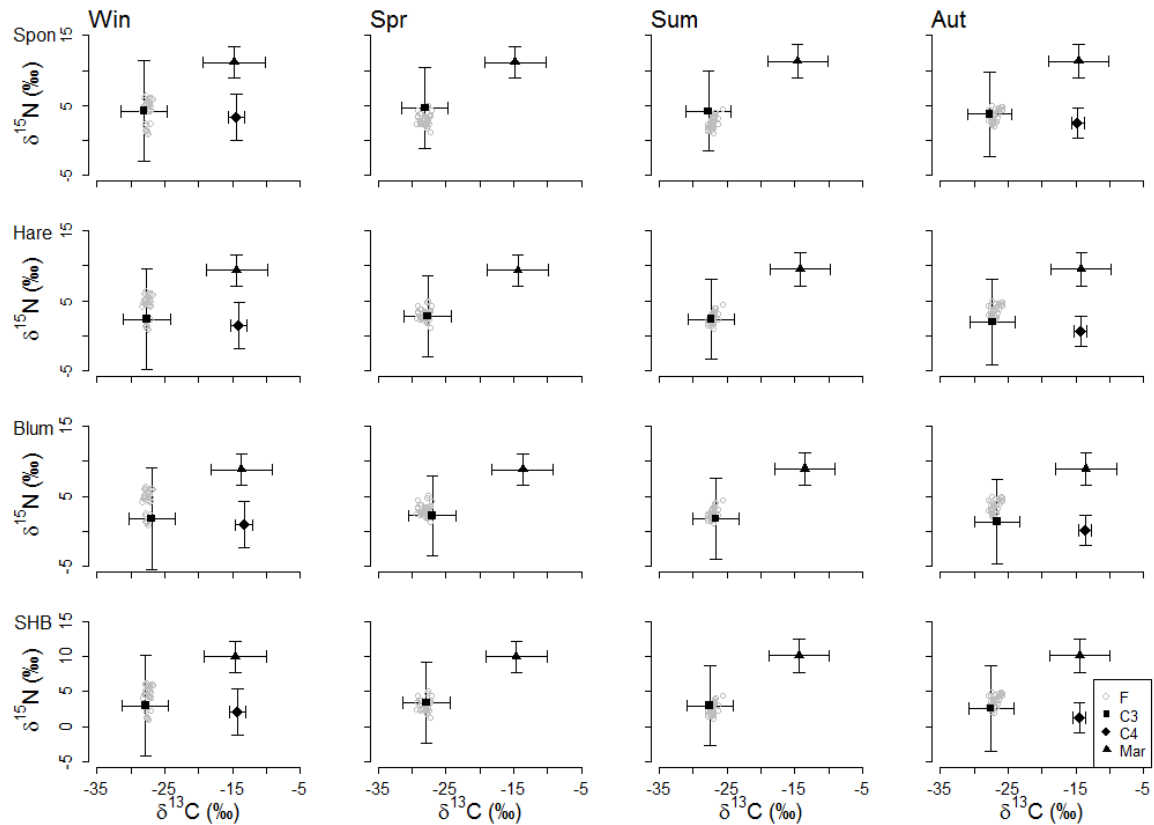


Fig. 3.4. Values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of faecal samples (grey circles) collected from a natural foraging troop of chacma baboons on the Cape Peninsula, South Africa during different seasons. Mean values ± 2 SD for food items (corrected for trophic enrichment; black symbols) consumed by the baboons are shown. Graphs in the same column present values for samples collected during the same season and graphs in the same row present values calculated using the same trophic enrichment factor. Trophic enrichment factors used were those calculated by Sponheimer et al., (2003 a; c) for large mammalian herbivores (Spon); Hare et al., (1991) for pigs (Hare); and Blumenthal et al., (2012) for gorillas (Blum); and an average of all of the above (SHB). F = faeces, C3 = terrestrial C₃ plant foods, C4 = terrestrial C₄ plant foods, Mar = marine foods.

values calculated by Sponheimer et al., (2003 a; c), Hare et al., (1991) and Blumenthal (et al., 2012).

The results of the model that incorporated the average TEF values indicated that baboons' diets were dominated by C₃ plant-derived foods in all four seasons, but there was some variation in the dietary contributions of different foods across seasons (Fig. 3.5). The percentages of winter and autumn diets comprised of different foods were very similar, as were those of spring and summer diets. The models indicate that the baboons certainly ate marine foods in winter and autumn, and that these foods may have comprised up to 9% of the diet in both seasons (CI_{95%} for marine invertebrates: 2 – 9% and 3 – 9% respectively). In

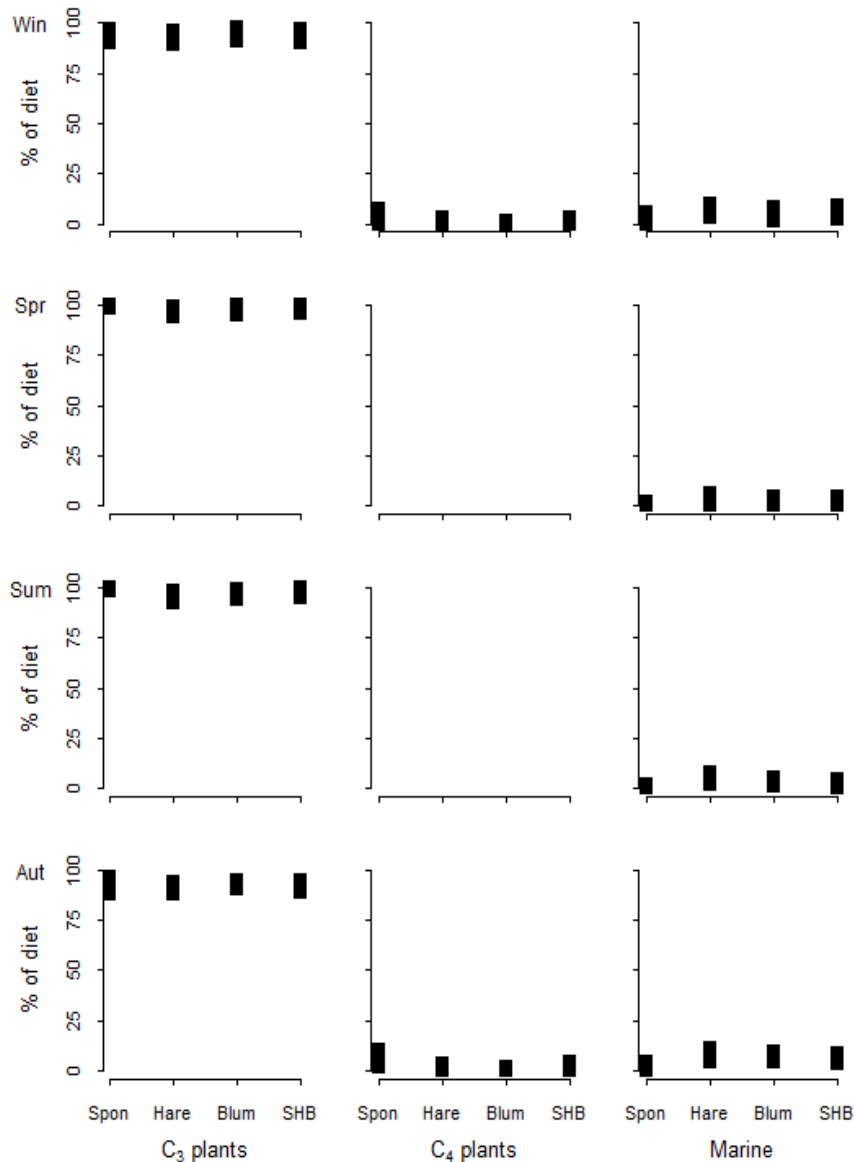


Fig. 3.5. Contributions of food groups to the seasonal diets of natural foraging baboons on the Cape Peninsula, South Africa, based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of faecal samples collected from unknown individuals. Contributions were estimated using models that incorporated $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (corrected for trophic enrichment as indicated on the horizontal axis), and percentage composition of carbon and nitrogen of food sources. Line segments indicate 95% credibility intervals of % contribution to diet (on the vertical axis) of different foods.. Trophic enrichment factors used were those calculated by Sponheimer et al., (2003 a; c) for large mammalian herbivores (Spon); Hare et al., (1991) for pigs (Hare); and Blumenthal et al., (2012) for gorillas (Blum); and an average of all of the above (SHB). Win = winter, Spr = spring, Sum = summer, Aut = autumn; C₃ plants = terrestrial C₃ plant foods, C₄ plants = terrestrial C₄ plant foods, Mar = marine invertebrates.

contrast, respective CI_{95%} for marine food contributions to spring and summer diets were 0 – 4% and 0 – 5%, indicating that the baboons ate very little marine food, if any, during these seasons. Thus, as the only other food type consumed in spring and summer, C₃ plant-derived

food comprised the balance of the diet in both seasons ($CI_{95\% \text{ spring}}: 96 - 100\%$ and $CI_{95\% \text{ summer}}: 95 - 100\%$). C_3 foods made up the majority of foods consumed in winter ($CI_{95\%}: 90 - 97\%$) and autumn ($CI_{95\%}: 89 - 95\%$), but the dietary proportions comprised of these foods were likely smaller than in the other two seasons. C_4 foods were not consumed during spring or summer (they were excluded from spring and summer models based on behavioural observations), and made up only small proportions of winter and autumn diets ($CI_{95\% \text{ winter}}: 0 - 3\%$ and $CI_{95\% \text{ autumn}}: 0 - 4\%$).

Isotope ratios of hair samples

Mean $\delta^{13}C$ and $\delta^{15}N$ values of hair collected from baboons of both sexes were -21.7‰ (± 0.2 , $n = 14$) and 4.5‰ (± 0.6 , $n = 14$) respectively (Fig. 3.6). Hair samples from males and females differed by just 0.1‰ in terms of $\delta^{13}C$, and this difference was not statistically significant. There was however a significant difference between $\delta^{15}N$ values of hairs from the two sexes ($W = 44$, $n_{\text{males}} = 7$, $n_{\text{females}} = 7$, $p < 0.05$); male baboon hairs (mean \pm SD = $4.9 \pm 0.3\text{‰}$, $n = 7$) were enriched in ^{15}N by 0.8‰ relative to female baboon hairs (mean \pm SD = $4.1 \pm 0.5\text{‰}$, $n = 7$).

Hair samples from KK baboons of both sexes were enriched in ^{13}C relative to C_3 plant foods, and depleted relative to C_4 plant foods and marine foods. In terms of ^{15}N , hair samples were similar to C_3 - and C_4 plant foods, and depleted relative to marine foods. Hair samples were however more similar to marine foods and C_4 plant foods than faecal samples. The differences between hair from

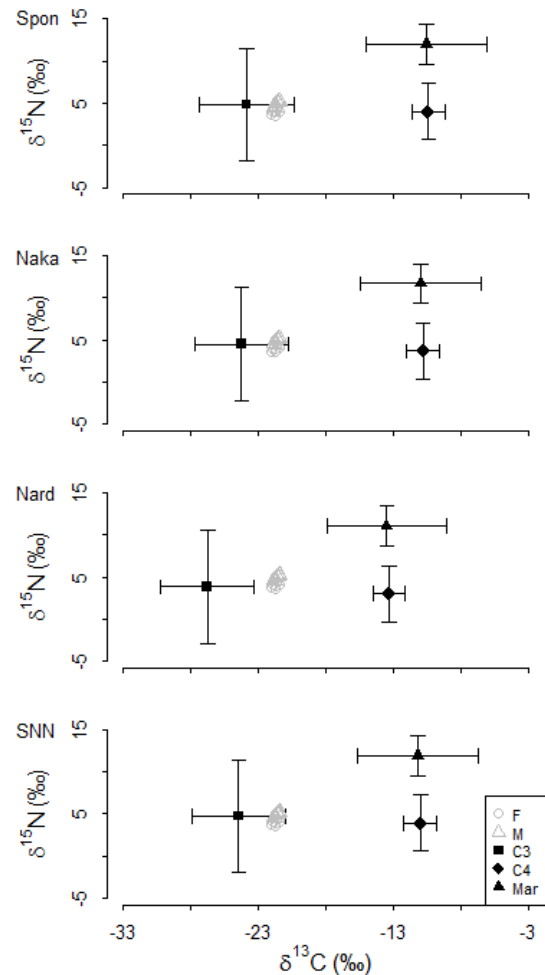


Fig. 3.6. Values of $\delta^{13}C$ and $\delta^{15}N$ of hair samples (grey symbols) collected from a natural foraging troop of chacma baboons on the Cape Peninsula, South Africa during different seasons. Mean values \pm 2 SD for food items (corrected for trophic enrichment; black symbols) consumed by the baboons are shown. Trophic enrichment factors used were those calculated by (Sponheimer et al., 2003b; c) for large mammalian herbivores (Spon); Nardoto et al., (2006) for pigs (Nard); and Nakashita et al., (2013) for Japanese macaques (Naka); and an average of all of the above (SNN). F = female, M = male, C3 = terrestrial C_3 plant foods, C4 = terrestrial C_4 plant foods, Mar = marine foods.

males and females meant that male hair was more similar to marine foods than female hair, in terms of carbon and nitrogen isotope ratios.

Diet based on hair isotopes

Results of models based on hair sample $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, and incorporating no prior information regarding diet composition, indicate that C_3 plants make up the majority of both female and male KK baboons' diets (Fig. 3.7). The full ranges of $\text{CI}_{95\%}$ values, across models incorporating different TEFs, were 55 – 91% and 54 – 90% in females and males respectively. Estimated percentages of female and male baboons' diets comprised of C_4 plant foods were smaller, but C_4 plants were included in diets of both males and females according to all four models ($\text{range}_{\text{female}}$: 5 – 43%, $\text{range}_{\text{male}}$: 4 – 42%). Marine foods made up the remaining small percentage of the diet in both females and males, and may in fact have been excluded from their diets altogether ($\text{range}_{\text{female}}$: 0 – 8%, $\text{range}_{\text{male}}$: 0 – 10%).

Irrespective of which TEF values were used, the above-mentioned pattern ($\text{C}_3 > \text{C}_4 >$ marine foods in terms of dietary contribution) was consistent in both males and females (Fig. 3.7). The modelled contribution of marine foods was remarkably consistent across models incorporating different TEF values. There was more variation in the modelled contributions of C_3 - and C_4 plants however, as models that incorporated the TEF values calculated by Nardoto et al., (2006) suggested lower percentages of C_3 foods, and higher percentages of C_4 foods, than models incorporating other TEF values (Fig. 3.7). As with faecal isotopes, there is uncertainty regarding which, if any, values from a single study, are appropriate for use in these models. In light of this, and considering the consistent pattern in the results of the models, further results will refer to the model which incorporated the averages of the TEF values calculated by Sponheimer et al., (2003 a; b), Nardoto et al., (2006) and Nakashita et al., (2013).

The models that incorporated the average TEF values show the same pattern described above, but also show subtle, but interesting, differences between males and females. The 95% credibility intervals for contributions of C_3 - and C_4 plants to the diets of females and males were almost the same, with minimum and maximum values of the respective intervals differing by no more than 1%. In the context of this study, the most important difference is the slightly larger percentage of male baboons' diets which was likely made up of marine foods—95% confidence intervals for contributions of marine foods to diets of female and male baboons were 0 – 7% and 0 – 10% respectively.

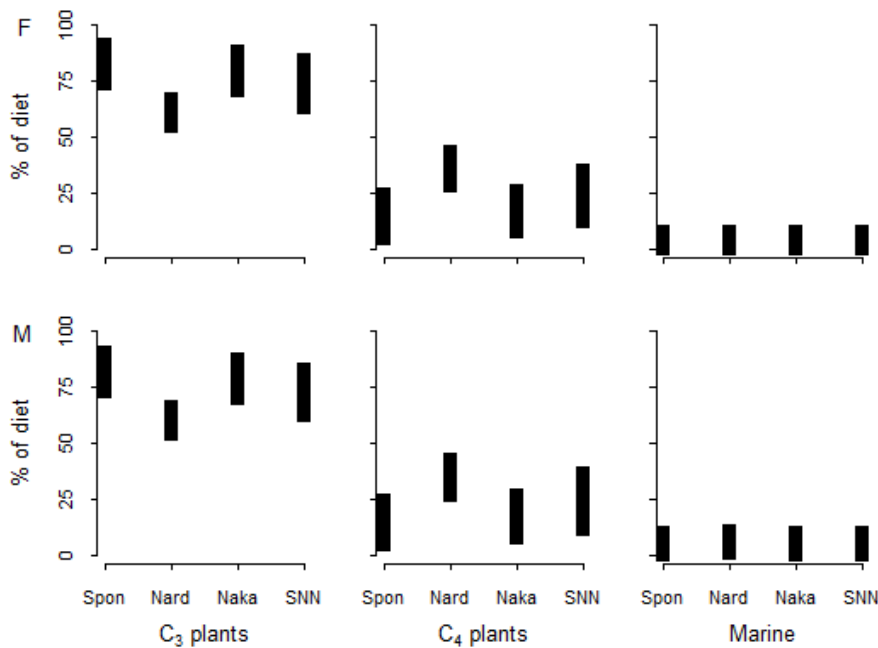


Fig. 3.7. Modelled diet composition of natural foraging baboons on the Cape Peninsula, South Africa, based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of hair samples collected from male (M) and female (F) adult baboons. Models incorporated $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (corrected for trophic enrichment), and carbon and nitrogen percentage composition, of foods. Line segments indicate 95% credibility intervals of % contribution to diet (on the vertical axis). Trophic enrichment factors were those calculated by Sponheimer et al., (2003 a; b) for mammalian herbivores (Spon); Nardoto et al., (2006) for pigs (Nard); and Nakashita et al., (2013) for Japanese macaques (Naka); and the average of the above (SNN). C_3 plants = terrestrial C_3 plants, C_4 plants = terrestrial C_4 plants, Marine = marine invertebrates.

Incorporating observation-based information regarding the diet of adult baboons in the troop into the models had a marked effect on the results (Fig. 3.8). The mean values (\pm SD in the case of C_4 plants) that were incorporated for C_3 plants, C_4 plants and marine foods were 0.942, 0.018 (\pm 0.025) and 0.040. Adding prior information had little effect on the estimated percentage of marine foods consumed (the only change was an increase in the maximum value of the 95% credibility interval for females from 7% to 8%), but caused notable changes to the estimated dietary contributions of C_3 and C_4 foods. In this model, the 95% credibility intervals of C_3 foods in diets of female and male baboons shifted up to 75 – 98% and 73 – 97% respectively. The 95% credibility intervals of dietary contributions of C_4 foods showed a corresponding shift in the opposite direction, with the result that lower and upper threshold values were 0 and 22% respectively, in both sexes. Thus, in terms of the general pattern of dietary contributions, the results of these models based on hair isotopes

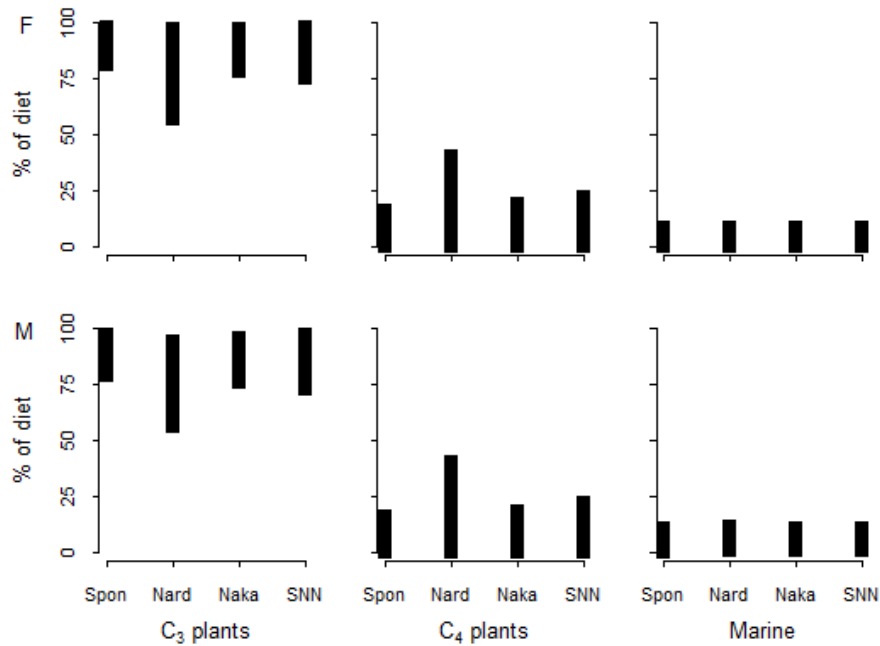


Fig. 3.8. Modelled contributions of food groups to the diet of natural foraging baboons on the Cape Peninsula, South Africa, based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of hair samples collected from male (M) and female (F) adult baboons. Contributions were estimated using models that incorporated $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (corrected for trophic enrichment as indicated on the horizontal axis), and percentage composition of carbon and nitrogen of food sources, as well as prior information regarding diet based on behavioural observations. Line segments indicate 95% credibility intervals of % contribution to diet (on the vertical axis) of different foods. Trophic enrichment factors used were those calculated by (Sponheimer et al., 2003b; c) for large mammalian herbivores (Spon); Nardoto et al., (2006) for pigs (Nard); and Nakashita et al., (2013) for Japanese macaques (Naka); and an average of all of the above (SNN). C_3 plants = terrestrial C_3 plant foods, C_4 plants = terrestrial C_4 plant foods, Mar = marine invertebrates.

were much more similar to those based on faecal isotopes, than were the hair models which did not incorporate prior information based on behavioural observations.

Isotopic comparison of Peninsula baboon troops

The average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of hairs collected from male baboons from different Peninsula troops (from which at least four hair samples were collected), ranged from -21.6 – -20.4‰, and from 4.9 – 6.1‰ respectively (Fig. 3.9). Hairs collected from MT1 males were significantly enriched in ^{13}C ($W = 0$, $n_{\text{KK}} = 7$, $n_{\text{MT1}} = 7$, $p < 0.001$) and ^{15}N ($W = 0$, $n_{\text{KK}} = 7$, $n_{\text{MT1}} = 7$, $p < 0.05$), relative to those collected from KK males. The differences between the average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of males from KK and MT1 troops were 0.3‰ and 1.2‰ respectively.

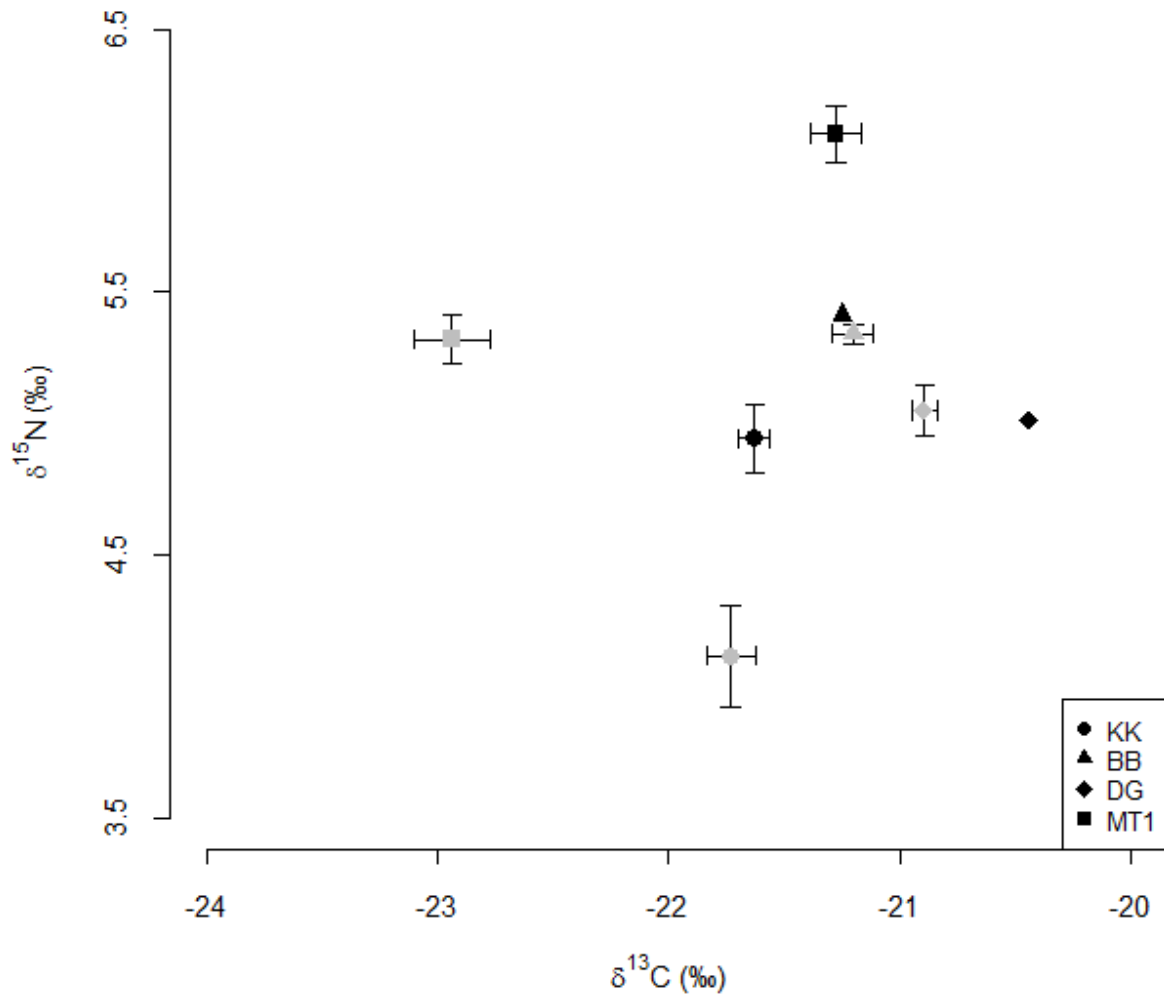


Fig. 3.9. Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of hair collected from males (black symbols) and females (grey symbols) from four chacma baboon troops on the Cape Peninsula, South Africa. Troops are arranged in ascending order of human-modified habitat use (i.e. from top to bottom in the legend sensu Hoffman and O’Riain, 2012 a). KK = Kanonkop, BB = Buffels Bay, DG = Da Gama Park, MT1 = Main Tokai 1; error bars denote standard errors around mean values.

Female baboons showed at least as much variation as their male counterparts in hair isotope ratios across troops, with average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values ranging from -22.9 – -20.9 ‰, and from 4.1 – 5.3 ‰ respectively. Hair samples from females from different Peninsula troops differed in terms of both $\delta^{13}\text{C}$ ($\chi^2 = 19.4$, $df = 3$, $p < 0.001$) and $\delta^{15}\text{N}$ ($\chi^2 = 16.2$, $df = 3$, $p < 0.01$) values (Fig. 3.9). Hairs from KK females were depleted in ^{13}C relative to those collected from Da Gama Park (DG; $p < 0.01$) and Buffels Bay (BB; $p < 0.05$) females, but enriched relative to MT1 females’ hairs ($p < 0.05$). Hairs from DG females were enriched in ^{13}C relative to BB females’ hairs ($p < 0.05$) and hairs from both troops were significantly enriched in ^{13}C relative to those collected from MT1 females ($p < 0.05$). In terms of $\delta^{15}\text{N}$, KK females’ hairs were significantly depleted relative to those of BB, DG and MT1 ($p < 0.05$ in all three cases).

As in KK troop, males and females from MT1 troop differed in terms of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ —hairs collected from MT1 males were significantly enriched in ^{13}C ($W = 35$, $n_M = 7$, $n_F = 5$, $p < 0.01$) and ^{15}N ($W = 35$, $n_M = 7$, $n_F = 5$, $p < 0.01$), relative to those from their female counterparts.

DISCUSSION

Kanonkop foods

As was expected, separation of natural baboon foods into terrestrial C_3 plants, terrestrial C_4 plants and marine foods was biologically meaningful, statistically sound, and appropriate for the purposes of using stable isotopes to model the diet of natural-foraging baboons. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of terrestrial plants and marine invertebrates consumed by the KK baboons fall within ranges of values reported previously for organisms of the respective types in this region (Sealy et al., 1986, 1987; Spriggs et al., 2003; Hill et al., 2006). Although the values reported here differ from some of those reported for terrestrial foods and foods of marine origin consumed by terrestrial mammals elsewhere, the patterns of variation are similar (Hobson et al., 1999; Szepanski et al., 1999; Stapp, 2002; Stapp and Polis, 2003; Ben-David et al., 2004).

One such pattern is a difference in $\delta^{13}\text{C}$ values of marine invertebrates and terrestrial C_3 plants. This difference arises at the level of the primary producer as marine algae are typically enriched in ^{13}C relative to terrestrial C_3 plants (O'Leary, 1988; France, 1995). The minimal fractionation of carbon by consumers at low trophic levels (DeNiro and Epstein, 1978), means that consumers of algae in the marine intertidal zone are, like their foods, enriched in ^{13}C relative to terrestrial C_3 plants (Hobson et al., 1999; Stapp, 2002).

The marine foods and C_4 plants consumed by the baboons could not be differentiated based on $\delta^{13}\text{C}$ values, but differed in terms of nitrogen ratios. This pattern may be explained, at least in part, by trophic enrichment in ^{15}N (Ehleringer et al., 1986; Kelly, 2000; Robinson, 2001). Trophic enrichment alone could not explain the large ($\sim 8\%$) difference reported here however (DeNiro and Epstein, 1981), as the Peninsula baboons' marine invertebrate prey feed at low trophic levels (Branch et al., 2005). This difference must therefore be caused by a combination of trophic enrichment and disparities in $\delta^{15}\text{N}$ values of the plants in question and the majority of marine primary producers (Hoering, 1955; Wada et al., 1975; Sealy et al., 1987).

Kanonkop faecal isotopes

There was statistically significant seasonal variation in faecal carbon- and nitrogen isotope ratios, which is indicative of seasonal variation in isotopic composition of baboon diet. Carbon isotope ratios of faeces suggest that the baboons consumed more ^{13}C -enriched foods (marine foods or terrestrial C_4 plants) in summer and autumn. Variation in faecal $\delta^{13}\text{C}$ across seasons is a reliable indicator of changes in dietary proportions contributed by foods with different $^{13}\text{C}/^{12}\text{C}$ ratios (Codron and Codron, 2009), because diet-tissue fractionation of carbon is consistent for a given consumer (Sponheimer et al., 2003b). Differences in $\delta^{13}\text{C}$ between faeces collected in different seasons were comparable to those reported elsewhere (Codron et al., 2006, 2008), and, although significant, were small ($< 1.1\%$) relative to differences between depleted foods (C_3 plants) and enriched foods (marine invertebrate tissue and terrestrial C_4 plants). A comparison of the enrichment/depletion patterns between faeces and foods reported here and elsewhere (Codron et al., 2006, 2008) suggests that ^{13}C -enriched foods (marine foods and terrestrial C_4 plants) comprised only small percentages of KK baboon diet during all four seasons.

Variation in faecal $\delta^{15}\text{N}$ values across seasons probably reflected seasonal differences in dietary ^{15}N content. Like variation in $\delta^{13}\text{C}$ values, differences in faecal $\delta^{15}\text{N}$ values do reflect differences in dietary isotopic values (Sponheimer et al., 2003d). Interpretation of faecal $\delta^{15}\text{N}$ variation across seasons is more complicated however, as nitrogen isotope variation might also reflect variation in TEFs (Ambrose, 1991; Vanderklift and Ponsard, 2003). Non-dietary factors which may affect nitrogen isotope fractionation can likely be disregarded in this instance (Vanderklift and Ponsard, 2003; Codron and Codron, 2009), as baboons always excrete nitrogenous waste in the same form (i.e., urea; Braun, 1998), and Peninsula baboons are, as a rule, not water-stressed (Hoffman and O'Riain, 2012b). Thus, if seasonal variation in faecal $^{15}\text{N}/^{14}\text{N}$ ratios is a reflection of differences in trophic enrichment, these differences would almost certainly be caused by shifts between diets which differ in terms of protein concentration (Codron and Codron, 2009). Although dietary protein may have profound effects on diet-tissue nitrogen isotope fractionation in other tissues (Sponheimer et al., 2003c), the effect of dietary protein content on diet-faeces fractionation is relatively small (Sponheimer et al., 2003d). It is therefore highly likely that seasonal variation in faecal $^{15}\text{N}/^{14}\text{N}$ reflects shifts between diets which differ in ^{15}N abundance across seasons.

Higher $\delta^{15}\text{N}$ values of faeces collected in winter and autumn almost certainly reflect increases in marine food intake during these seasons. Higher ^{15}N values could reflect either decreased intake of depleted foods ($\delta^{15}\text{N} < 0$) within the C_3 food group (e.g., *Watsonia sp.*),

or increased intake of more enriched foods ($\delta^{15}\text{N} > 0$), either within the C_3 food group (e.g., *Carpobrotus sp.*) or from the intertidal zone (Ambrose and Deniro, 1986; Codron et al., 2006). Although these factors are not mutually exclusive, the higher frequency of marine foraging in winter and autumn (indicated by behavioural observations), and concomitant increase in %N of faeces, suggest that the enrichment in faecal ^{15}N is certainly due, at least in part, to increased marine food intake. This suggestion is given further credence by the strong significant correlations between MFI_f and faecal $\delta^{15}\text{N}$ in spring and autumn, and across all seasons.

Nitrogen isotope ratios of baboon faeces suggest that although there is seasonal variation in marine food intake, invertebrates from the intertidal zone do not comprise large proportions of baboon diet during any season. The differences among nitrogen isotope ratios of baboon faeces collected in different seasons, while statistically significant, were small relative to differences between plant foods and marine foods. The enrichment/depletion patterns in ^{15}N reported here are similar to those between foods and more enriched faeces collected by Codron et al. (2006, 2008). Thus, KK baboon faeces displayed similar $\delta^{15}\text{N}$ values (relative to foods consumed at each site) to faeces of baboons elsewhere that did not engage in extensive faunivory.

Inferences based on comparison of patterns of enrichment/depletion in carbon and nitrogen isotopes, and results of faecal isotope-based models, are therefore in agreement. Interpretation of faecal isotopes following either method suggests that, although there was some variation, KK baboons ingested little marine- and C_4 food, and that terrestrial C_3 plant parts comprised the majority of their diet, during all four seasons (Sponheimer et al., 2003b; d; Codron and Codron, 2009).

Kanonkop hair isotopes

Hair isotope ratios indicate that male and female baboons consumed diets that differed in terms of nitrogen isotope ratios, but not in terms of carbon isotope ratios. The latter conclusion is sound, as primate hair reflects carbon isotope ratios of diets (Loudon et al., 2007; Nakashita et al., 2013), and animal diet-hair carbon isotope enrichment is remarkably consistent (Sponheimer et al., 2003b). The enrichment/depletion patterns of hair from baboons of both sexes, relative to different foods, can therefore be interpreted simultaneously.

The patterns of enrichment/depletion in ^{13}C observed here (relative to different food groups) suggest that these baboons may have included as much as 20–30% ^{13}C -enriched

foods (marine invertebrates or terrestrial C₄ plants) in their diet. These patterns were similar to those observed in the Waterberg (a mountainous area in the far north of South Africa) between different foods and hair samples collected from baboons which had included 20–30% “C₄ food” (i.e., C₄ grasses and succulents which use the CAM photosynthetic pathway) in their diet (Codron et al., 2008). In the context of Codron et al.’s (2008) study, an estimate of the proportion of diet comprised of ¹³C-enriched food (based solely on δ¹³C values) was highly informative. This is not the case here however, as marine foods and terrestrial C₄ foods are similarly enriched in ¹³C relative to terrestrial C₃ foods, and δ¹³C values alone cannot be used to resolve the contributions of these foods to KK baboon diet (Crowley, 2012; Phillips, 2012). Consideration of isotope ratios of a second element such as nitrogen, which distinguished these foods from each other in isotope space, is therefore necessary.

Mathematical models represent the only justifiable isotope-related approach for determining the extent of faunivory in KK baboons. This is the case because few studies have included isotope ratios of both primate hair and specific food items consumed (Oelze et al., 2011). A comparison of hair isotope values with those reported in other studies (Schoeninger et al., 1997, 1998, 1999; O’Regan et al., 2008) should be treated with caution, because any differences could, at least in part, be attributed to variation in food source isotope ratios across study sites (Schoeninger et al., 1997, 1998; Crowley et al., 2011; Oelze et al., 2011). The δ¹⁵N values reported here are generally lower than those reported for hair of congenics in the Awash National Park, Ethiopia, though there is some overlap (Moritz et al., 2012). This could be indicative of lower levels of faunivory (Schoeninger et al., 1998), or a greater reliance on nitrogen-fixing plants (Schoeninger et al., 1997, 1999) on the part of Peninsula baboons. It is however difficult to state with any degree of certainty which of these explanations is correct, as Moritz et al., (2012) did not report δ¹⁵N values of baboon food items in the Awash National Park.

Comparison of estimated diets

Models which incorporated isotope ratios of baboon hair, and those that incorporated faecal isotope ratios, both indicated that KK baboon diet is dominated by C₃ foods and that C₄- and marine foods make up small proportions of the diet. The exact dietary proportions estimated by the two sets of models differed however. These dissimilarities are in part due to differences in food source input—C₄ foods were not included in Spring and Summer faeces models—but there are several other factors that might have contributed to the discrepancies between the results of the models.

Firstly, it is plausible that not all components of the model input, which determines the accuracy and reliability of output from models such as these (Caut et al., 2008; Parnell et al., 2010; Bond and Diamond, 2011), were entirely accurate. It is likely that the isotope ratios and elemental concentrations incorporated into the models were accurate and appropriate, as geographic and temporal isotopic variation were accounted for (Heaton et al., 1986; Swap et al., 2004; Crawford et al., 2008; Codron and Codron, 2009), but this may not be true of TEF values.

The TEF values applied here were not baboon-specific values, because no such values are available in the literature. Diet-hair- and diet-faeces carbon and nitrogen TEFs have been determined for a variety of taxa (DeNiro and Epstein, 1978, 1981; Hobson et al., 1996; Sponheimer et al., 2003b; c; d; Hwang et al., 2007; Blumenthal et al., 2012; Nakashita et al., 2013), but not yet for baboons. The extent of enrichment in carbon between animal diet and tissue is relatively constant across diets, but not across species (Sponheimer et al., 2003b). Diet-tissue enrichment in nitrogen on the other hand has been shown to vary with a number of factors including the form in which nitrogenous waste is excreted (Vanderklift and Ponsard, 2003), dietary protein quantity (Codron and Codron, 2009) and quality (Robbins et al., 2005), and rainfall (presumably a proxy for water stress; Codron and Codron, 2009). In situations such as this, where species-specific values are unavailable, researchers must use values determined for other appropriate animals as proxies (Codron et al., 2006; Bond and Diamond, 2011). The values applied in this study were determined for animals that are ecophysiologically similar to baboons and were not water-stressed during experiments (Hare et al., 1991; Sponheimer et al., 2003b; c; d; Nardoto et al., 2006; Blumenthal et al., 2012; Nakashita et al., 2013), and were therefore the most appropriate values available. It has however been shown that these models are extremely sensitive to changes in TEF (Bond and Diamond, 2011). If, despite being the best current proxies, the TEF values used here are in fact not correct for baboons, the model output would not provide accurate estimates of KK baboon dietary composition.

Secondly, a factor which is not inherent in the models, but might affect estimates of dietary composition, is the dietary integration period, which varies hugely across tissues (Chisholm et al., 1982; Tieszen et al., 1983; Hilderbrand et al., 1996). Faeces reflect integrated diet consumed over just a few days (Coates et al., 1991; Sponheimer et al., 2003b), while hair may reflect diet integrated over several months (Schwertl et al., 2003; Ayliffe et al., 2004). The exact period reflected in hair is determined by hair growth rate and length (longer hairs reflect diet integrated over longer periods) as hair is biologically inert once it

has been produced (Voigt et al., 2003). Peninsula baboons are known to exploit different food items in different seasons (Davidge, 1978; Van Doorn et al., 2010; Hoffman and O’Riain, 2011), and the isotopic composition of their diet might therefore change through time. If this were true, the dietary proportions estimated using the two sets of models should differ.

Thirdly, isotopes in hair and faeces may reflect isotopic composition of different components of an animal’s diet (Tieszen and Fagre, 1993; Codron et al., 2011). Faeces reflect the stable isotope ratios of animals’ ingested diets (Sponheimer et al., 2003b; d; Steele and Daniel, 2009; Blumenthal et al., 2012), but may over-represent dietary items with lower digestibility (Codron et al., 2011). Hair isotopes on the other hand reflect the isotope ratios of assimilated nutrients, particularly the protein component of the animal’s diet (Tieszen and Fagre, 1993). Hair isotope ratios might therefore indicate greater dietary contributions of marine invertebrates, as these are richer in protein than all of the KK baboons’ plant foods except the seeds of one species (see Chapter 2). Thus, even if the correct TEF values were used, and the dietary integration periods represented were the same, the output of the hair- and faeces-based models are expected to differ to some extent. Due to the uncertainty associated with both models, the model results should be compared not only to each other, but also to dietary estimates based on behavioural observation, in order to assess their accuracy (Schoeninger et al., 1997; Kurlle and Worthy, 2002).

Importantly, the estimates of seasonal diet composition based on faecal isotope ratios are remarkably similar to those generated from observational data. In all four seasons, the marine dietary contributions estimated from behavioural data fell well within the 95% credibility intervals for this food source generated by the models (see Chapter 2). Furthermore, the model output indicates that even in spring and summer, marine foods were definitely ingested by baboons, even if only in small quantities. Not surprisingly therefore, the total intake of terrestrial plant foods estimated from behavioural observations also fell well within the relevant 95% credibility intervals (combined for the purposes of this comparison).

Comparison of diet contributions estimated from hair isotope ratios to those based on behavioural observation is more complex in the context of this study. This is largely because the dietary integration period reflected in baboon hair is unknown, as there is a paucity of information regarding primate hair growth in the literature. It has however been shown that some primates exhibit synchronous hair growth, (Inagaki and Nigi, 1988), while others, including humans, exhibit asynchronous hair growth (Harkey, 1993; Isbell, 1995). In both cases, hair growth may occur throughout the year, as hair grows continuously between moults

in species with synchronous hair growth (Inagaki and Nigi, 1988). In light of this, and our current poor understanding of baboon hair growth, it was assumed that homogenised baboon hair samples reflect diet integrated throughout all four seasons. Dietary estimates based on hair isotope ratios were therefore compared to estimated diets of adult baboons based on behavioural observations collected throughout the year.

As in the comparison described above, observation-based estimates of marine food components in diets of adult baboons fell within the 95% credibility intervals for marine food generated by the models that incorporated hair isotope ratios, but no prior information. There was also concordance between model- and observation-based estimates of marine food intake differences between the sexes (both indicated that male baboons ingest slightly more marine foods than females). The 95% credibility intervals for C₃- and C₄ foods generated by these models did not include the estimated contributions of these foods derived from behavioural observation however (see Appendix C). Relative to observation-based estimates, the model overestimated the dietary contribution of C₄ plants, and underestimated the C₃ component of baboon diet.

The second set of SIAR models incorporated the same isotope ratios and elemental concentration values as the first, but also incorporated prior information regarding diet. The 95% credibility intervals for marine intake generated by these models were very similar to those generated by the first set of models, and also included the observation-derived estimates of marine food intake. As with the first set, the model output and estimates derived from observation records suggested similar differences between males and females. The C₃- and C₄ food 95% credibility intervals generated by these models differed sufficiently from those generated by the first set of models however, such that the observation-based estimates fell within these credibility intervals. Thus there is agreement between the model output and observation-derived dietary estimates, but it is important to note that the model output does not rule out a relatively large (>20% of total diet) C₄ food input to baboon diet, or C₃ contribution as low as 75% of diet.

The high values of the upper limits of 95% confidence intervals for C₄ foods in the models based on hair isotope ratios are surprising. If anything, hair isotope values might be expected to over-represent marine invertebrate dietary input, because these foods provide a disproportionately large amount of protein (see Chapter 2; Tieszen and Fagre, 1993). This incongruity could be indicative of an erroneous value in the model input (Caut et al., 2008; Phillips, 2012). Considering the precision of the isotope ratios, the values which are more likely to be incorrect are the TEFs, which, if incorrect, may have profound adverse effects on

the accuracy of the model output (Bond and Diamond, 2011). Diet-hair carbon TEFs are relatively consistent across conspecific individuals on the same diet (Hobson et al., 1996), and across species (Sponheimer et al., 2003b). Thus, it seems unlikely that the carbon TEF used here are inappropriate. Animal diet-hair nitrogen TEFs show much greater variation than carbon TEFs (Sponheimer et al., 2003b; c), and may differ markedly across conspecific individuals on the same diet, and individuals of different species on the same diet (Sponheimer et al., 2003c). It is therefore plausible, that the nitrogen TEF used here could have been incorrect and had a smaller TEF value been used, the hair would have been more enriched in ^{15}N relative to terrestrial C_4 plants, and less depleted relative to marine invertebrates. Use of such a value would therefore have resulted in the model producing larger estimates of marine food intake and smaller estimates of terrestrial C_4 plant intake. In light of this, further research is needed to determine the true diet-hair ^{15}N TEF for baboons on a diet which includes small amounts of animal protein.

Output from models that incorporated faecal isotope ratios indicated that consumption of marine foods varied across seasons, but that marine foods comprised only small dietary proportions (<10%) during all four seasons. Davidge (1978) reported a similar pattern based on observational study of another troop of Peninsula baboons that did not raid and included marine invertebrates in their diet. Insects, the other animals which might be ingested by these baboons, comprise an even smaller proportion of Peninsula baboon diet than marine foods (Hall, 1962; DeVore and Hall, 1965; Davidge, 1978; Chapter 2 of this thesis). The results of faecal isotope-based models presented here therefore agree not only with the companion study on this troop (see Chapter 2), but also with previous studies of Peninsula baboons.

All available evidence therefore suggests that natural-foraging Peninsula baboons do not ingest large amounts of protein-rich animal tissue. This is not unusual in baboons—congeners elsewhere also include only small amounts of animal tissue in their diets (Altmann and Altmann, 1970; Post, 1982; Byrne et al., 1993; Altmann, 1998; Okecha and Newton-Fisher, 2006). The %N values of Peninsula baboons faeces are generally similar to those on the upper end of the spectrum of reported by Codron et al. (2006) for faeces of baboons from the Kruger National Park and Waterberg regions. This suggests that the diet of Peninsula baboons is in fact relatively rich in protein, which is surprising considering that plants in the Peninsula's dominant terrestrial habitat (fynbos), generally have nutrient-poor tissues (Campbell, 1986; Stock and Allsopp, 1992; Coetzee et al., 1997). Despite this, it seem that Peninsula baboons simply may not need to marine forage more in order to fulfil their nutritional requirements. This may be because their dexterity allows them to fulfil the

majority of their nutritional requirements by selectively ingesting those parts of fynbos plants which are relatively rich in nutrients.

Isotopic comparison of Peninsula baboons

There were significant isotopic differences between males and females in both KK and MT1 troops. This pattern, which is unusual in primates (Schoeninger et al., 1997; O'Regan et al., 2008; Oelze et al., 2011), indicates that males and females from the same troop differ in terms of dietary intake (Schoeninger et al., 1997; Nakashita et al., 2013). MT1 males were enriched in ^{13}C by $\sim 1.7\%$ relative to females from the same troop. This suggests that diets of males include at least 10% more C_4 plant-derived food than females (Codron et al., 2008). This could represent either increased consumption of alien C_4 grasses in residential gardens, or C_4 plant-derived human foods (e.g. corn and sugar, and foods in which these are major ingredients) which could be obtained from human dwellings, rubbish bins and vehicles in the troop's home range (Hoffman and O'Riain, 2012a; Johnson et al., 2013).

In both KK- and MT1 troops, males were on average enriched in ^{15}N relative to females. This suggests that males either ingest greater amounts of enriched animal tissue (Schoeninger et al., 1998) or less food derived from depleted nitrogen-fixing plants (Schoeninger et al., 1997, 1999). Based on the other results presented here, and incidence of faunivory in baboons reported elsewhere (Altmann and Altmann, 1970), the former seems more likely.

In both males (KK and MT1 troops) and females (BB, KK, DG and MT1 troops), individuals from different troops differed in terms of both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. The most striking aspect of inter-troop variation in ^{13}C is the depletion of MT1 females relative to other females. Considering that KK females ate so little C_4 food, this could imply that the MT1 females fed exclusively on C_3 foods (Schoeninger et al., 1999). It could however, also be indicative of the fact that these baboons spend a great deal of time in the closed-canopy plantations of Tokai (Hoffman and O'Riain, 2011). It has been shown elsewhere that tissues of C_3 plants in closed canopy habitats are depleted in ^{13}C relative to those of C_3 plants in nearby open habitats (Schoeninger et al., 1997; Cerling et al., 2003, 2004). Thus, baboons that spend much of their time in closed-canopy habitats, and feed mostly on C_3 foods from these habitats, should be expected to have tissues that are depleted in ^{13}C relative to those of baboons that frequent more open habitats. If this is true, and the C_3 plants consumed by Tokai baboons are markedly depleted relative to those consumed by other Peninsula baboons, the difference in dietary composition of KK and MT1 males is in fact greater than it appears

based only on hair isotope ratios. Unfortunately, there are no carbon isotope data for plants in the Tokai plantation in the literature, so further study is required to quantify the true extent of the differences in C₃- and C₄ food consumption between Tokai baboons and baboons from other Peninsula troops. If one ignores the $\delta^{13}\text{C}$ values of MT1 females, and considers the values of females from other troops, it is apparent that across troops, as time spent in human-modified habitats increases (Hoffman and O’Riain, 2012a), so does enrichment in ^{13}C . This suggests that those baboons that spend time in human-modified habitats switch to a diet that includes more C₄ plant-derived foods (probably C₄ alien grasses and C₄ crop-derived human foods) (Codron et al., 2008).

Both males and females of KK troop were depleted in ^{15}N relative to individuals of the same sex from other troops (females of the other troops were not significantly different from each other). KK animals might therefore either consume significantly less animal tissue (Schoeninger et al., 1998), or significantly more nitrogen-fixing plant tissue (Schoeninger et al., 1997, 1999), than the individuals from other troops. It is interesting to note however that the individuals which are enriched in ^{15}N are those from troops which are known to come into contact with, and raid food from, humans (Hoffman and O’Riain, 2012a). A similar pattern was observed in the Kruger National Park, where faeces from baboons that had access to human foods were enriched in ^{15}N relative to natural-foraging troops (Codron et al., 2006). Based on this, it must be assumed that baboons are either raiding animal tissues from humans or that human foods derived from plants are enriched in ^{15}N relative to natural foods. The former is unlikely, as baboons rarely take meat from humans and human dwellings, preferring foods such as fruits, vegetables and grain-based products (Kaplan et al., 2011). The latter on the other hand is plausible as manure and other non-synthetic fertilizers are enriched relative to atmospheric nitrogen (Bateman and Kelly, 2007), and crops fertilized with these substances have correspondingly high $\delta^{15}\text{N}$ values (Bogaard et al., 2007). Baboons that ingest these crops (e.g., MT1 troop), the foods derived from them (e.g., BB, DG and MT1 troops), or insects that have fed on them (Park and Lee, 2006; Birkhofer et al., 2011), would be enriched relative to individuals that do not do so (Sponheimer et al., 2003c). Whether this is the correct explanation or not, the fact remains that there is a general pattern of enrichment in both ^{13}C and ^{15}N of baboon hair with increasing association with humans and human-modified habitats.

Conclusion

The results presented here suggest that stable isotope analysis may allow for accurate estimation of contributions of marine foods to natural-foraging Peninsula baboon diet. The estimates of marine dietary input generated by models that incorporated faecal isotope ratios were more similar to dietary estimates based on behavioural data, than were those of models that incorporated hair isotope ratios. Stable isotope ratios of baboon hair might provide a better indication of how much of the baboons' dietary protein is assimilated from marine foods, but further research is required to ascertain the best TEF value for use in hair isotope-based models. That said, analyses of both tissues indicated that natural-foraging Peninsula baboons incorporate only small amounts ($\leq 10\%$) of marine foods into their diet. Variation in baboon hair isotope ratios across troops suggests that foods obtained from humans and human-modified habitats are enriched in both ^{13}C and ^{15}N relative to natural plants foods. Stable isotope analysis might therefore be of limited use in quantifying the extent of marine food use in baboons that access human foods, but could in fact be used as a remote means for assessing raiding. This precludes the use of stable isotope analysis in quantifying the extent of ingestion of marine foods by non-natural foraging baboons.

CHAPTER 4

Factors affecting exploitation of marine
intertidal organisms by natural-foraging
baboons on the Cape Peninsula

ABSTRACT

Baboons are highly adaptable generalist omnivores that are known to exploit a wide variety of foods within a given habitat. On the Cape Peninsula, South Africa, where terrestrial systems are largely oligotrophic, chacma baboons (*Papio ursinus*) supplement their diet with protein-rich invertebrates from the marine intertidal zone. No study to date has provided a detailed account of seasonal variation in exploitation of marine foods, or the potential factors which might influence this behaviour. In this study behavioural observations were used to determine how the frequency and duration of marine foraging bouts varied seasonally. Generalized Additive Models (GAM) were used to determine which environmental factors predicted the probability and intensity of marine foraging during a given hour. Marine foraging was recorded on up to 67% of days during a given season, but the troop members typically only spent short periods feeding on the shore (marine foraging by any member of the troop was observed during just 8.4% of total observation time). There was seasonal variation in both the frequency of marine foraging by the troop and the duration of MF bouts (the troop foraged in the intertidal zone most frequently in winter, but bouts were longest in autumn). GAMs indicated that multiple environmental factors (both biotic and abiotic) explained significant amounts of residual deviance of models of probability and intensity of MF. Both the intensity and the probability of MF declined with increasing tide height and swell height; probability increased slightly as offshore wind speed increased; and intensity fluctuated with wind speed and direction, and varied significantly across seasons and between coasts. The results therefore suggest that abiotic oceanic factors limit the exploitation of marine foods by the baboons, and that biotic factors play a role in when and where this behaviour is carried out.

INTRODUCTION

Exploitation of marine foods by Peninsula baboons has been documented multiple times in the literature (Hall, 1962, 1963; DeVore and Hall, 1965; Davidge, 1978), but no study to date has provided an explanation of the factors that influence the occurrence or frequency of this unusual behaviour. Hall (1962, 1963) described the behaviour and identified the marine organisms that are consumed by Peninsula baboons, but did not quantify the amount of marine food eaten. Davidge (1978) quantified the proportional contribution of marine foods to the diet of a troop of chacma baboons on the Cape Peninsula over the course of a year, but her estimate was based on limited monthly observations (as little as 12.5 hours of observation per month). Considering the likely effects of tidal cycles on marine foraging (MF) (Hall, 1962; Nielsen, 1991; Conrads, 2000), any study of MF should, at the very least, control for variation in tide heights through lunar cycles (Palmer, 1995). Davidge (1978) makes no mention of tides and it therefore seems unlikely that she accounted for tidal variation in her sampling. She might therefore have underestimated (or overestimated) the amount of time that her study animals allocated to feeding on marine foods depending on when she collected data. Also, Davidge's (1978) study troop had access to abundant protein-rich seeds of alien trees and might therefore have been less dependent on marine foods as a source of protein than baboons living exclusively in nutrient-poor fynbos vegetation.

The few studies in which the effects of environmental variables on exploitation of marine foods by other terrestrial mammals have been quantified, suggest that the behaviour is limited by advancing tides (Nielsen, 1991; Bonesi et al., 2000). It seems likely that these patterns would hold true in other systems, as maritime mammals seldom enter the water fully (if at all) while foraging (Dalquest, 1948; Conrads, 2000; Sleeman et al., 2001; Hansen et al., 2003; Smith and Partridge, 2004). Hall (1963) stated that Peninsula baboons exploit marine foods "almost daily when wind and tide allow... easy access to intertidal rock pools and to the sea verge", but while in the intertidal zone, baboons "would rush away on the approach of a large wave." The potential effects of environmental factors such as tides and wave height have however, not yet been quantified.

Observations of baboon behaviour (Chapter 2), and stable isotope ratios of the same animals' hair and faeces (Chapter 3), indicate that marine foods comprise small proportions of the diet of the Peninsula's last remaining non-raiding baboons. This is surprising considering the protein-rich nature of these foods, and it seems likely that some

environmental factors limit this behaviour. Further investigation of the behaviour and the environmental factors that may limit exploitation of marine foods is therefore warranted.

Aims and predictions

The aims of this chapter are to quantify in greater detail the use of marine food resources by the same study troop investigated for Chapters 2 and 3, and to elucidate the potential effects of a suite of environmental factors that may limit this behaviour. In light of results reported in Chapters 2 and 3, seasonal variation in marine invertebrate condition reported elsewhere, and trends described in other studies of maritime mammals (*sensu* Carlton and Hodder, 2003), and based on Hall's (1963) statement mentioned above, I predict that:

1. The frequency and duration of marine foraging bouts, and the number of animals exploiting marine foods during these bouts will show marked seasonal variation.
2. KK baboons will be less likely to marine forage when the tide is in, or when rough seas (a result of large swells, strong winds, or a combination of the two) restrict safe access to the intertidal zone.
3. If they do feed on marine foods when conditions are not optimal, I predict that the intensity of exploitation will increase with improving conditions (lower tide heights, smaller swells and lower wind speeds).

METHODS

Study animals

The study troop for this research was the Kanonkop troop (KK). The troop's home range encompasses 45.26 km² of largely untransformed fynbos habitat in the northern section of the CoGH section of the TMNP (see Chapter 2), and includes almost 13 km of coastline on the Peninsula's east and west coasts. In March 2010 (when the most accurate count was obtained), KK numbered 56 baboons, with an adult sex ratio (M:F) of 1:3.4. Thus, the per capita area of the troop at this time was 0.81 km².baboon⁻¹ (see Chapter 2).

Data collection

With the help of a team of volunteer field assistants, I collected data on 136 days during five discrete fieldwork sessions spread across all four seasons between May 2009 and June 2010 (see Chapter 2; Kruger, 1979). During each of the first four fieldwork sessions (June and September 2009, and January and March 2010) we attempted to collect data on 30

consecutive days within the calendar month in order to account for fluctuations in tide height through lunar cycles (Palmer, 1995). Although we lost the troop on a few occasions (in two of the four months), we nevertheless collected data on a minimum of 30 days during each of the first four sessions (see Chapter 2).

The baboons of KK troop had been habituated to human presence at a distance of ~20 metres for a previous study (Hoffman and O’Riain, 2012a), so it was possible for observers to follow the troop on foot at this distance. We performed instantaneous scan samples (Altmann, 1974) at 10 minute intervals on the troop throughout each day, while following the troop from their morning to evening sleeping sites. When the troop entered the intertidal zone and at least one baboon was observed feeding on marine organisms we changed the observation protocol. We recorded the start-time and end-time of each MF bout, where a bout was defined as a continuous period throughout which at least one baboon was feeding on marine organisms in the intertidal zone, and noted whether the bout took place on the Peninsula’s east or west coast. Throughout each bout, we recorded counts of the number of animals (excluding infants) foraging on marine organisms at one minute intervals (hereafter referred to as MF scans). All animals that were visible within 20 s of the beginning of the MF scan, and were handling or ingesting marine organisms were included in the scan. These data were collected in this manner because initial observations suggested that feeding on marine organisms is a sporadic, short-duration behaviour. Although MF scans did not allow analysis of individual-level differences in exploitation of marine foods, this method did provide a robust estimate of the frequency, duration and intensity of MF at a troop level.

I used MF scan values and bout durations to determine the average percentage of time available that KK baboons spent feeding on marine foods. I did so by summing MF scan values during a given season (and the whole study period) and then dividing this figure by the total number of animals in the troop (49, excluding infants) and then by the total number of daylight minutes during the period in question. Based on the activity budgets determined in Chapter 2, this value was then translated to the percentage of total feeding time spent feeding on marine foods. Unfortunately, feeding rates and individual-level differences in behaviour could not be determined as this would have required focal sampling and close proximity to individual troop members (see Altmann, 1974). Collecting these data would have involved a violation of the conditions of my SANParks research permit, which stipulated that troop members could not be followed and habituated for the close individual observation required for focals. This condition was imposed to prevent further habituation of the Peninsula’s last ‘non-commensal’, free-ranging troop.

External organisations provided the abiotic environmental variable data for the study. Tide height data (metres above chart datum), were collected at Simonstown (10 km north of KK troop's home range on the east coast of the Peninsula), by the South African Navy Hydrographic Office. The South African Council for Scientific and Industrial Research (CSIR) provided swell height data (m) collected with a Directional Waverider buoy located ~5.5 km off the Peninsula's west coast at 34°12.24'S, 18°17.20'E. The Cape Town Weather Office of the South African Weather Service (SAWS) provided temperature-, precipitation-, and wind speed- (ms^{-1}) and wind direction data collected at the Cape Point Weather Station (34°21.20'S, 18°29.35'E). I obtained sunrise and sunset data for Cape Town from the South African Astronomical Observatory Website (SAAO, 2010). Together, these data were used to investigate the potential effects of abiotic factors on the exploitation of marine foods by KK baboons.

Ideally, food availability in marine intertidal habitats would also have been investigated using detailed numerical observations. This was not possible however, due to the scale of the undertaking required to accurately determine marine food availability within the troop's home range. The density of baboons' marine invertebrate prey, as well as the size and condition of these organisms, may differ between coasts (Branch, 1974; Xavier et al., 2007), and along each coast over small spatial scales (Van Erkom Schurink and Griffiths, 1991; Steffani and Branch, 2003a), and condition may vary through time (over the course of seasons; Branch, 1974; Van Erkom Schurink and Griffiths, 1991). An accurate assessment of marine food availability within KK troop's home range would therefore, at the very least, require a large number of counts along multiple transects in the intertidal zone on each coast. Even these data might not provide a true indication of marine food availability because of the rapid changes in accessibility resulting from periodic submergence (Branch et al., 1998). The effects of tidal cycles (and associated factors that affect submergence) should therefore be incorporated into assessments of marine food availability, but this cannot be done if these effects are not well-understood. The effects of abiotic factors on exploitation of marine foods will be ascertained in this chapter, and the results reported here could then be used to inform an accurate assessment of marine food availability. The latter was unfortunately beyond the scope of this study. Thus, the variables "Season" and "Coast" were used as broad-scale proxies for food availability in the models of marine food exploitation.

Statistical analyses

Data preparation

The vast majority of MF bouts throughout the study were shorter than 1 hour (mean \pm SD = 23.7 ± 25.3 min, $n = 224$). In light of this, and given the resolution of the environmental data (weather variable- and swell height values were provided for each hour and half-hour respectively), I divided the observation time into hour-long sampling periods for the purposes of investigating the frequency and intensity of MF. I included all full hours between sunrise and sunset. I calculated the average tide height-, swell height- and wind speed values, and determined the predominant wind direction, during each hour. Depending on the wind direction, and which coast the baboons were closer to during the hour in question, I classified wind as either on- or offshore. I determined “tide status” (i.e., whether the tide was advancing or receding) by comparing average tide height (THT) during the hour in question and the preceding hour. I defined tides as advancing if $THT_t < THT_{t-1}$, and receding if $THT_t > THT_{t-1}$, where t represents time at the start of the hour in question. Box plots revealed that there was adequate spread in tide height, wind speed and swell height during observation time over the study period and that there were no true outliers in any of these variables. To test for collinearity, I performed Pearson correlations between all pairs of predictor variables (following Dormann et al., 2013), and found that no two variables were strongly linearly related ($r < 0.7$ in all cases).

The baboons did not marine forage at all during the majority of observation hours (86%, $n = 1417$ hours). In 41% of those hours, the baboons were more than 1063 m (mean + $1 \times$ SD KK troop’s hourly travel distance) from the coast and were thus not able to marine forage, irrespective of intertidal conditions. I thus excluded all of these samples to provide a subset of foraging data in which the troop was sufficiently close to the coast (< 1063 m) and could thus choose, based on the environmental conditions at the time, whether or not to marine forage and at what intensity to do so.

I created two variables based on MF observations to use as response variables in the models described below. The first was a binary descriptor of MF, to which I assigned a value of 0 if no baboon ingested marine foods and 1 if at least one animal ingested marine food items during a given hour. The second was the average proportion of the troop that fed on marine foods within a given hour (this was only calculated for hours which had been assigned a value of 1). I calculated the average proportion of the troop that fed on marine foods during hour T using the formula:

$$Average Prop_T = \left(\frac{\sum_{i=0}^{59} MF scan_{T+i}}{49} \right) / 60,$$

where T is the time at the turn of the hour, $MF scan$ is the number of animals ingesting marine foods (see above) and i is the number of minutes since time T . Count values might range from 0 to 49 within a given hour, because the 7 infants in the troop were not included in MF counts. Due to the inclusion of minutes during which no animals marine foraged ($count = 0$), this value is a composite measure of the time spent MF, and the number of animals MF, during each hour. It is thus referred to as the intensity of MF.

Models

I used Generalized Additive Models (GAMs; Hastie and Tibshirani, 1990; Wood, 2006) to examine the relationships between the probability, and intensity, of MF and predictor variables. GAMs are semi-parametric extensions of Generalized Linear Models (GLMs) which may incorporate both non-parametric smooth- and parametric model components (Wood, 2006). Unlike GLMs, GAMs are not based on an assumed relationship between the response variable and the predictor variables that is specified *a priori*. Rather, GAMs fit ‘smooth’ functions to continuous predictor variables and then use a link function to establish relationships between these functions and the response variable (Wood, 2006; Zuur et al., 2009). As a result, they are referred to as “data-driven models”, because the fitted values are not determined by a pre-specified function (Yee and Mitchell, 1991). GAMs can therefore be used to model highly non-linear and non-monotonic relationships (Guisan et al., 2002; Zuur et al., 2009) such as are predicted with tidal and diurnal patterns. In all models, I included predictor variables based on findings of previous studies on other maritime mammals (Nielsen, 1991; Bonesi et al., 2000), and observations of MF in Peninsula baboons (Hall, 1962, 1963).

I used tensor splines to generate smooth functions in all GAMs. I did so because this allows for the use of tensor product splines, which can generate a single smooth function of an interaction between two (or more) continuous predictor variables (e.g., tide height and swell height) (Wood, 2006).

I investigated the relationships between the probability of MF during a given hour and predictor variables using GAMs assuming a binomial error model. I ran one set of GAMs to investigate the relationships between the response and predictor variables across both coasts, and one set of models to investigate these relationships when the troop was nearer to the west coast (see below for explanation). I evaluated the main effects of season, coast, time since

sunrise, tide height, tide status, wind speed, and wind direction, and an interaction between wind speed and wind direction, as potential predictors of probability in the models of MF across both coasts. I ran the second set of models primarily to determine the potential effect of swell height on MF. This could not be done in the first set because swell height data were only available for the west coast. I therefore evaluated the main effects of season, time since sunrise, tide height, tide status, swell height, wind speed, and wind direction, and interactions between tide height and swell height, and between wind speed and wind direction, in the models of MF on the west coast only.

Thus, the full model used to investigate the probability of MF across both coasts during a given hour is described by the equation:

$$\text{logit}(p) = \beta_0 + f_1(\text{Tide height}) + f_2(\text{Time since sunrise}) + f_3(\text{Wind speed}) + \text{Season} + \text{Coast} + \text{Tide status} + \text{Wind direction} + f_4(\text{Wind speed} \times \text{Wind direction}),$$

where $\text{logit}(p)$ denotes the binomial link function, p is the probability of MF occurring (i.e., response = 1), and f_{1-4} denote the smooth functions realised by tensor splines (Wood, 2006). The full model including only hours during which the troop was nearer to the west coast on the other hand, is described by the equation:

$$\text{logit}(p) = \beta_0 + f_1(\text{Tide Height}) + f_2(\text{Time Since Sunrise}) + f_3(\text{Swell Height}) + f_4(\text{Wind Speed}) + \text{Season} + \text{Tide Status} + \text{Wind direction} + f_5(\text{Wind speed} \times \text{Wind direction}) + f_6(\text{Tide height} \times \text{Swell height}),$$

where the symbols denote the same quantities and functions, with the addition of the smooth function of swell height (f_3); and the resultant changes to functions involving wind speed) and f_6 , which denotes the smoothing function realised by tensor product splines (Wood, 2006).

I investigated the relationships between the intensity of MF and predictor variables using GAMs that assume a binomial error model. This type of model was appropriate because the values of the response variable were proportions (Zuur et al., 2009). Once again, I ran one set of models to investigate the relationships between the response and predictor variables across both coasts, and another set to investigate these relationships when the troop was on the west coast. I evaluated season, coast, tide height, tide status, wind speed and wind direction as potential predictors in the former, and season, tide height, tide status, swell height, wind speed and wind direction in the latter. Sample sizes for these models were not large enough to allow for an evaluation of interactions between variables.

The full model used to investigate relationships between intensity and predictor variables is described by the equation:

$$\text{logit}(P) = \beta_0 + f_1(\text{Tide Height}) + f_2(\text{Wind Speed}) + \text{Season} + \text{Coast} + \text{Tide Status} + \text{Wind direction},$$

where logit denotes the binomial link function, P is the average proportion of the troop MF during a given hour, and f_{1-2} denote the smooth functions realised by tensor spline functions (Wood, 2006). The full model used to investigate the same relationships when the troop marine foraged on the west coast is described by the equation:

$$\text{logit}(P) = \beta_0 + f_1(\text{Tide Height}) + f_2(\text{Swell Height}) + f_3(\text{Wind Speed}) + \text{Season} + \text{Tide Status} + \text{Wind direction},$$

where the symbols denote the same quantities and functions as in the equation above, with addition of the smooth function of wind speed (f_3).

Model building

In each set of models, I first evaluated the full model (main effects only) with and without the random effect of day (run as generalized additive mixed models), to determine whether the addition of this random effect improved the model. I did so because I was unsure whether there was temporal autocorrelation between observations which should be accounted for in the model (Zuur et al., 2009). I assessed candidate models using second-order Akaike's Information Criterion (AIC_c) because this criterion is more appropriate than first-order Akaike's Information Criterion (AIC) if $n/K \leq 40$, where n is the number of observations and K is the number of parameters in the full model (Burnham and Anderson, 2004). In all cases, the model without the random effect was the more parsimonious model (indicated by lower AIC_c) and the random effect was therefore omitted from further models.

I used analysis of deviance tests to ascertain which predictor variables in the full models contributed significantly to the deviance explained by the model (Table 4.1 and Table 4.2). I used $p < 0.01$ as the threshold for immediate inclusion in the model because the p -values generated by the these tests are approximate, and values close to 0.05 might therefore not indicate true significance (Zuur et al., 2009). In cases where interactions were found to contribute significantly to the deviance explained by the model, the main effects of variables included in the interaction were not investigated. Those predictor variables that did not contribute significantly ($p > 0.05$) were dropped from the model. If a variable's contribution was significant, but not highly so ($0.05 < p < 0.01$), I ran two intermediate models (one that

Table 4.1. Results of analysis of deviance tests for significance of contributions to deviance explained by GAMs fitted to probabilities of marine foraging¹

Predictor	Both coasts		Predictor	West coast	
	Resid. dev.	<i>p</i> -value		Resid. dev.	<i>p</i> -value
none	780.74	-	none	411.49	-
te(Tide height)	861.35	< 0.001	te(Tide height)	-	-
te(Time since SR)	807.33	< 0.001	te(Time since SR)	426.20	< 0.01
Te(Wind speed)	-	-	te(Swell height)	-	-
Season	787.28	0.108	te(Wind speed)	-	-
Coast	781.01	0.609	Season	415.38	0.290
Tide status	780.76	0.885	Tide status	411.49	0.972
Wind direction	-	-	Wind direction	-	-
te(WSP × WDR)	791.07	< 0.01	te(WSP × WDR)	428.86	< 0.001
			ti(TDH × SWH)	417.56 *	0.015

¹Residual dev. = residual deviance; te = tensor spline smooth; ti = tensor product spline smooth; Time since SR = time (in hours) since sunrise; WSP = wind speed; WDR = wind direction; TDH = tide height; SWH = swell height; highly significant values ($p < 0.01$) are in boldface; * denotes variables that were significant at the 5% significance level and were retained in the final model based on the AIC_c values of the intermediate models.

Table 4.2. Results of analysis of deviance tests for significance of contributions of deviance explained by GAMs fitted to intensity of marine foraging¹

Predictor	Both coasts		Predictor	West coast	
	Residual dev.	<i>p</i> -value		Residual dev.	<i>p</i> -value
none	831.19		none	478.84	
te(Tide height)	868.36	< 0.001	te(Tide height)	520.48	< 0.001
te(Wind speed)	831.23	0.842	te(Swell height)	492.25	< 0.01
Season	904.63	< 0.001	te(Wind speed)	489.67	< 0.01
Coast	855.14	< 0.001	Season	556.08	< 0.001
Tide status	834.86	0.053	Tide status	480.80	0.164
Wind direction	831.35	0.681	Wind direction	485.50 *	0.012

¹Residual dev. = residual deviance; te = tensor spline smooth; Time since SR = time (in hours) since sunrise; highly significant values ($p < 0.01$) are in boldface; * denotes variables that were significant at the 5% significance level and were retained in the final model based on the AIC_c values of the intermediate models.

included the variable in question and one that did not) and chose the more parsimonious model (i.e., the model with the lower AIC_c value) as the final model. I then compared AIC_c values of the respective full- and final models, to check whether the final model was more parsimonious than the full model in each case. In all cases, the final model was more parsimonious than the full model (Table 4.3).

I used the final models to predict the probability, and intensity, of MF for all significant environmental variables under “optimal conditions” (i.e., conditions at which predicted probability and intensity of MF were at their maxima). Models were fitted using the mgcv package (Wood, 2013) in the statistical platform R (R Core Team, 2014).

Table 4.3. Second-order Akaike’s Information Criterion (AIC_c) values of models of probability and intensity of marine foraging during a given hour¹

	Prob. (both)	Prob. (West)	Intensity (both)	Intensity (West)
Full model	808.78	445.75	1292.35	784.15
Final model	804.80	441.29	1289.78	783.86

¹Prob. = probability; both = both coasts; West = west coast.

RESULTS

On average, over the entire study period, KK baboons spent 1.0% of their time feeding on marine foods (Fig. 4.1A). KK baboons exploited marine resources during all four seasons, but there was seasonal variation in the amount of time spent feeding on these foods (Fig. 4.1A) and the percentage of feeding time allocated to marine foods (Fig. 4.1B).

The proportions of days on which KK troop members marine foraged, and the percentage of time spent MF, varied seasonally. MF occurred on more than 60% of days during winter and spring, and on only 33% of days in summer (Fig. 4.2A). Although KK baboons marine foraged on a high proportion of days in winter, feeding on marine organisms was observed during only 8.4% of observation time during this season. In other seasons, the percentage of time during which MF occurred ranged from 2.0 to 7.5% (Fig. 4.2B). The frequency of exploitation of marine foods also varied seasonally; MF occurred, on average, during 1 in every 15.8 hours in summer, and 1 in every 4.6 hours in winter. The proportion of observation hours during which MF occurred (hereafter referred to as “MF hours”) was higher in the morning than in the afternoon.

The members of KK troop spent more time feeding on marine foods during MF hours in autumn (mean \pm SD = 34.0 \pm 18.9 min, n = 49) than during any other season (Fig. 4.3A). There was little variation in time spent feeding on marine foods during MF hours on east and west coasts (Mean \pm SD_{east} = 26.9 \pm 17.8 min, n = 77; Mean \pm SD_{west} = 24.6 \pm 17.1 min, n = 132).

There was seasonal variation in the number of animals MF during MF hours (Fig. 4.3B), with means ranging from 8.6 (\pm 6.3, n = 49) in autumn, to 5.5 (\pm 5.1, n = 51) in spring (Fig. 4.3B). The number of animals MF during MF hours also differed between coasts, with means of 8.0 (\pm 5.9, n = 77) animals per count on the east coast and 6.8 (\pm 5.7, n = 132) on the west coast.

Probability models

East and west coasts

Tide height, time since sunrise and the wind speed \times wind direction interaction were significant predictors of probability of MF across both coasts (Table 4.4). The model including these variables, and the main effects of wind speed and wind direction, explained 17.5% of the deviance in the data. With time elapsed since sunrise held constant at four hours, and wind speed of an offshore wind held constant at 25.4 m.s⁻¹, the final model predicted that the probability of MF occurring across both coasts decreased from 0.87 to 0.06 as tide height increased from 0.131 to 2.201 m above chart datum (Fig. 4.4A). The probability of MF dropped below 0.1 (i.e., MF would be expected during one in ten hours under these conditions) at a tide height of 1.681 m above chart datum. The widest confidence

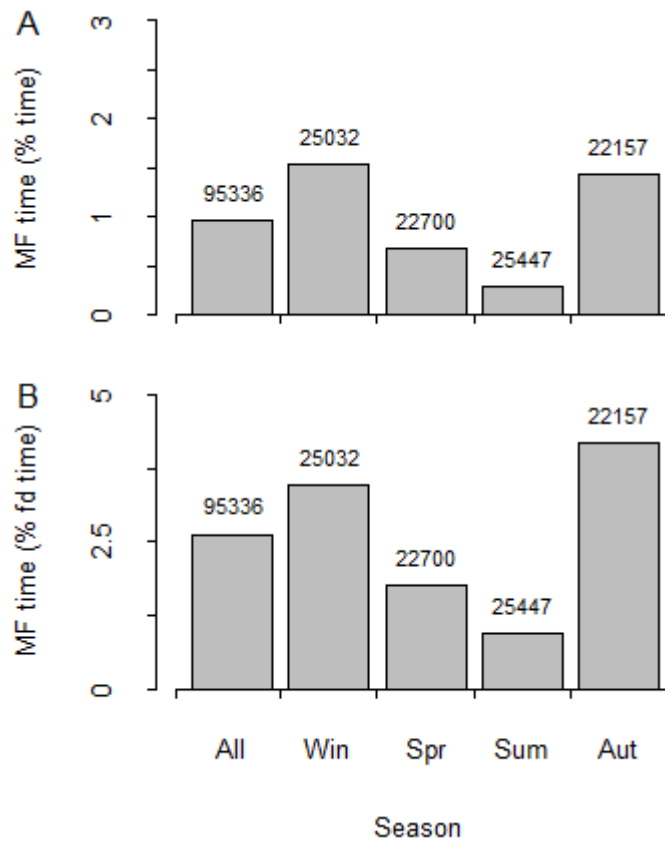


Fig. 4.1. Average time KK baboons spent feeding on marine foods as a percentage of time available (A) and total feeding time (B) available to each baboon. Values in graph B were calculated from those in graph A and previously determined activity budgets (see Chapter 2). Numbers above bars indicate observation time (in minutes) during each season; Win = winter, Spr = spring, Sum = summer, Aut = autumn.

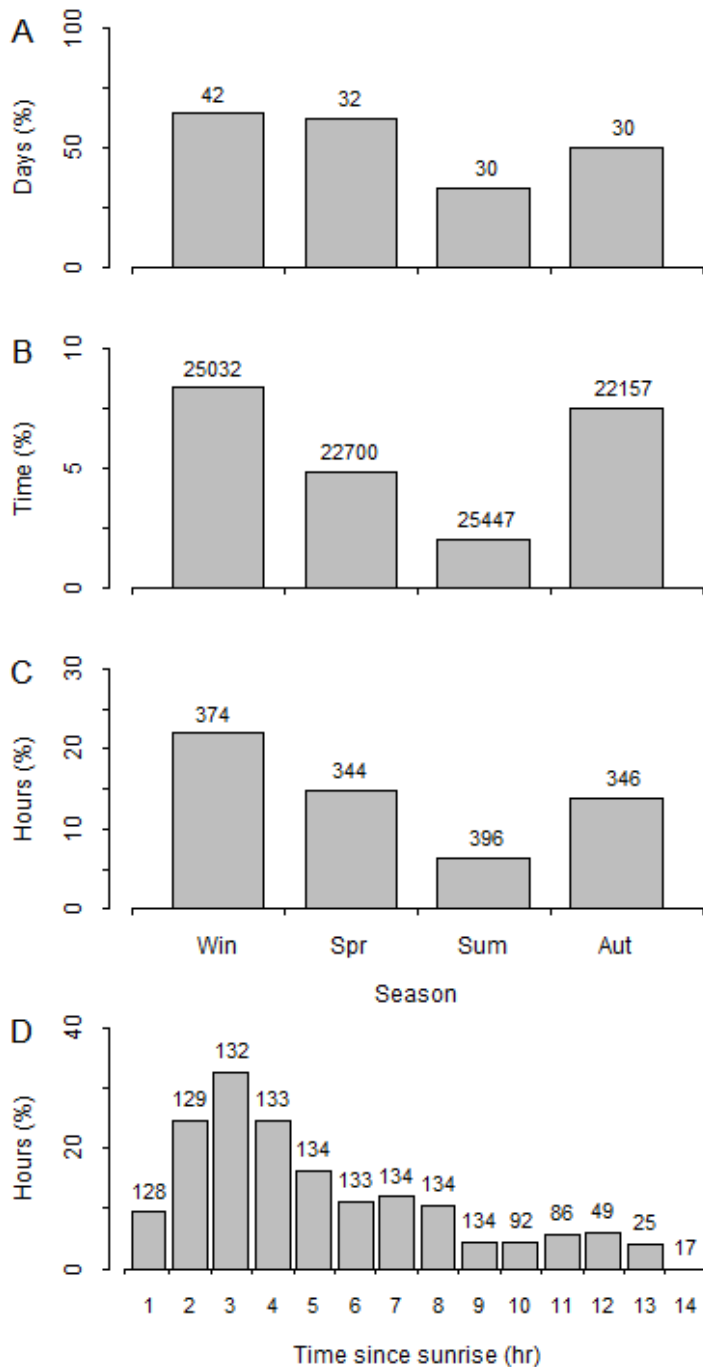


Fig. 4.2. Percentages of days (A), total daylight time in minutes (B) and total numbers of observation hours (C) in different seasons, and percentages of hours at different times of day (D), during which marine foraging occurred. Numbers above bars indicate sample sizes; Win = winter, Spr = spring, Sum = summer, Aut = autumn.

interval around the mean predicted probability of MF, for a given tide height, was 0.356 (with tide height at 1.011 m above chart datum).

The probability of MF across both coasts varied considerably through daylight hours (Fig. 4.4B). With tide height held constant at 0.131 m above chart datum, and wind speed of an offshore wind held constant at 25.4 m.s⁻¹, the model predicted that the probability of MF increased from 0.65 at the turn of the first hour after sunrise, to 0.87 four hours after sunrise. Predicted probability then decreased at a mildly fluctuating, but moderate rate with increasing time, until 10 hours after sunrise ($p_{T=10} = 0.70$), after which it decreased rapidly again ($p_{T=14} = 0.39$). The predicted probabilities later in the day (especially from 10 hours after sunrise onwards) were however less reliable than those earlier in the day as indicated by greater width of 95% confidence intervals (95% CI). This was a

result of there being fewer observed values in the latter part of the day due to seasonal variation in day length—mean (\pm SD) day lengths in winter and summer were 9.9 (\pm 0.1) and

14.1 (± 0.2) hours, respectively.

The effect of increasing wind speed on probability of MF was dependent on wind direction (Table 4.4)—probability of MF increased with increasing offshore wind speed (Fig. 4.4C), but was not significantly affected by wind speed if the wind was blowing onshore. With tide height held constant at 0.131 m above chart datum, and time since sunrise held constant at four hours, probability of MF during a given hour increased from 0.72 in still conditions to 0.87 as offshore wind speed increased to $25.4 \text{ m}\cdot\text{s}^{-1}$. The reliability of these predictions

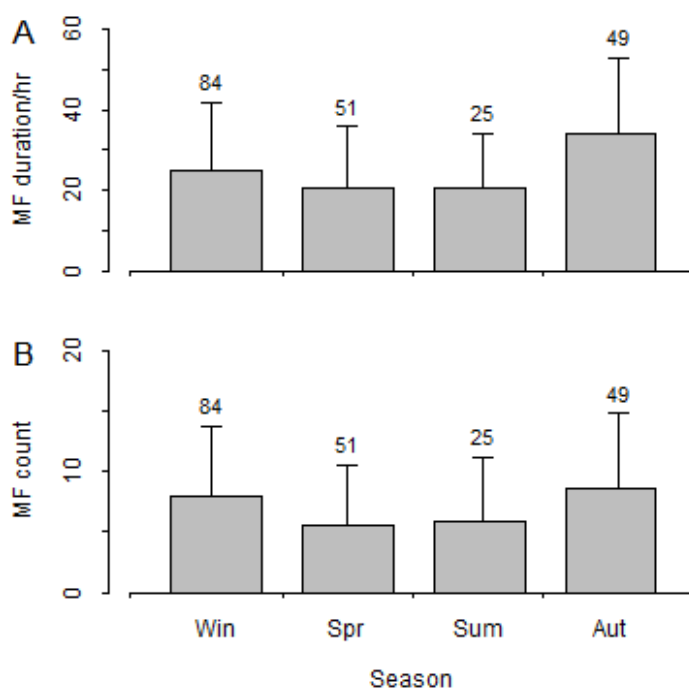


Fig. 4.3. Average duration (A) and average count values (B) within hours during which marine foraging occurred in each season. Error bars indicate standard deviation; numbers above bars indicate sample sizes (no. hrs); Win = winter, Spr = spring, Sum = summer, Aut = autumn.

Table 4.4. Summary statistics for predictor variables assessed for significance in GAMs fitted to probabilities of marine foraging¹

Predictor variable	Both coasts		Predictor variable	West coast	
	χ^2	<i>p</i> -value		χ^2	<i>p</i> -value
te(Tide height)	75.843	< 0.001	te(Tide height)	60.386	< 0.001
te(Time since SR)	29.305	< 0.001	te(Time since SR)	13.966	< 0.01
te(Wind speed)	3.941	0.047	te(Swell height)	8.588	< 0.01
Wind direction	2.698	0.100	te(Wind speed)	0.000	0.999
te(WSP: Off)	5.862	< 0.05	Wind direction	1.892	0.169
te(WSP: On)	0.056	0.813	te(WSP: Off)	0.085	0.771
			te(WSP: On)	3.623	0.298
			ti(TDH \times SWH)	5.299	< 0.05

¹te = tensor spline smooth; Time since SR = time (in hours) since sunrise; WSP = wind speed; TDH = tide height; SWH = swell height; Off = off-shore wind; On = on-shore wind; significant values ($p < 0.05$) are in boldface.

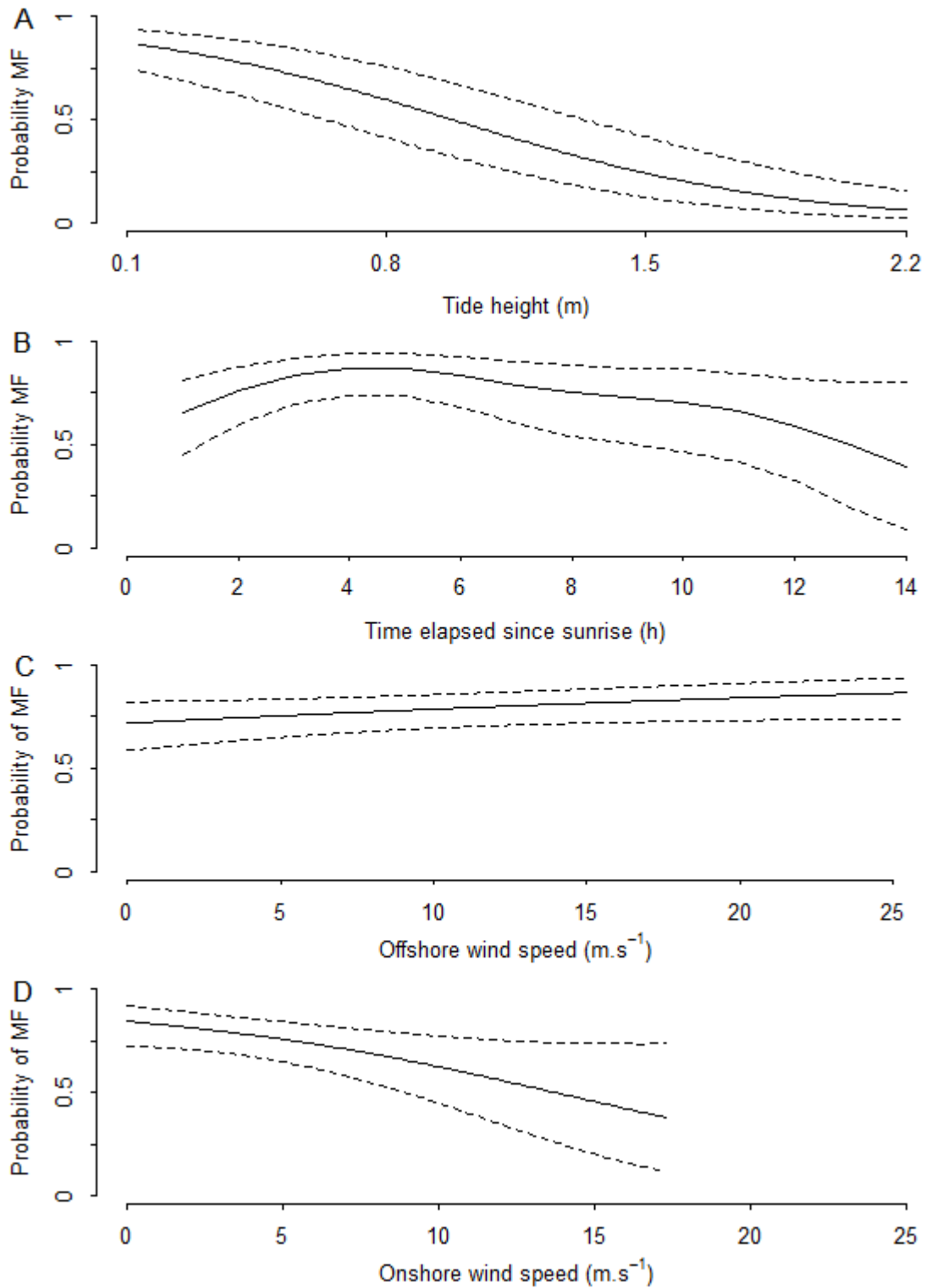


Fig. 4.4. Relationships between predicted probability of marine foraging (across both coasts) and tide height (A), time elapsed since sunrise (B), offshore wind speed (C) and onshore wind speed (D) based on results of a GAM. Dashed lines indicate 95% confidence intervals.

varied little with changes in wind speed, as the width of the 95% CI remained similarly small throughout the range of offshore wind speeds recorded.

West coast

The interaction between tide height and swell height, and time since sunrise, were significant predictors of probability of MF on the west coast (Table 4.4). The model that included these variables, as well as the main effects of tide height, swell height, wind speed and wind direction, and the interaction between wind speed and wind direction, explained 33.1% of the deviance in the data. Similar to the probability of MF across both coasts, the predicted probability of MF on the west coast generally decreased with increasing tide height (Fig. 4.5A). The rate of decrease varied considerably with tide height however, and, perhaps more importantly, was affected by swell height. When tide heights were extremely low, swell height had little effect on probability of MF (probability actually increased with decreasing swell height when tide heights were at their lowest). Through the range of intermediate tide heights on the other hand, the rate at which the probability of MF decreased with increasing tide heights, increased with increasing swell height. Thus, probabilities of MF (which were greater than 0.90 across the entire range of swell heights when tide height was at its minimum) were 0.89 and 0.20 with swell heights of 1.11 and 6.26 m respectively. Also, the tide height at which probability of MF dropped to little more than zero decreased with increasing tide height. Finally, when swell height was at its lowest, probability of MF did not fall below 0.10, even when tide height was at the maximum observed value.

As with the output from the model predicting MF probability across both coasts, the predicted probability of MF on the west coast peaked in the latter part of the morning (four hours after sunrise) and then decreased. The main differences between the outputs of the two models were that the predicted probabilities were higher under optimal conditions (minimum observed tide height, maximum observed swell height, and still conditions with wind direction set as on-shore), and that the range of values was much smaller, on the west coast (Fig. 4.5B). Also, the rate of decrease through the latter part of the day was almost constant in the predicted probability on the west coast only (Fig. 4.5C). The output of this model suggested that KK baboons were highly likely to exploit marine foods at any time of day if they were near the west coast when conditions were optimal (see above). If these conditions were met during the fourth hour after sunrise, it was a near certainty that the baboons would have exploited marine foods. The reliability of these inferences might be questioned however, as the 95% CI around the mean were wide, particularly during the latter part of the day.

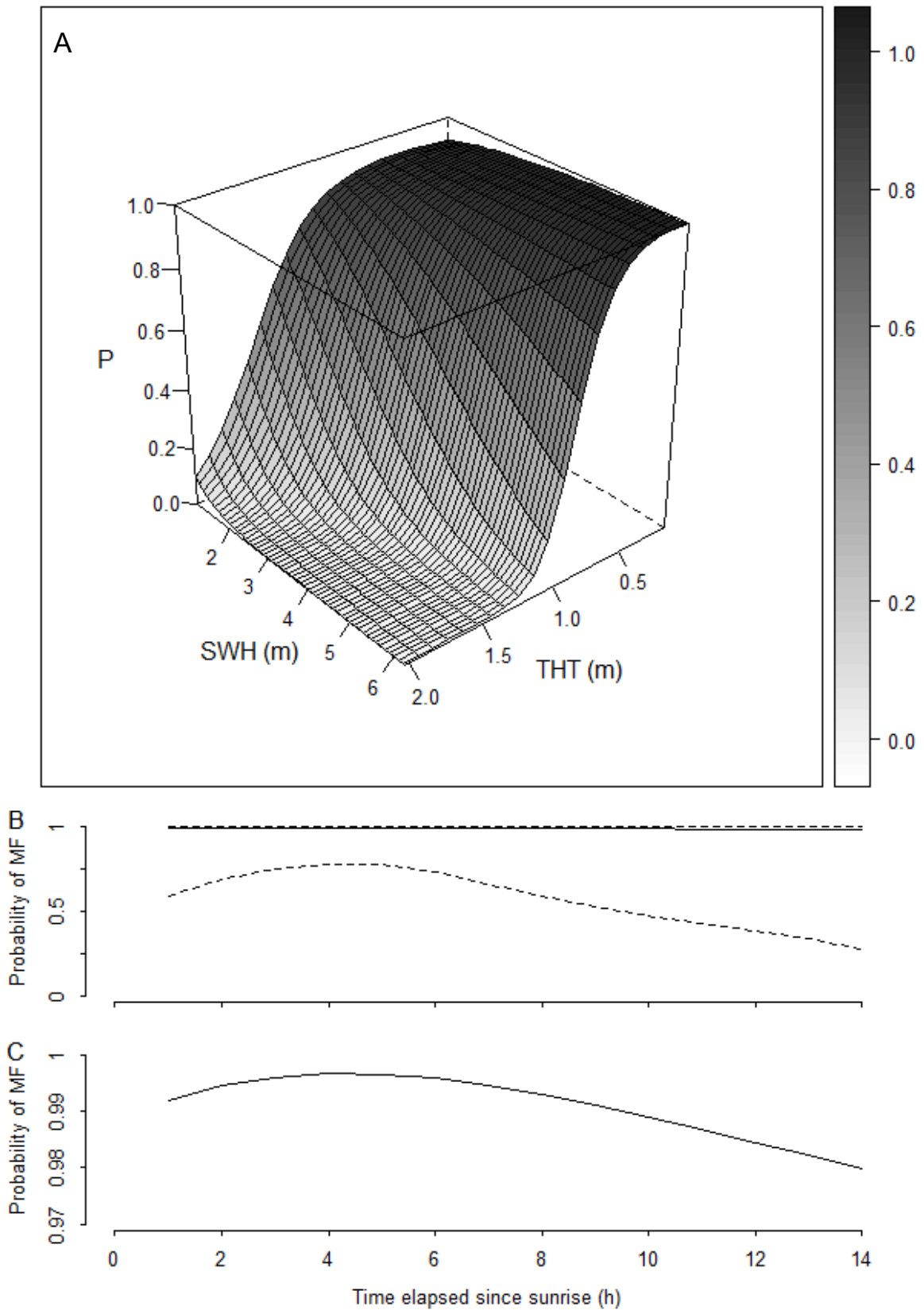


Fig. 4.5. Relationships between predicted probability of marine foraging (on the west coast) and tide- and wave height (A), and time elapsed since sunrise showing the full range of probabilities (B), and showing a smaller range of probabilities (C), based on results of a GAM. P = probability; WVH = wave height; TDH = tide height; dashed lines indicate 95% confidence intervals; note the difference in scale on the vertical axis

Proportion models

East and west coasts

Season, coast and tide height were significant predictors of the average proportion of the troop MF during a given hour (Table 4.5), and were included in the final model. This model explained 13.5% of the deviance in the data. The predicted average proportion of the troop decreased with increasing tide height (A), similar to the predicted probability of MF (see Fig. 4.6). The predicted average proportion of the troop MF decreased rapidly as tide height increased from 0.131 (the minimum observed tide height) to 0.561 m above chart datum and from 0.771 to 1.141 m above chart datum. The model predicted that the maximum predicted average proportion of the troop marine foraging (which would occur when the troop marine foraged on the east coast, in autumn, with tide at 0.131 m above chart datum), was 0.26. Differences between upper and lower limits of confidence intervals were highest at the extreme lower and upper tide height values, but did not exceed 0.15 at any tide height.

The model predicted that the average proportion of the troop MF during MF hours was higher in autumn than in any other season (Fig. 4.6B). During spring and summer MF hours, the predicted average proportions of the troop feeding on marine foods were similar, and were markedly lower than during MF hours in winter and autumn. Even under optimal conditions (minimum observed tide height while the troop forages on the east coast) the predicted average proportions during spring and summer MF hours were less than 0.13. This means that during those seasons, even under optimal conditions, the intensity of MF was low. The predicted average proportion of the troop that marine foraged during a given hour was higher if the baboons were foraging on the east coast than on the west coast (Fig. 4.6C). If the troop marine foraged on the east coast during autumn, with the tide at the lowest observed

Table 4.5. Summary statistics for predictor variables assessed for significance in GAMs fitted to hourly average proportions of the troop marine foraging¹

Predictor variable	Both coasts		Predictor variable	West coast	
	χ^2	<i>p</i> -value		χ^2	<i>p</i> -value
te(Tide height)	45.85	< 0.001	te(Tide height)	36.48	< 0.001
Season	72.50	< 0.001	te(Swell height)	10.11	< 0.05
Coast	26.21	< 0.01	te(Wind speed)	11.97	< 0.05
			Season	68.23	< 0.001
			Wind direction	5.712	< 0.05

¹te = tensor spline smooth; significant values (*p* < 0.05) are in boldface.

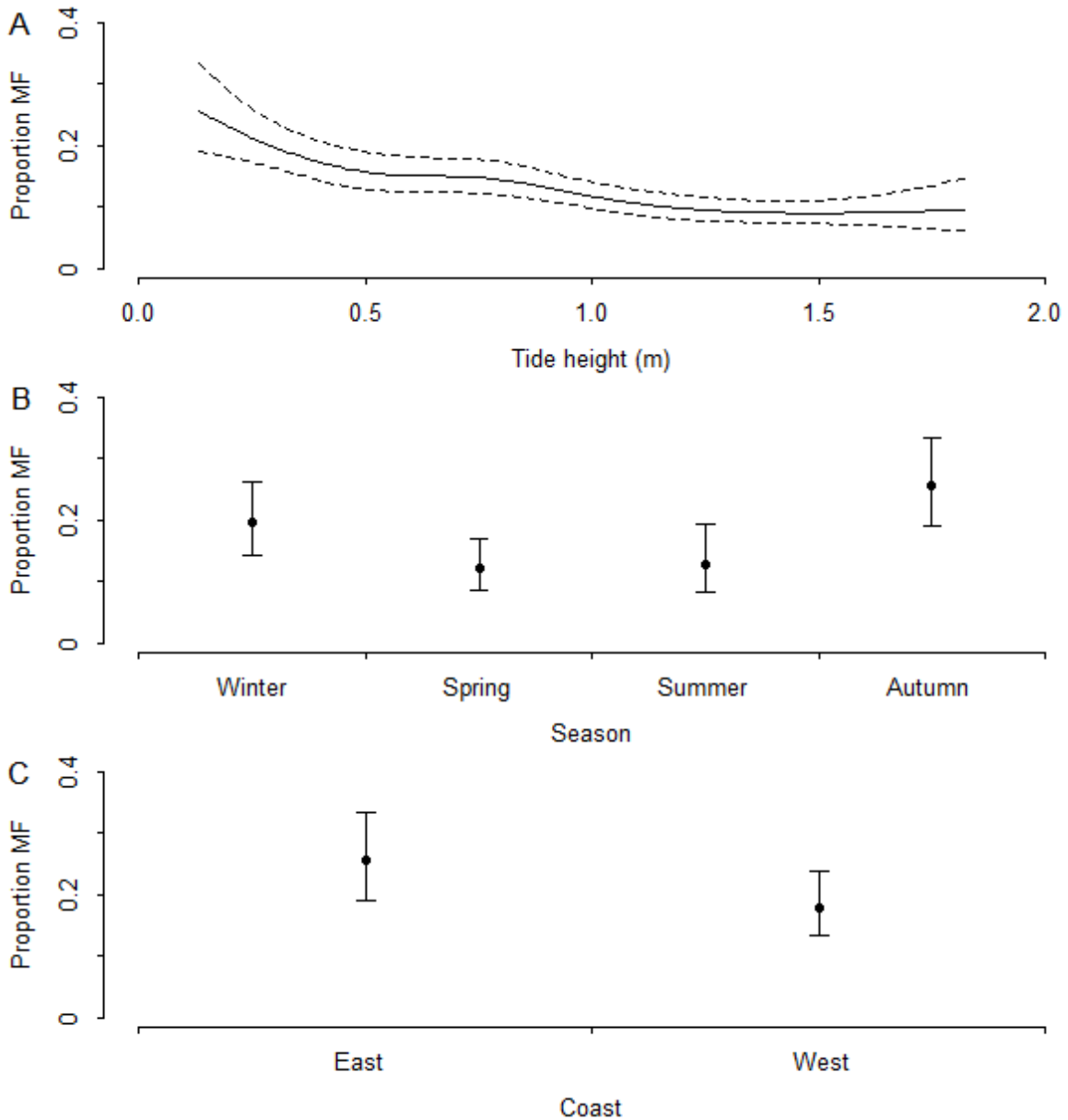


Fig. 4.6. Relationships between predicted average proportion of the troop marine foraging during a given hour (on both coasts) and tide height (A), season (B) and coast (C), based on results of a GAM. Dashed lines (in A) and error bars (in B – C) indicate 95% confidence intervals.

height above chart datum, the model predicted that the average proportion of the troop doing so was 0.26.

West coast

Tide height, swell height, season, wind speed and direction were significant predictors of average proportion of the troop MF on the west coast during MF hours (Table 4.5). The model that included these predictor variables explained 21.6% of the deviance in the data. As in the model described above, the general pattern is that the predicted average proportion

decreased with increasing tide height (Fig. 4.7A). There was however a small increase in the predicted proportion of the troop MF (0.26 to 0.30 under optimal conditions) as tide height increased from 0.671 to 0.891 m above chart datum. The minimum predicted proportion (at a tide height of 1.391 m above chart datum) was just 0.05. The maximum predicted average proportion (at a tide height of 0.131 m above chart datum) was 0.48, which is markedly higher than the maximum proportion predicted by the model across both coasts. The 95% CI around the mean predicted proportions generated by this model were wider than those generated by the model of hours on both coasts (Fig. 4.6 and Fig. 4.7; both coasts model width of 95% CI mean \pm SE: 0.06 ± 0.0016 , west coast model width of 95% CI mean \pm SE: 0.26 ± 0.0049).

The model predicted that as swell height increased, the predicted proportion of the troop MF decreased through the lower range of swell heights (< 3.52 m) and then increased slightly as swell height increased from 3.52 to 4.61 m (Fig. 4.7B). The minimum predicted average proportion of the troop MF was 0.33 (with 3.52 m high swell). The increase in predicted proportion as swell heights increased beyond this value was accompanied by a slight increase in the width of the 95% confidence intervals. This increase was due to a low number of samples at the maximum extreme of tide heights observed during west coast MF hours.

As wind speed increased, the model predicted that the average proportion of the troop MF during a given hour would first increase (from still conditions to wind speeds of 3.68 m.s^{-1}), then decrease (as wind speeds increased from 3.69 to 11.62 m.s^{-1}) and then increase again (as wind speed increased to 21.20 m.s^{-1} ; Fig. 4.7C). The minimum predicted proportion (0.28) was predicted when wind speed was 11.62 m.s^{-1} . The width of the confidence intervals around the mean predicted proportions changed little with increasing wind speed for the most part, but increase slightly at the upper extreme of wind speeds observed during the study.

The seasonal pattern in west coast MF hours was very similar to that predicted across both coasts (Fig. 4.7D). The main difference between the outcomes of the two models was that the predicted proportion of the troop MF during MF hours on the west coast was higher than those predicted by the model across both coasts (range $P_{W \text{ Coast}} - P_{E+W \text{ coast}}$: $0.05 - 0.23$). As with tide height, the model of MF on the west coast generated wider 95% CI around these predicted proportions than the model that included hours on both coasts (Fig. 4.6B and Fig. 4.7D; both coasts model width of 95% CI mean \pm SE: 0.11 ± 0.012 , west coast model width of 95% CI mean \pm SE: 0.34 ± 0.037). The highest predicted proportion for hours

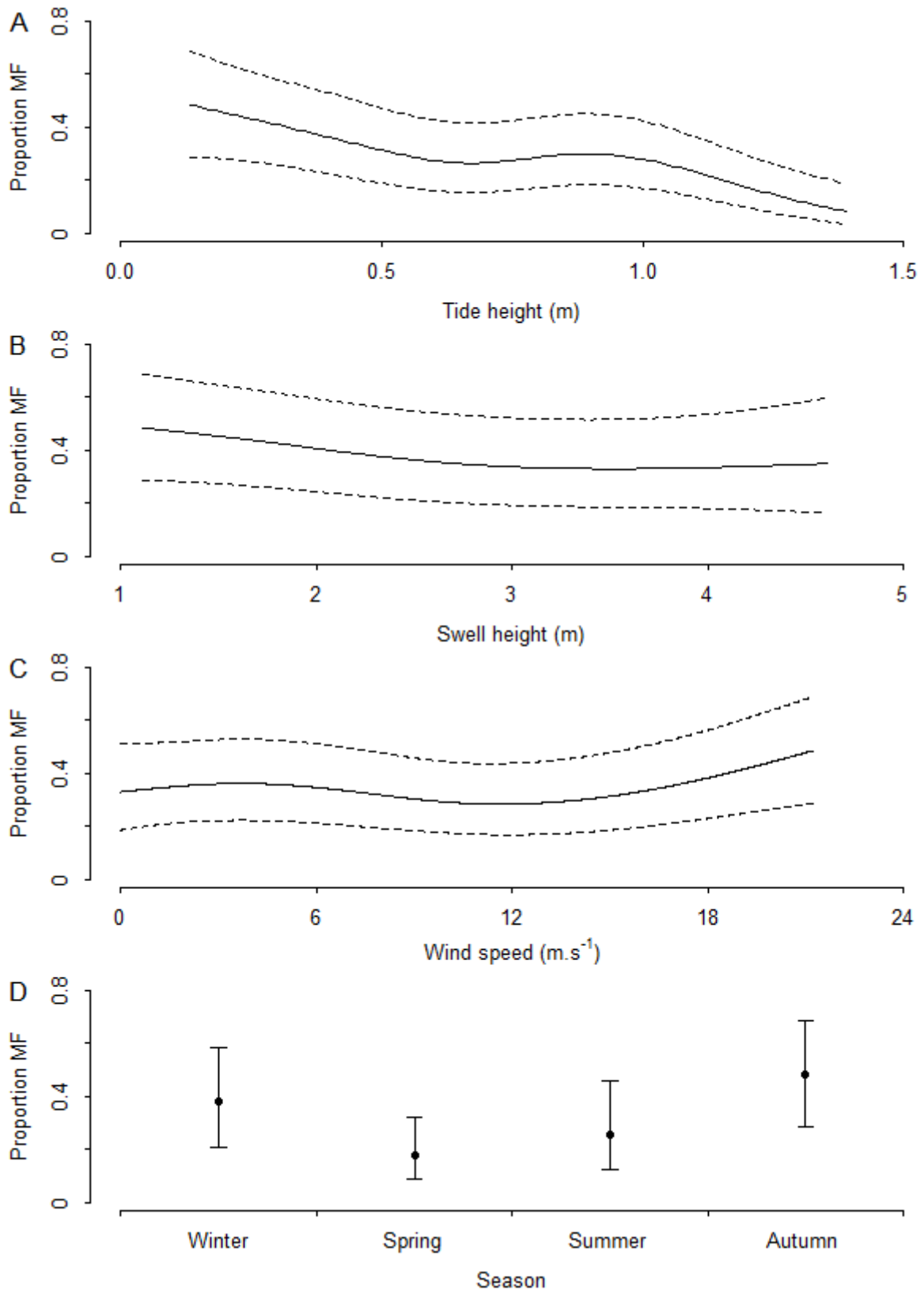


Fig. 4.7A – D. Relationships between predicted average proportion of the troop marine foraging during a given hour (on the west coast) and tide height (A), swell height (B), wind speed (C) and season (D), based on results of a GAM. Dashed lines (in A – C) and error bars (in D) indicate 95% confidence intervals.

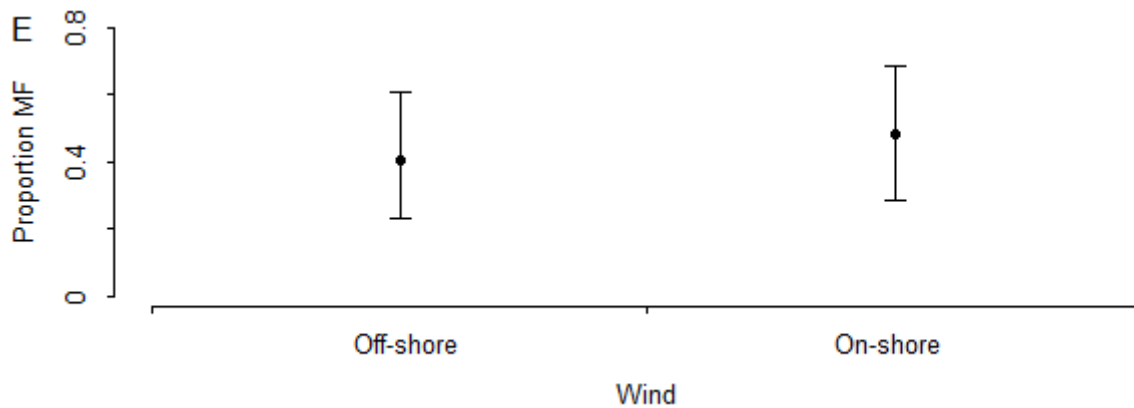


Fig. 4.7E. Relationship between predicted average proportion of the troop marine foraging during a given hour (on the west coast) and wind direction relative to the shore. Error bars indicate 95% confidence intervals.

during which the troop was MF on the west coast (which was predicted in Autumn) was 0.48, which was 0.23 higher than the predicted proportion across both coasts.

The model predicted that a larger proportion of the troop marine foraged during MF hours in which on-shore winds were blowing, than during hours in which offshore winds were blowing (Fig. 4.7E). With tide height and swell height at their respective minima, the predicted proportions in Autumn were 0.40 and 0.48, with offshore and on-shore winds respectively. There was however considerable overlap between the 95% confidence intervals around the means.

DISCUSSION

On average, across all four seasons, KK baboons spent just 1.0% of the total time available feeding on marine organisms in the intertidal zone. Based on previously estimated activity budgets (which indicated that feeding time comprised 37.2% of percentage time activity budgets; see Chapter 2), this equates to just 2.6% of feeding time allocated to exploiting marine invertebrates. This finding is consistent with findings at other research sites where baboons have been shown to feed almost exclusively on plant foods, and only very occasionally on animals (Hamilton et al., 1978; Whiten et al., 1987; Okecha and Newton-Fisher, 2006). Baboons have however been shown to favour plant parts (e.g. seeds; Jones and Earle, 1966; Altmann et al., 1987) that are rich in protein relative to other tissues, and other locally available plant foods (Whiten et al., 1991; Barton and Whiten, 1994). These food items may enable baboons to maintain a constant daily proportional intake of dietary protein without consuming large amounts of animal food (Johnson et al. 2013). However, given that

animal tissues are, by and large, rich in protein (DeFoliart, 1975; Defoliart et al., 1982; Calvert, 1985; Smith and Partridge, 2004), and that many plant parts consumed by Peninsula baboons are low in macronutrients such as protein (see Chapter 2), the small contribution of animal foods (inferred from feeding time values) to KK troop's diet was unexpected.

Although relatively small throughout the year, the proportion of the troop's feeding time allocated to exploiting marine foods did fluctuate seasonally. Not surprisingly, these fluctuations were matched by differences in the percentages of days and hours during which the troop marine foraged, as well as the frequency and duration of MF bouts. Changes in time allocated to feeding on different foods are typically linked to variation in either the availability or quality of foods in primates' home ranges (Agetsuma and Nakagawa, 1998; Di Fiore and Rodman, 2001; McConkey et al., 2003; Alberts et al., 2005). Indeed, baboons elsewhere include large amounts of animal tissue, including invertebrates (Hamilton et al., 1978), in their dietary intake when abundances are unusually high. The results presented here therefore suggest that either availability or quality of marine foods consumed by the baboons increased (or, conversely that terrestrial foods exhibited declines in availability or quality), through autumn and winter. Nevertheless, the proportions of time allocated to feeding on marine foods remained small during these seasons. The results reported by Hamilton et al. (1978) suggest that baboons are capable of including higher proportions of animal foods in their diet than has been observed in KK troop. This begs the question: are there other factors limiting their exploitation of this resource?

Abiotic factors limiting MF

The probability of KK baboons ingesting marine foods, and the intensity of exploitation within a given hour when they did so, were, at least in part, determined by tide height—both quantities decreasing with increasing tide height. This finding corroborates part of Hall's (1963) statement that Peninsula baboons marine forage “when wind and tide height allow easy access to intertidal rock pools and the sea verge.” Thus, it seems that periodic submersion of marine foods limits baboons' access to these foods, thereby decreasing the probability and intensity of marine food exploitation. The two studies that have quantified the effects of tidal cycles on exploitation of marine foods by other maritime mammals (*sensu* Carlton and Hodder, 2003), revealed that Arctic foxes (*Alopex lagopus*) only forage for marine foods when the tide has almost fully retreated (Nielsen, 1991) and mink (*Mustela vison*) spend less time feeding on marine foods, and feed in less productive high-shore habitats, when the tide is high (Bonesi et al., 2000). KK baboons are therefore typical of

maritime mammals in being limited to some extent in their exploitation of marine foods by advancing tides.

The limiting effects of advancing tides on intensity of exploitation could be particularly pronounced because marine resources are clumped foods (*sensu* Shopland, 1987). As tides rise and further reduce the availability of these foods, the baboons might experience increased within-group contest competition (Barton and Whiten, 1993; Koenig, 2002). Further research, involving investigation of feeding rates in marine intertidal- and terrestrial habitats, and rates of agonistic encounters (which could not be carried out in this study), would however be required to determine whether or not this is the case.

The effect of tide height on probability of MF is not unaffected by other variables, as evidenced by the significance of the tide height–swell height interaction. Predictably, and in line with Hall’s (1963) observation that baboons on the shore “often had to dash away to avoid a wave,” probability of MF decreased more rapidly with increasing tide height as offshore swell heights increased. There are two likely explanations for this. The first is that a smaller area of the intertidal zone is exposed (and the baboons therefore have access to fewer marine food items) when larger swells approach the coast, because runup increases with wave size (Raubenheimer and Guza, 1996). The second likely explanation for the above-mentioned pattern is that baboons reduce their risk of drowning by not feeding in the intertidal zone when the likelihood of being washed offshore is great. Drowned baboons occasionally wash up on the Peninsula coast, and Hall (1962) suggested that these animals are most likely washed offshore by unexpectedly large waves while foraging in the intertidal zone. This seems a plausible explanation as similar events involving humans have occurred on the Peninsula (Brundrit, 2009). Baboons are capable of swimming, but they are not particularly strong swimmers (Busse, 1980) and being washed offshore might therefore result in death by drowning. The likelihood of a baboon being washed offshore should increase as swell height increases, but only if said baboon is foraging in close proximity to the waterline. As tide height increases so baboons must feed increasingly close to the waterline if they are to obtain marine foods, because the area of the intertidal zone that is exposed decreases. It is therefore plausible that the effect of the tide height–swell height interaction on probability of MF is, at least in part, a result of increased risk of drowning that arises with concomitant increases in tide height and swell height.

The general decline in intensity of MF with increasing swell height can almost certainly be explained by the same wave-related factors that limit probability of marine foraging (described above). The slight increases in predicted MF intensity on the west coast,

as swell height increased beyond 3.52 m, and also as tide height increased from 0.671 to 0.891 m above chart datum, are more difficult to explain than the general patterns. One possible explanation is that these anomalies were caused by an undetected interaction between wave height and tide height. The significance of such an interaction seems likely in light of the interaction described in the model of probability of MF on the west coast. If such an interaction was in fact significant, the severity with which advancing tides limit intensity of MF could be expected to increase with increasing swell heights, and vice versa. Unfortunately, the sample size for this model was too small to allow for testing of the significance of such an interaction, because only hours during which the troop foraged on the west coast were included in the model.

Explaining the relationship between probability of MF and time elapsed since sunrise is somewhat more difficult than explaining the trends mentioned above (anomalies aside). The relatively low probabilities in the early hours of the morning and the late hours of the afternoon are likely the results of two other behavioural patterns. Firstly, KK baboons, like baboons elsewhere (Altmann and Altmann, 1970), tend to spend time grooming and socialising at their sleeping sites in the early morning and, to a lesser extent, the evening (see Chapter 2). Time spent grooming is important for maintaining and strengthening social bonds (Silk, 2007), which in turn enhance longevity (Silk et al., 2010) and, ultimately, fitness (Silk et al., 2003, 2009; Wittig et al., 2008; Sapolsky, 2009). The importance of grooming is emphasised by baboons' reluctance to reduce time spent engaged in this activity, even when nutrient-stressed (Alberts et al., 2005; Chapter 2). In light of this, it is unlikely that the baboons would sacrifice time spent grooming in the early morning or late evening in order to increase time spent feeding on marine foods, irrespective of conditions in the intertidal zone.

Secondly, the baboons' use of specific sleeping sites imposes limitations on their ranging (Rasmussen, 1979; Whiten et al., 1987), as they start and end each day's journey at either cliffs or trees that are large enough to accommodate all members of the troop (DeVore and Hall, 1965; Altmann and Altmann, 1970). KK troop used 16 different sleeping sites during the course of this study, none of which were on the actual coast. Thus, no matter which sleeping site they used, KK baboons were required to travel hundreds of metres at least between sleeping sites and locations at which they might obtain marine foods. It is therefore plausible that a combination of this limitation on ranging behaviour, and the baboons' tendency to groom in the early morning and late afternoon, accounts for the lower probabilities of MF at the beginning and end of the day.

The higher probability of MF in the mid- to late morning (relative to the afternoon) could also be linked to the location of sleeping sites. Like baboons elsewhere (Hamilton et al., 1976; Hausfater and Meade, 1982; Zinner et al., 2001; Pebsworth et al., 2012), the KK baboons use rocky outcrops, cliffs, and large trees as sleeping sites. Of the 16 sleeping sites used by KK baboons during the study period, 12 are at relatively high altitudes (in the context of their home range) and offer unobstructed views of the shoreline. On days when they have slept at these sites, KK baboons may be capable of discerning (through a combination of olfactory and visual cues) whether or not environmental conditions are potentially suitable for MF, prior to leaving the sleeping site. In other systems, such direct assessment is unnecessary, as changes in food availability over weeks or even months are more common (Rowell, 1966; Alberts et al., 2005). In such systems baboons' ability to learn from experience (Fagot and Cook, 2006) and build cognitive maps of their home range means that they are able to engage in goal-oriented ranging behaviour to maximise their exploitation of dispersed food patches (Noser and Byrne, 2007, 2010). Changes in marine food availability however occur over the course of hours, and the temporal window of peak availability shifts on a daily basis, due to tidal variations alone (Palmer, 1995). Thus, the success of goal-oriented ranging behaviour is contingent on the baboons' ability to determine favourable environmental conditions in the marine intertidal zone from afar. The location of the majority of their sleeping sites means that they are more likely to be aware of favourable conditions in the morning, which could explain the higher probability of MF at this time of day.

The effect of offshore wind speed on probability of MF is unlikely to be a manifestation of a direct influence of wind on the baboons themselves. Wind may affect animals directly by, for example, increasing energetic costs of thermoregulation (Ames and Insley, 1975; Walsberg and Wolf, 1995), but such an effect would be largely independent of wind direction. Offshore wind speed must therefore affect probability of marine foraging by acting on other variables that influence this quantity. In this case, it seems likely that strong offshore winds mitigate the limiting effects of increasing tide- and wave height to some extent. Wind has profound effects on behaviour of oceanic waves (Neshyba, 1987), and also affects when and how waves break as they approach the shore (Douglass, 1990; Fedderson and Veron, 2005; Holthuijsen, 2008). The effects of moderate-to-strong ($> 4 \text{ m}\cdot\text{s}^{-1}$) offshore winds on breaking wave behaviour and runup have not been quantified, but it has been shown that wave height (Masselink and Pattiaratchi, 1998) and runup elevation (Ward et al., 1996, 1998) increase with increasing onshore wind speeds above $6.5 \text{ m}\cdot\text{s}^{-1}$. This is not surprising considering the role of wind stress in wave generation and behaviour (Neshyba, 1987) and

the relationship between wind speed and drag coefficient (Smith and Banke, 1975; Smith, 1988). In light of the above (and the fact that strong offshore winds may generate currents directed offshore; McCreary et al., 1989), it seems highly likely that strong offshore winds should cause a decline in wave height, and reduce runup elevation. These effects could explain the observed pattern as more of the intertidal zone should be exposed, and the threat of being washed offshore should be reduced, as offshore wind speed increased.

The effect of wind speed on intensity of MF is also likely a manifestation of the effect of wind on wave behaviour and runup. The general pattern of change in MF intensity is similar to that of probability (an increase with increasing wind speed), but there was a decrease in intensity of marine foraging through a range of intermediate wind speeds. The irregularity could be a result of an undetected interaction between wind speed and wind direction. This seems likely, in light of the significance of the interaction in the model of probability across both coasts, and also the difference in the effects of light onshore and offshore winds on wave behaviour (Douglass, 1990). It is important to note that the ranges, and distributions, of wind speeds recorded for off-shore and on-shore winds during this study were markedly different. The highest speed recorded for an onshore wind during an hour in which the troop fed on marine foods was 8.4 m.s^{-1} (this was 12.8 m.s^{-1} lower than the highest speed recorded for an offshore wind). Thus, the proportion of recorded wind speeds comprised of values for onshore winds was higher in the lower part of the recorded range, and the higher wind speeds recorded ($> 8.4 \text{ m.s}^{-1}$) were those of offshore winds only. It is therefore plausible that the decline in predicted intensity of MF as wind speed increased from 3.7 m.s^{-1} to 11.6 m.s^{-1} reflects a change in the proportion of speeds recorded for onshore wind speeds through this range. The increase in predicted MF intensity with increasing wind speeds above 12.5 m.s^{-1} is likely driven by the same factors implicated above in the increase of probability of MF with increasing offshore wind speed.

The explanation above is given further credence by the small, but significant difference between predicted intensity of MF under the influence of offshore- and onshore winds. This difference is likely caused by the influence of wind on waves prior to breaking and the perceived threat to the baboons on the shore. If wind speeds are low ($< 3.9 \text{ m.s}^{-1}$) waves break earlier and in deeper water under the influence of onshore winds, and later and closer to the shore under the influence of offshore winds (Douglass, 1990). As a result of the difference in depth of breaking mentioned above, waves exhibit lower crest elevation under the influence of light onshore winds (Douglass, 1990). This seems the more likely effect of onshore winds during the hours included in the model of MF intensity on the west coast,

because wind speed of onshore winds during hours included in this model did not exceed 8.4 m.s⁻¹ (Masselink and Pattiaratchi, 1998). If wave height and proximity to the shore at breaking point are seen as indicators of the potential threat of being washed offshore, baboons might perceive the threat posed by breaking waves as less serious when waves are affected by light onshore winds.

The above-mentioned abiotic factors clearly affect exploitation of marine foods by KK baboons, but the relatively low percentages of deviance explained by the models suggest that other factors also play some role in determining how and when marine foods are exploited.

Biotic factors that affect MF and future study

It has been shown that baboons in other regions alter their diets in response to seasonal changes in food availability (Alberts et al., 2005). In the case of the KK baboons, the seasonal change in diet could be driven by relative changes in terrestrial and marine food availability and nutritional quality (Van Erkom Schurink and Griffiths, 1991; Van Doorn et al., 2010; see Chapter 2). The results presented in Chapter 2 suggest that the nutritional rewards offered by marine foods vary little seasonally, but it seems likely that this is an artefact of limitations of the dataset—the condition of marine intertidal organisms is known to fluctuate markedly through time (Branch, 1974; Van Erkom Schurink and Griffiths, 1991; Kreeger, 1993; Steffani and Branch, 2003 a). Future research involving detailed surveys of food availability in marine and terrestrial Peninsula habitats would be necessary to determine which of these factors affects how and when Peninsula baboons exploit marine foods. Such research would also provide insight into the differences in MF intensity across the two coasts. It is important to note however, that due to the heterogeneity of density and condition of marine invertebrates along the Peninsula's coasts (Branch, 1974; Steffani and Branch, 2003b; Xavier et al., 2007), surveys of marine foods would have to be carried out at the myriad sites where Peninsula baboons marine forage.

Other properties of the foods consumed by these baboons should also be investigated, as it is possible that the nature of the animal foods available to KK baboons precludes more extensive exploitation. Marine invertebrates typically accumulate certain elements in their tissues over time, with the result that concentrations of elements such as iodine may attain extraordinarily high levels (Galtsoff, 1934). Consumed in small to moderate quantities, iodine is beneficial to primates, as it plays an important role in various physiological functions, particularly during natal and neonatal development (Mano et al., 1985; Cunnane and

Crawford, 2003). It becomes toxic however when large amounts are consumed (Zemlyn et al., 1981; Backer and Holloweii, 2000), and this alone may moderate baboons' intake of marine invertebrates. To the best of my knowledge, no study has attempted to determine how much iodine primates might safely consume, although it has been suggested that upper limits are markedly higher than that for humans (Oftedal et al., 1991). Marine foods may comprise up to 20% of the diet of crab-eating macaques (*Macaca fascicularis*) in the mangrove forests of Vietnam (Son, 2003), suggesting that marine foods may comprise larger proportions of primate diet than that observed in KK baboons. Drawing parallels between the macaques and baboons may be of limited use however as the two feed on different types of marine foods (Hall, 1962, 1963; Davidge, 1978; Son, 2003) and different marine animals accumulate iodine to different extents (Galtsoff, 1934). The chemical composition of the organisms consumed by Peninsula baboons should therefore be investigated in future studies.

The lack of an effect of season on probability of marine foraging is surprising, given the seasonal fluctuation in frequency of marine foraging bouts reported above. This finding is however almost certainly a result of the modelling approach employed here. Any seasonal effects on time spent in close proximity to the intertidal zone were excluded from the model because I excluded hours during which the troop was further than 1063 m from the coast (in order to test for the immediate effects of conditions on probability of MF). Considering that the troop made use of different parts of their full home range during each season (see Chapter 2), it seems highly likely that this would account for the absence of a seasonal effect on the probability of marine foraging.

If circumstances on the Peninsula change in the future, and more intensive research protocols are allowed, focal sampling of baboon behaviour (see Altmann, 1974) should be used to determine feeding rates for different foods at the level of the individual. The combination of data regarding the availability of different foods, the rates at which these foods are ingested, and the chemical properties of both terrestrial and marine foods, could help to further elucidate the foraging strategies of the Peninsula's MF baboons.

Conclusions

Marine foods comprised only a very small percentage (< 3%) of the diet of KK baboons during the study period. Although this percentage was consistently low (< 5%) during all four seasons, there was seasonal variation with more frequent bouts, time spent feeding on marine foods, and a greater number of animals on the shore during autumn and winter. GAMs indicated that increasing tide- and wave height had a significant negative impact on MF

frequency and intensity. Time of day was another significant predictor of frequency of MF, while wind direction, coast and season significantly affected the intensity of MF. The relatively low percentages of deviances (13.5% – 29.7%) explained by the models suggest that there are other factors not included in this study that affect baboons' decisions regarding when, and how much, to exploit this abundant source of protein in a generally oligotrophic environment. We might greatly improve our understanding of factors affecting use of marine foods by Peninsula baboons if future research can be performed at the level of the individual, and if temporal and spatial variation in the distribution, relative abundance and quality of marine foods can be determined.

CHAPTER 5

Synthesis: current understanding of marine foraging in chacma baboons and recommendations for future research

The Cape Peninsula's oligotrophic terrestrial habitats (Cowling et al., 1996) are juxtaposed with productive marine habitats that are home to a variety of abundant, sedentary or extremely slow-moving invertebrates (Branch, 1974, 1976; Bayne et al., 1984; Van Erkom Schurink and Griffiths, 1991; Robinson et al., 2005). In light of this, and considering baboons' remarkable adaptability and dietary breadth (DeVore and Hall, 1965; Altmann and Altmann, 1970; Hamilton et al., 1978; Whiten et al., 1991), it is unsurprising that the Peninsula's chacma baboons (*Papio ursinus*) include marine organisms in their diet (Hall, 1962, 1963; Davidge, 1978). The tissues of marine invertebrates are known to be an important source of protein for maritime mammals (*sensu* Carlton and Hodder, 2003) elsewhere (Smith and Partridge, 2004), and it seems likely that this would hold true in the case of Peninsula baboons. Despite the novelty of exploitation of marine foods by baboons, there was a paucity of information on this behaviour in the literature prior to the commencement of this study. The first major aim of this study was to provide ecological context for this behaviour by investigating the behaviour and diet of a troop of natural-foraging Peninsula baboons (of which only one remains). The second major aim was to quantify the extent of marine foraging in the study troop, and elucidate some of the effects of environmental variables that might influence this behaviour. Thus, the five overarching questions, to which I sought answers, were:

1. How do ranging patterns and activity budgets of a non-raiding, marine foraging troop of baboons vary seasonally and how do they compare with other baboon troops, both on the Peninsula and elsewhere?
2. How much time do natural-foraging Peninsula baboons allocate to exploiting marine foods, and does this vary seasonally?
3. Do stable isotope signals of hair and faeces reflect proportional contributions of terrestrial and marine foods to the diet of non-raiding Peninsula baboons?
4. If the extent of marine foraging is reflected in the isotope ratios of hair (see above), could isotope analysis of hair be used to determine whether or not an unknown baboon exploits marine foods?
5. How frequent are marine foraging bouts, and what environmental factors influence the frequency and intensity of exploitation?

Taken in isolation (in Chapters 2 – 4), the answers to these questions provide insights into distinct aspects of marine foraging, and how this behavioural phenomenon might be investigated in other contexts. In this final chapter, I synthesise the key findings from each chapter and illustrate how these relate to the broader literature regarding primate foraging

ecology and the feeding behaviour of maritime mammals. I also highlight some of the limitations of the study and provide recommendations for future research on this subject matter.

Key findings

Ranging behaviour and activity budgets

The Kanonkop (KK) troop (the only extant non-raiding troop on the Peninsula) occupied a home range (HR) covering approximately 45 km² and travelled a little more than 6 km each day, on average. Comparison of per capita area (derived from home range area) and daily path length (DPL) with ranging data for other troops both on the Peninsula and elsewhere (DeVore and Hall, 1965; Rowell, 1966; Stoltz and Saayman, 1970; Hamilton et al., 1976; Harding, 1976; Anderson, 1981; Whiten et al., 1987; Barton et al., 1992; Hoffman and O’Riain, 2012a) suggest that KK troop is nutrient-stressed (Barton et al., 1992; Henzi et al., 1992).

The above-mentioned conclusion was given further credence by the results of a model of HR cell use frequency. The better of two statistical models (a sparse spatial Generalized Linear Mixed Model; SGLMM) indicated that frequency of cell use was affected by habitat type, and was positively related to slope, and negatively related to distance-to-coast, altitude and distance-to-fresh water. In this context, the effects of habitat type, altitude and distance-to-coast are all thought to be driven by the baboons’ nutritional needs as these cell characteristics were tied to productivity, or ease with which foods could be accessed. These findings suggest that the baboons’ primary need for food is the main driver of area use. Peninsula baboons are not unusual in the regard, as area use has been linked to food availability in baboon populations elsewhere (Harding, 1976; Henzi et al., 1992).

Importantly, KK did not use the entire home range during each season; the troop used a larger proportion of their home range in summer, and a smaller proportion in winter, than during other seasons. Also, the DPL varied seasonally, and was longest in summer and shortest in winter. Primates in other regions are known to travel further on a daily basis during times of food scarcity (Barton et al., 1992; Henzi et al., 1992; Di Bitetti, 2001; Hanya et al., 2005; Riley, 2008). The findings reported here therefore suggest that levels of nutrient-stress fluctuated through the year, being more severe in the warm, dry months.

The inference regarding nutrient stress, based on ranging data, was corroborated by the activity budgets reported in Chapter 2. The dominance of foraging behaviours (*sensu* Bronikowski and Altmann, 1996) in activity budgets is typical of troops that feed only on

natural foods (Post, 1981; Whiten et al., 1987), as opposed to those that supplement natural foods with human-derived foods (Forthman Quick, 1986; Altmann and Muruthi, 1988). As with ranging patterns, there was however seasonal variation in time spent engaged in different behaviours. Similar variation has been reported in previous studies, which have shown that baboons increase time allocated to foraging when preferred foods are in short supply (Post, 1981; Alberts et al., 2005). In the case of KK troop, foraging time (in minutes) was longest in summer and shortest in winter, which once again suggests that nutrient stress is more severe during the warm, dry summer than during the cool, wet winter.

The troop's diet (estimated from behavioural observations) showed relatively little variation across seasons in terms of composition based on broad food types (above-ground plant, subterranean plant and marine animal). The only significant difference across seasons was that the troop consumed a higher proportion of above-ground plants in spring than in summer or autumn. Marine foods comprised only a very small proportion ($\leq 3\%$) of the troop's diet during all four seasons. This was surprising considering that marine foods were richer in protein than the vast majority of the baboons' terrestrial foods, and baboons typically show a preference for foods that are relatively rich in protein (Whiten et al., 1991; Barton and Whiten, 1994).

Stable isotope ratios

The results of the stable isotope analysis (Chapter 3) were in accordance with estimates of marine food consumption based on scan sample data. As expected (Sealy et al., 1986, 1987), terrestrial C₃- and C₄ foods, and marine animal tissues, were isotopically distinct, with the result that isotope-based models could be used to estimate baboon diet composition. Models based on isotope ratios of both hair and faeces indicated that marine foods comprise only small proportions of the troop's diet, and that there is a small amount of seasonal variation in this quantity. The marine signal in baboon hair is not very strong however, and would be overwhelmed by the signal of human foods (inferred from comparisons with other troops) in an animal that consumed both. Stable isotope analysis is therefore only a viable tool for identifying marine foraging individuals where the individuals in question are known to feed only on natural foods. Nonetheless, the stable isotope ratios proved informative here. Both stable isotope ratios and scan sample-based estimates indicated that over the course of a year, and within each season, marine foods comprised only small proportions of KK baboons' diet. This might not be the case over shorter periods however, as availability of marine foods

fluctuates rapidly through time, and the baboons might therefore exploit these foods to a greater extent, when they are available.

Factors affecting marine foraging

MF scan data, like general scan data and stable isotope ratios, indicated that marine foods comprise only small percentages of seasonal diets. The proportions of hours (during which the baboons fed on marine foods) and the numbers of animals feeding on marine foods during these hours varied markedly through the seasons however. Modelling of probability and intensity of marine foraging indicated that several environmental variables limit the extent to which Peninsula baboons are able to feed on marine foods (Chapter 4). Thus, as was expected, high tides and large waves limited marine foraging, but this limiting effect was mitigated to some extent by strong offshore winds. Season and coast were also shown to be significant predictors of probability and intensity of marine foraging. It stands to reason that the differences across seasons, and between coasts, were driven by variation in availability or quality of food. Interestingly, the season during which nutrients stress was apparently most severe (summer), was also one of the seasons during which the baboons exploited marine foods very little and marine foraging intensity was low. This is surprising, and could be indicative of a stronger limiting effect of some chemical property of marine foods, such as secondary metabolite concentration, which is known to vary through time in marine invertebrates (López-Legentil et al., 2007; Sacristán-Soriano et al., 2012).

Limitations of the study

A major limitation of the study is the lack of individual-level observations of feeding behaviour. This limitation arises, albeit indirectly, from the KK troop's unique status among Peninsula troops. Observations of this nature could only have been recorded through close-up focal sampling (Altmann, 1974), and would have allowed for estimation of feeding rates for different foods by baboons of different age and sex classes. A sampling protocol of this nature could not be implemented under the conditions of the research permit granted to me by SANParks Scientific Services—time with the troop and proximity to the animals were both strictly limited (see Chapter 2). These conditions were specified because the SANParks staff wished to minimise human-baboon interactions which might result in KK baboons losing their fear of humans and habituating to close human presence. This is understandable as fear of humans is one of the major obstacles that baboons must overcome if they are to employ raiding as a foraging strategy (Strum, 2010). KK baboons are therefore less likely to become

habitual raiders if they remain fearful of humans. Habitual raiding results in greater spatial overlap with humans (Kaplan et al., 2011), which is in turn linked to more intense human–baboon conflict (Hoffman and O’Riain, 2012c). Increased conflict between humans and baboons results in higher rates of human-induced injury and death in semi-commensal troops (Beamish, 2010), and raiding baboons may fall victim to human parasites and pathogens (Drewe et al., 2012). Thus, it is in the baboons’ best interests to minimise their interactions with humans, thereby reducing the likelihood of initiating a behavioural progression that ultimately leads to habitual raiding. It is worth noting that both troops to the immediate south of KK troop’s home range are comprised of habitual raiders despite being within the same section of TMNP. Hence the threat of habituation and raiding remains high for this troop. In summary, the lack of individual-level data could not have been redressed without increasing the probability of compromising the KK baboons’ wellbeing in the long term.

Another shortcoming of the study is a lack of data regarding the abundance of different foods, and how this might vary through seasons. Food abundance affects food choice and, therefore, diet composition in a variety of primates (Heiduck, 1997; Conklin-Brittain et al., 1998; McConkey et al., 2003) including baboons (Byrne et al., 1993). This variable might therefore be one of the factors that determines how much marine food KK baboons consume. An accurate assessment of the availability of all foods available to the KK baboons, and how this varies through time, would have been an enormous undertaking however, due to the number of species consumed by Peninsula baboons (Hall, 1962, 1963; Davidge, 1978) and the rapid fluctuations in the availability of marine intertidal foods (Palmer, 1995; Branch et al., 1998). Such an undertaking was, unfortunately, beyond the scope of this study. Also, the findings presented in Chapter 4 should inform which variables are controlled for in such an assessment of food availability. Thus, an assessment conducted without the knowledge gained through this study would have likely been flawed.

Recommendations for future research

Analysis of secondary metabolites

The models of probability and intensity of marine foraging described in Chapter 4 explain notable amounts of deviance in the data, but a substantial amount of deviance in each data set remains unexplained. One of the contributing factors to this could be a somewhat unexpected biotic variable that limits exploitation of marine foods by the baboons (Whiten et al., 1991; Barton and Whiten, 1994), namely the presence of alkaloids in tissues of marine invertebrates (Chapter 3). The presence of secondary metabolites has, to the best of my knowledge, not

previously been suggested as a potential factor limiting consumption of marine foods by maritime mammals. In the only study in which this issue was investigated, it was shown that the two algae species preferred by sheep on North Ronaldsay island both contained phenolic antinutritive compounds (Hansen et al., 2003). The presence of secondary metabolites in plant and animal tissues typically acts as a consumer deterrent however, and is known to affect baboon food choice (Whiten et al., 1991; Barton and Whiten, 1994).

In light of the above, it is plausible, even probable, that the presence of alkaloids in marine invertebrate tissues could be a factor that limits exploitation of marine foods by baboons. The deleterious effects of ingestion of secondary metabolites differ according to the consumer and the compound, ranging from impaired digestion (Griffiths, 1986) to reduced hair growth (Crouse et al., 1962), to lesions on internal organs, and, in some cases, even death (Hutton et al., 1958; Glick and Joslyn, 1970; McLean, 1970; Levin, 1971). There is interspecific variation in the methods that animals use to mitigate negative effects of consuming secondary metabolites (Dearing et al., 2005; Barbehenn and Constabel, 2011), as well as the extent to which they are able to neutralise these compounds (Freeland and Janzen, 1974). It is therefore unsurprising that the effects of particular compounds on consumers vary across species (Hutton et al., 1958), as does tolerance of specific compounds (Basey et al., 1990; Marsh et al., 2003; Bailey et al., 2004, 2007; Wooley et al., 2008; Diner et al., 2009). Mammals are known to learn rapidly which foods may cause illness (Bell and Janzen, 1971), and will avoid these foods (Kenagy, 1972; Freeland, 1974), even to the point of refusing to eat if no other foods are available (De Muelenaere, 1965; Glick and Joslyn, 1970). The fact that baboons elsewhere prefer foods with low alkaloid content (Whiten et al., 1991) suggests that they are not able to overcome the effects of these chemical compounds with ease. Further studies of marine foraging in baboons should therefore place greater emphasis on the chemical properties of different foods (specifically the concentrations of secondary metabolites), how these change through time and whether they influence the amount of that item ingested.

Nutritional rewards and feeding rates

The seasonal differences in the intensity of marine foraging reported here could have been driven by seasonal changes in food availability and, perhaps, food quality in both terrestrial and intertidal habitats. Seasonal variation in baboon diet has been documented in other troops both on the Peninsula (Van Doorn et al., 2010), and in other populations (Post, 1982; Barton and Whiten, 1993; Byrne et al., 1993), and is attributed to seasonal variation in food

availability and quality of available foods in different habitats (Byrne et al., 1993; Alberts et al., 2005). The KK troop might be expected to exploit marine foods more intensely when marine foods offer particularly rich nutritional rewards, and/or when the abundance or quality of terrestrial foods is particularly low (Barton and Whiten, 1994; Codron et al., 2006; Dunbar et al., 2009). The results presented here (Chapter 2) suggest that this was the case, as intensity of marine foraging was higher in autumn and winter than in summer or spring. The average protein content of marine foods was higher in autumn than during other seasons, and the terrestrial foods consumed in winter were lower in protein than those consumed during other seasons, thus rendering marine foods more attractive to baboons (see Chapter 2; Barton and Whiten, 1994; Codron et al., 2006). Unfortunately, the abundance of KK troop's foods was not quantified here (see above), so the potential effects of fluctuations in availability cannot be directly accounted for. Future studies should therefore include investigation(s) of abundance and availability of different foods, and how these quantities vary through time.

Interestingly, the only terrestrial foods that were analysed that are not markedly poorer in protein than marine foods are *Leucodendron* sp. seeds (which were in fact richer in protein than marine foods). Although rich in nutrients, exploitation of these seeds requires complex, time-consuming processing of the exceptionally hard cones, which means that the seeds might represent fallback foods. This term is frequently used to refer to abundant low-quality foods, but it may also refer to relatively high-quality foods, the yield of which is offset by high processing costs (Alberts et al., 2005). In light of this, theory predicts that the baboons should prefer marine foods over *Leucodendron* sp. seeds as a source of protein (Dunbar, 1992; Dunbar et al., 2009) if both are equally readily available. The rapid temporal fluctuations in the availability of marine foods, and potential risk of death associated with spending time in the intertidal zone, mean that exploitation of these foods is not without cost however. The seasons during which marine foods were most intensively exploited were also the seasons during which *Leucodendron* sp. seeds are exploited to greater extents (see Chapter 2). This pattern suggests that both foods are in fact fallback foods, which are used more extensively when preferred terrestrial foods are in short supply (Marshall et al., 2009). Proving that *Leucodendron* sp. seeds and marine foods are in fact fallback foods (due to the costs incurred by baboons through exploitation), would require focal sampling (Altmann, 1974) to determine feeding rates, and thus nutrient intake rates, for different foods (Marshall et al., 2009). These data could then also be used to confirm that the KK baboons, like those with access to human foods and agricultural food products (Johnson et al., 2013), forage selectively in order to maintain a constant daily intake of protein as a proportion of the diet.

The last point in the previous paragraph could in fact be extremely important. It has been shown that allocating relatively small amounts of time to feeding on protein-rich marine foods may greatly reduce the time required for a maritime omnivore to fulfil its daily nutrient requirements (Smith and Partridge, 2004). Considering how much richer in protein the baboons' marine foods are than most of their terrestrial foods (and indeed foods consumed by the baboon studied by Johnson et al., 2013), it is plausible that the small amounts of marine foods that they consume do in fact allow them to significantly reduce time spent feeding. This would however be dependent on feeding rates, and thus foraging reward obtained per unit effort, of different foods. If circumstances ever allow, future study should be carried out to determine abundance of different foods, and rates at which different foods are consumed, to further elucidate the factors that drive or limit marine foraging in chacma baboons on the Peninsula.

Trophic enrichment factors

Although there was general agreement between the models of KK troop's diet based on stable isotope ratios, and estimated diet composition based on behavioural observation, the results of the models were not identical. The models that incorporated faecal isotope ratios generated estimates of dietary composition that were more similar to those based on behavioural observations. This suggests that the TEF values incorporated into the faeces-based models were closer to the correct tissue-specific values for baboons than those used in the models that incorporated hair isotope ratios (Caut et al., 2008; Bond and Diamond, 2011). This is perhaps not surprising, as diet-hair fractionation of nitrogen isotopes has been shown to be highly variable (Sponheimer et al., 2003c), and the factors that affect this are still poorly understood (Codron et al.; Sponheimer et al., 2003c). Also, isotope ratios of hair may in fact not reflect isotope ratios of the bulk diet, but rather protein uptake from different food groups (Petzke et al., 2005), due to metabolic routing (Gannes et al., 1997; Voigt et al., 2008). In the absence of observational data, it seems that isotope models incorporating isotope ratios of baboon foods and faeces, and the TEF values used here, should be used to quantify contributions of C₃-, C₄- and marine foods to the diet of Peninsula baboons (Caut et al., 2008). Stable isotope analysis of baboon hair might still be used to determine contributions of marine foods to baboon protein intake, but further research is required to determine correct diet-hair TEF values for baboons (Bond and Diamond, 2011).

Conclusion

Behavioural indicators suggested that natural-foraging baboons on the Cape Peninsula, South Africa experienced nutrient-stress that is comparable to that experienced by troops in harsh environments elsewhere. Seasonal changes in ranging patterns and time allocated to different activities indicated that the study troop's levels of nutrient stress varied through time however. Ecological theory dictates that these baboons should maximise exploitation of foods that offer great nutritional rewards, particularly during the season(s) when nutrient stress is most severe. Unlike baboons in other regions that are restricted to terrestrial habitats, baboons on the Peninsula have access to protein-rich foods in the marine intertidal zone, which might provide at least partial relief from nutrient stress. The study animals consumed only small amounts of marine food however. Models that incorporated a suite of abiotic factors, and proxies for biotic factors, explained some of the deviance in a set of marine foraging data. This amount of unexplained deviance suggests that as yet unexplored factors (likely biotic factors such as chemical composition of foods) also play important roles in driving or moderating exploitation of marine foods by the baboons.

Nonetheless, this thesis has enhanced our understanding of marine foraging, a behaviour which displays baboons' remarkable ability to exploit novel food types in diverse habitats. This adaptability is one of the key traits that has allowed baboons to thrive in human-modified habitats (Else, 1991; Swedell, 2011). Time spent in such habitats is associated with frequent contact with humans, and invariably leads to conflict between the baboons and their human neighbours (Naughton-Treves, 1998; Naughton-Treves et al., 1998; Hill, 2000; Tweheyo et al., 2005; Kaplan et al., 2011; Kaplan, 2013). Costs are incurred by both parties (Naughton-Treves et al., 1998; Tweheyo et al., 2005), but those incurred by baboons are perhaps the greater, as encounters with humans may result in serious injuries or even death (Beamish, 2010). It is therefore imperative that local conservation agencies and land managers should take all necessary precautions to ensure that the study troop does not make the switch to raiding as a foraging strategy.

Welfare issues aside, this troop is particularly important from a research perspective as baboons are considered to be appropriate analogues for research into human evolution and early human diets (Jolly, 2001; Codron et al., 2008; Wrangham et al., 2009). Considering the well-documented importance of marine foods in the diets of humans in the southern and south-western parts of South Africa over the last one-hundred-and-fifty-thousand years (Sealy et al., 1986; Sealy, 1997; Marean et al., 2007; Jerardino and Marean, 2010; Marean, 2010), and the hypothesised role of these foods in human evolution (Broadhurst et al., 2002;

Cunnane and Crawford, 2003), this troop may provide a rare and valuable window into the challenges faced by early humans as they sought to exploit these foods. Further studies of this troop that do not involve habituation or protracted close human contact might therefore provide valuable insights in the context of research on human evolution.

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APPENDICES

Appendix A. Table of nutritional and chemical properties of different foods consumed by KK baboons over the course of the study¹

Food group	Genus	Structure(s)	AP (%)	NDF (%)	ADF (%)	CT (%)	PLP (%)	D	M	W
Above-ground	<i>Arctotheca</i>	Whole plant	2.44	24.08	17.45	0.09	0.94	-	-	-
	<i>Aspalathus</i>	Flowers	3.00	33.20	21.91	0	5.60	-	-	-
	<i>Carpobrotus</i>	Leaf-bases	7.54	18.68	11.60	4.46	5.54	-	-	-
	<i>Centella</i>	Whole plant	6.49	25.91	17.81	0	2.47	-	-	-
	<i>Chrysanthemoides</i>	Flowers	5.26	28.43	18.11	0	2.72	-	-	-
	<i>Cullumia</i>	Flowers	2.39	42.87	24.35	0	0.99			
	<i>Elegia</i>	Stems	3.27	54.59	21.42	0.70	0.72	-	-	-
	<i>Erica</i>	Flowers	7.14	28.43	21.63	2.04	6.66	-	-	-
	<i>Leucodendron</i>	Seeds	48.85	31.04	20.57	0.08	0.27	+	+	+
	<i>Leucospermum</i>	Seeds	9.61	40.10	31.89	0.22	2.50	+/-	+/-	+/-
	<i>Lolium</i>	Leaves	4.73	30.28	16.47	0	1.36			
	<i>Mimetes</i>	Flowers	2.74	63.84	49.59	0.50	1.89	-	-	-
	<i>Nylandtia</i>	Fruit	1.91	66.23	45.80	0	0.3	-	-	-
	<i>Olea</i>	Fruit	2.15	51.73	33.03	0.17	2.45	-	-	-
	<i>Otholobium</i>	Whole plant	2.95	26.75	17.76	0.17	1.49			
	<i>Pterocelastrus</i>	Leaves	7.90	33.75	20.51	3.02	4.86	-	-	+/-
	<i>Salvia</i>	Flowers	5.94	24.65	15.95	0	4.63	-	-	-
	<i>Searsia</i>	Fruit	6.94	43.37	26.38	0.69	1.43	-	-	-
	<i>Stenotaphrum</i>	Leaves	4.49	53.96	23.50	0	0.56	+	-	+

Appendix A continued.

Food group	Genus	Structure(s)	AP (%)	NDF (%)	ADF (%)	CT (%)	PLP (%)	D	M	W
	<i>Stoibrax</i>	Leaves	5.86	28.42	18.99	0	1.36	-	-	-
	<i>Tetralia</i>	Stems	2.50	46.32	19.92	0.33	0.29	-	-	-
	<i>Willdenowia</i>	Seeds	5.03	73.01	31.61	0.21	0.96	-	-	-
Subterranean	<i>Eriospermum</i>	USO	2.91	29.63	19.81	0.80	0.77	-	-	-
	<i>Hyobanche</i>	USO	1.95	32.77	20.18	0	4.48			
	<i>Sporobolus</i>	Rhizome	2.61	48.13	22.60	0	0.29	-	-	-
	<i>Watsonia</i>	USO	5.67	31.41	7.90	3.61	2.43	-	-	-
Marine	<i>Cymbula</i>	Soft tissue	28.45	11.15	0.84	0	0.28	+	+	+
	<i>Mytilus</i>	Soft tissue	24.79	10.74	0.84	0	0.28	+	+	+
	<i>Scutellastra</i>	Soft tissue	31.14	10.48	2.10	0	0.30	+	+	+

¹Values are averages where multiple samples from a genus were analysed; Missing values indicate that insufficient sample mass was available for the test in question; AP = available protein, NDF = neutral detergent fibre, ADF = acid detergent fibre, CT = condensed tannins, PLP = polyphenols, D = Dragendorff reagent, M = Mayer reagent, W = Wagner reagent; CT and PLP percentages are equivalent to quebracho tannin and pyrogallol respectively; USO = underground storage organ; “-” denotes a negative results, “+” denotes a positive result, “+/-” denotes positive and negative results for different samples of the same genus.

Appendix B. Table of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of hair sub-samples used in experiment testing for effects of trapping glue and mineral turpentine on hair isotope ratios¹

Troop	$\delta^{13}\text{C}$ (‰)		$\delta^{15}\text{N}$ (‰)	
	Control	Treatment	Control	Treatment
DG	-20.8	-21.0	5.5	5.4
JTR	-20.3	-20.2	6.2	6.3
MT1	-21.1	-21.3	6.2	6.2
UNK	-23.5	-22.8	5.5	6.0

¹all samples were plucked either from animals that had been anaesthetised for other research projects or had died as a result of conflict with humans; “control” hairs were wiped down with 95% ethanol three times and allowed to dry; “treatment” hairs were stuck to an unused dart and then processed following the methods described in Chapter 3; Wilcoxon’s paired rank sum tests indicated that control and treatment hairs did not differ in terms of either $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$; DG = Da Gama Park, JTR = John Travolta, MT1 = Main Tokai 1, UNK = Unknown.

Appendix C. Table of Diet composition estimates (of food groups based on photosynthetic pathways in the case of terrestrial foods) of adult male and female baboons in KK troop based on time spent feeding on different foods recorded through instantaneous scan sampling.

	Terrestrial C ₃	Terrestrial C ₄	Marine
Female	94.7	1.7	3.6
Male	92.9	2.1	5.0