A Comparison of the Subspecific Divergence of Two Sympatric African Monkeys, *Papio hamadryas* & *Chlorocebus aethiops*: Morphology, Environment, Diet & Phylogeny

By

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ABSTRACT

The baboon and vervet monkey exhibit numerous similarities in geographic range, ecology and social structure, and both exhibit extensive subspecific variation corresponding to geotypic forms. This thesis compares these two subspecific radiations, using skull morphology to characterise the two taxa, and attempts to determine if the two have been shaped by similar selective forces.

The baboon exhibits clinal variation corresponding to decreasing size from Central to East Africa, like the vervet. However West African baboons are small, unlike the vervet. Much of the shape variation in baboons is size-related. Controlling for this reveals a north-south pattern of shape change corresponding to phylogenetic history. There are significant differences between the chacma and olive baboon subspecies in the proportion of subterranean foods in the diet. No dietary differences were detected between vervet subspecies. Baboon dietary variation was found to covary significantly with skull variation. However, no biomechanical adaptation was detected, suggesting morphological constraint owing to the recent divergence between subspecies. Phylogeny correlates with morphology to reveal an axis between northern and southern taxa in baboons. In vervets *C. a. sabaeus* is the most morphologically divergent, which with other evidence, suggests a West African origin and radiation east and south, in contrast with a baboon origin in southern Africa. Path analyses of all the factors discussed revealed markedly different relationships between the two taxa, with baboons responding to the environment via diet rather than directly.

The two subspecific radiations have different relationships with diet, environment and phylogeny. In spite of superficial similarities, the study taxa are sufficiently different that similar ecological and environmental selective forces have not produced convergent patterns of radiations. The baboon exhibits greater flexibility and larger size freeing it from limiting constraints faced by vervets. Additionally the two have distinct sites of origins and patterns of dispersals adding a stochastic element to the differences between radiations.

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AUTHOR'S DECLARATION

I confirm that this work is original and that if any passage(s) or diagram(s) have been copied from academic papers, books, the internet or any other sources these are clearly identified by the use of quotation marks and the reference(s) is fully cited. I certify that, other than where indicated, this is my own work and does not breach the regulations of HYMS, the University of Hull or the University of York regarding plagiarism or academic conduct in examinations. I have read the HYMS Code of Practice on Academic Misconduct, and state that this piece of work is my own and does not contain any unacknowledged work from any other sources.

CHAPTER 1. INTRODUCTION TO THE STUDY TAXA AND CONCEPTS OF SUBSPECIFIC VARIATION

1.1 QUESTION AND AIMS

The vervet *Chlorocebus aethiops* and baboon *Papio hamadryas* are the most widespread and abundant non-human African primates (Altmann and Altmann, 1970, Fedigan and Fedigan, 1988, Struhsaker, 1967a). They are largely sympatric and virtually ubiquitous in sub-Saharan Africa (Fedigan and Fedigan, 1988, Jolly, 2001). They inhabit semi-arid savannah (Altmann, 1998, Isbell and Young, 1993), woodland (Gaynor, 1994, Young and Isbell, 1994), and latitudes ranging from the equator to the temperate cape (Anderson, 1982, Kingdon, 1997), failing only to inhabit desert and the deepest parts of the rainforest (Kingdon, 1997, Jolly, 1993). This considerable ecological breadth is achieved through flexibility in group size (Henzi et al., 1997), activity (Hill et al., 2003, Willems and Hill, 2010) and life history (Whitten and Turner, 2009, Jolly and Phillips-Conroy, 2006). In particular a generalist and opportunistic foraging behaviour enables the vervet and baboon to survive in an array of environments (Alberts and Altmann, 2006, Fedigan and Fedigan, 1988, Bercovitch and Harding, 1993). Morphological features such as skull shape in vervets (Cardini et al., 2007) correlate with environmental variation suggesting anatomical adaptation. In both baboons (Jolly, 2001, Frost et al., 2003, Jolly, 1993) and vervet (Cardini et al., 2007) the change in morphology over any given geographic axis is clinal or gradistic. However, this is steeper in places (stepped), corresponding to pelage differences on which subspecific classification is based (Grubb et al., 2003, Groves, 2001).

These two species are both polytypic, generalist and flexible. Both arose in Africa and have radiated into approximately the same geographic distribution (Jolly, 2001, Fedigan and Fedigan, 1988). A fascinating ecological question is whether these two subspecific radiations show any affinities. Natural selection might be posited to exert the same forces and thus produce similarities in both the overall pattern of subspecific variation and environmental correlates. Alternatively it may produce two unique subspecific radiations. The purpose of this thesis is to answer this question by comparing the divergences of two subspecific radiations, in terms of environmental and geographic variation (Chapter 2), diet (Chapters 3 and 4), phylogeny (Chapter 5) and the interrelation of these factors (Chapter 6). This is of considerable importance in understanding the covariation between environmental and morphological variation in primates, giving us insight into the processes of differentiation, adaptation and speciation.

1.2 TAXONOMY & EVOLUTIONARY HISTORY

Both the vervet and the baboon belong to the Cercopithecinae in the order Primates and as such are similar in body plan and physiology (Fleagle and McGraw, 1999). They are united by their caeco-colic method of fermentative digestion, as opposed to foregut-dominated digestion of their sister group the colobines (Lambert, 1998). In contrast with the colobines, cercopithecines have cheek pouches for storing food (Napier and Napier, 1985). The baboon belongs to the tribe Papionini (hereafter referred to as the papionins) and the vervet to the Cercopithecini (hereafter referred to as the guenons) which diverged approximately 11.5 Ma (Tosi et al., 2005, Raaum et al., 2005).

The papionin lineage has diversified into numerous species of middle to large sized terrestrial monkeys with drab pelage. Extant animals include the macaques, mangabeys, gelada, baboons and mandrills (Fleagle, 1988). In spite of morphological convergence between the large bodied, long- or “dog”-faced *Mandrillus* and *Papio* (Collard and O'Higgins, 2001), the latter are more closely related to their sister group *Theropithecus* and the smaller mangabeys of the genus *Lophocebus* (Harris, 2000). *Mandrillus* is more related to the other mangabey genus, *Cercocebus*, exposing the mangabeys as a polyphyletic group (McGraw and Fleagle, 2006). The similarity of the two mangabeys is almost certainly the result of their retention of the ancestral characteristics rather than convergence (Collard and O'Higgins, 2001, Leigh et al., 2003).

The modern baboon lineage is estimated to have split from its extant sister taxon, *Theropithecus*, approximately 4 Ma (Zinner et al., 2009b), which is within the range of dates derived from the fossil record (7 - 3.5 Ma (Jablonski, 1993)). While the theropiths were once widespread in Africa in the Plio-Pleistocene they now are restricted to one species endemic exclusively to the highlands of Ethiopia (Jablonski, 1993). The modern genus *Papio* is likely to have arisen from the genus *Parapapio* (Williams et al., 2007), an extinct genus of Plio-Pleistocene papionins, well represented in southern African sites (Williams et al., 2007). These are at the smaller end of extant baboon size spectrum (Delson et al., 2000) and have a correspondingly short muzzle and low sexual dimorphism. They are characterised by the absence of an ante-orbital drop in the cranium, have a steeply sloping facial angle and less prominent supraorbital tori. (Williams et al., 2007).

The genus *Papio* arose at 2.6 million years ago with *Papio angusticeps*, *P. izodi* and an extinct subspecies of the baboon *P. hamadryas robinsoni* (McKee and Keyser, 1995, Szalay and Delson, 1979, Newman et al., 2004). The other two congenerics *P. izodi* and *P. angusticeps* are both small bodied, retaining the ancestral *Parapapio* condition. *P. izodi* is notable in having large teeth for its size. Indeed these early *Papio* shared their environment with the large bodied, macrodontic forms *Gorgopithecus*, *Dinopithecus* and *Theropithecus* now extinct (Williams et al., 2007), suggesting large teeth may have been a common dietary adaptation for these sympatric species. *Papio hamadryas* is found in the fossil record from 2.6 million years ago (Newman et al., 2004, Delson et al., 2000). These early specimens of *P. h. robinsoni* are as different from modern subspecies as the subspecies are from each other (Frost, 2007, Szalay and Delson, 1979) arguing for its subspecific designation.

The modern species *Papio hamadryas* is divided into five “forms” (Jolly, 1993), which are here termed subspecies. There is no taxonomic consensus and some consider *Papio hamadryas* a superspecies (Thorington and Groves, 1970, see section 1.8 on species concepts) while some authors have considered these forms full species (Groves, 2001). This study considers the forms subspecies of the species *Papio hamadryas.*, recognising a sixth *P. h. kindae* as distinct from *P. h. cynocephalus*, in which group it is usually subsumed, on the basis of its differentiated morphology (Leigh, 2006) and genetics (Jolly et al., 2011). The subspecies recognised here are *Papio hamadryas anubis* (the olive baboon), *P. h. hamadryas* (the hamadryas baboon), *P. h. papio* (the Guinea baboon), *P. h. cynocephalus* (the yellow baboon), *P .h. ursinus* (the chacma baboon) and *P. h. kindae* (the Kinda baboon).

Genetic evidence yields a fascinating insight into the pattern of this subspecific diversification of *Papio hamadryas*. Mitochondrial DNA evidence suggests chacma baboons diverged shortly after at 1.79 Ma (Newman et al., 2004). Zinner et al. (2003) found the yellow baboon, including Kinda, and chacma baboons formed a clade to the exclusion of the remaining, northern subspecies. Their date was approximately the same. Added to the strong southern Africa fossil record, this suggests a northern expansion and diversification, placing the hamadryas and Guinea baboons on the edge of the expanded range (Jolly, 2009). Climatic fluctuation in the Pleistocene is thought to have been instrumental in creating dispersal barriers thus facilitating divergence (Jolly, 2001, Zinner et al., 2009b). This is corroborated by more recent work that has documented a number of haplogroup populations providing evidence of past refugial populations (Zinner et al., 2009b). Indeed while there is current contact between the olive and hamadryas baboons it is thought that in the mid-Pleistocene the two taxa were separated by desert that has since disappeared enabling contact (Wildman et al., 2004).

Establishing the true phylogenetic relationship of the baboon subspecies is hampered by the fact that mtDNA often tells quite a different story from nuclear DNA in species with male dispersal (Zinner et al., 2009b, see Chapter 5). This is because of the matrilineal descent of mtDNA. In cases of introgression, where one subspecies makes a genetic contribution to another, with male dispersal that contribution is nuclear and not mitochondrial DNA. An mtDNA study by Zinner et al. (2009b) groups distinct subspecies and splits others in keeping with expectation under a scenario of past introgression. However, until a nuclear DNA phylogeny is produced mtDNA can provide a useful, if biased, insight into the phylogenetic relationship of modern subspecies

The guenons constitute a clade that today consists of numerous small bodied, colourful, largely arboreal specimens in the forests of sub-Saharan Africa, as well as a terrestrial clade comprising the vervet, patas and l'Hoest's monkey (Tosi et al., 2005). Piecing together guenon evolutionary history is difficult owing to the rarity of guenon fossils (Frost and Alemseged, 2007, Leakey, 1988). The earliest guenon fossils are found in the Pliocene, circa 2.9 Ma (Leakey, 1988). Arboreal species are often poorly represented in the fossil record as they do not fossilise well. Even with that in mind, the rarity of these fossils suggests they were simply not present in southern Africa and present only in small numbers in East Africa, as other fossil primates are well preserved (Leakey, 1988, Elton et al., 2010). Genetic evidence for an earlier split from baboons (Tosi et al., 2005) however suggests a much deeper evolutionary history.

The terrestrial Guenons split from the arboreal Guenons circa 8 Ma and started to diverge into the three extant species at approximately 4 Ma (Tosi et al., 2005). The most parsimonious hypothesis would put this terrestrial substrate shift between these dates (Tosi et al., 2004). This window contains the putative time for the origin of hominin bipedality at the Miocene-Pliocene boundary (Xing et al., 2007). This raises the interesting possibility that the shift to greater terrestriality was caused by similar environmental forces during this period (Xing et al., 2007). The monophyly of this clade demands their grouping in the same genus or three genera distinct from their arboreal relatives (*Cercopithecus*). *Chlorocebus*, originally proposed for the vervet, is the valid generic name for the three terrestrial species (Tosi et al., 2004) and is used here.

Chlorocebus aethiops, formerly *Cercopithecus aethiops,* is also split into six taxa, and like the baboon the taxonomy is contested. Grubb (2006) termed this a single "geospecies" to reflect the highly geographic nature of vervet variation. The common name "vervet" is used here in its broader sense for the entire subspecies rather than its restricted use for just *C. a. pygerythrus*. Following Grubb et al. (2003), this thesis considers the six forms subspecies, recognising *C. a. sabaeus* (the green monkey), *C. a. tantalus* (the tantalus monkey), *C. a. aethiops* (the grivet), *C. a. pygerythrus* (the "true" vervet), *C. a. cynosuros* (the malbrouck), and *C. a. djamdjamensis* (the djam-djam or Bale monkey).

The lack of fossil evidence makes reconstructing the origin of the vervets difficult. While there are definite fossils of *C. aethiops* at Asbole, Ethiopia at 0.6 Ma, this date is very recent (Frost and Alemseged, 2007). Genetic information can once again provide an insight, with mitochondrial DNA suggesting a Pleistocene origin at 2.3 Ma (Shimada et al., 2002). With regard to location Fedigan and Fedigan (1988) suggested a southern African origin. However more recent considerations of the fossil record (Elton, 2007) and genetics (Hauser, personal communication) suggests an origin probably in West Africa (see Chapter 5). Little work has been done on subspecific variation in vervets, and DNA studies are often hampered by poor sampling of this widespread species (Shimada et al., 2002). As such less is known about intraspecific divergence than the baboon. However recent evidence suggests *C. a. sabaeus* diverged earliest from the other subspecies (Hauser, personal communication, see Chapter 5).

1.3 GEOGRAPHIC DISTRIBUTION

From their sites of origin in Africa both the vervet and the baboon have dispersed widely across the majority of the continent (fig. 1a & b). Aside from an isolated group of baboons living in Arabia (Winney et al., 2004) and a translocated population of vervets in the West Indies (Horrocks, 1986) the two species inhabit most of sub-Saharan Africa, absent only from the central African rainforest in the Congo Basin.

The olive baboon, *P. h. anubis*, is a large-bodied subspecies ranging from West Africa to East Africa. In East Africa the olive baboon hybridises with the yellow baboon in the south east (Alberts and Altmann, 2001) and the hamadryas baboon in the north east (Nagel, 1973). The olive baboon penetrates as far south as Tanzania and expansion north is limited by the Sahara. Its range excludes much of the Congo Basin, though forest baboons do occur (Rowell, 1966, Jolly, 1993) on the fringes and baboons penetrate as much as 500 miles inside the forest (Gautier-Hion et al., 1999).

The hamadryas baboon is confined to the north east of sub-Saharan Africa and a small section of the Arabian Peninsula. It hybridises with the Olive baboon when present at Awash , Ethiopia, (Nagel 1973), though not in parts of Eritrea (Zinner et al., 2001). On the other side of the continent from the hamadryas baboons but bordering the olive, is the Guinea baboon, *P. h. papio*. It is found from Senegal to Guinea in West Africa (Sharman, 1981). It is recorded as hybridising with the olive baboon (Grubb et al., 2003) though the extent and ecological conditions under which this takes place as well as the fertility and fitness implications are unknown. A more well studied hybrid zone exists between the olive and yellow baboon (Samuels and Altmann, 1986, Alberts and Altmann, 2001). The yellow baboon inhabits East Africa, with olive baboons to the north-west and chacmas to the south. Between the yellow baboon and the Kinda baboon there is a morphological cline as opposed to a discrete split (Dechow, 1983, Freedman, 1963). The Kinda baboon inhabits land north of the Zambezi in Zambia and Angola. The chacma baboon inhabits southern Africa encountering the Kinda and yellow baboons north of the Zambezi (Jolly et al., 2011).

Among the vervets *C. a. sabaeus* is the westernmost subspecies inhabiting land west of the Volta River (fig. 1a). Whether *C. a. tantalus* meets this subspecies is unknown (Groves, 2001); *C. a. sabaeus* inhabits the region of the upper Volta river while *C. a. tantalus* inhabits the lower reaches (IUCN, 2011). *C. a. tantalus* ranges across from Senegal to East Africa where it hybridises with *C. a. pygerythrus* in Uganda. It does not appear to meet *C. a. aethiops* (Groves, 2001), which is the most northerly subspecies, inhabiting Ethiopia, Eritrea and the Sudan. *C. a. djamdjamensis* has the smallest range as it is restricted to the Bale mountains There is some evidence that the southern forms of *C. a. aethiops* are contiguous with this subspecies (Groves, 2001). *C. a. pygerythrus* hybridises with *C. a. tantalus* in East Africa and *C. a. aethiops* further north, and sweeps down to South Africa, though failing to occupy as full an extent as the baboon (fig. 1). Between Southern Africa and the Congo Basin lies *C. a. cynosuros*.

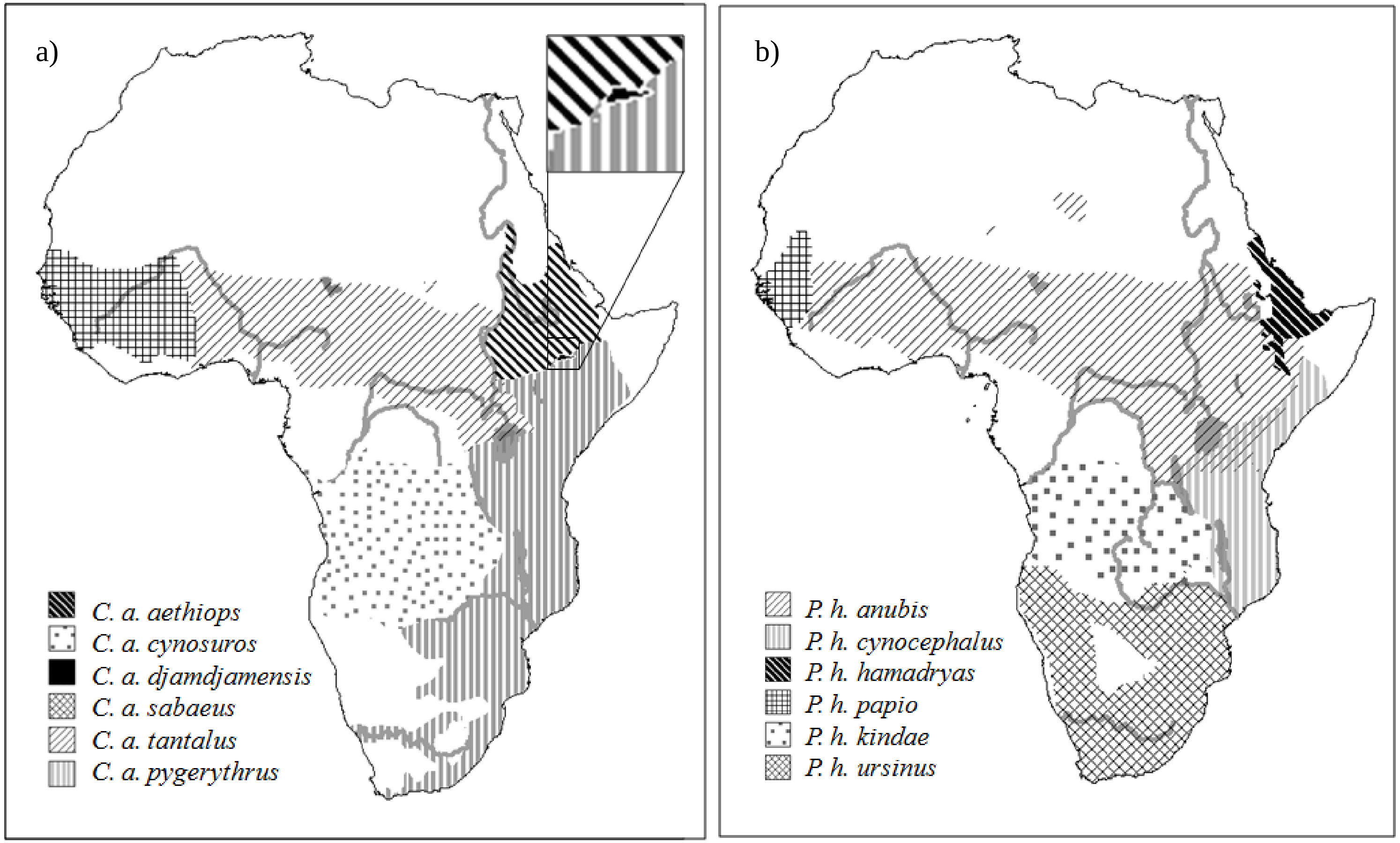


Figure 1.1. The geographic distribution The geographic distribution of the subspecies of ***a)*** *the vervet monkey* Chlorocebus aethiops *spp. and* ***b)*** *the baboon* Papio hamadryas *(data from IUCN, 2011).*

1.4 ENVIRONMENT & HABITAT

There is extensive overlap of vervet and baboon geographic ranges (fig. 1.1a & b), with both inhabiting latitudes from the equator to the Cape, exposing them to extensive variation in temperature and rainfall seasonality. The two are specifically recorded as being sympatric in the open savannah in East Africa (Fedigan and Fedigan, 1988) where they use the same sleeping trees at Amboseli (Altmann, 2009). In South Africa, at Lajuma, baboons prey on vervets (Willems and Hill, 2009). Both are found in savannah, woodland and riparian forests (Kingdon, 1997). Olive baboons inhabit evergreen forest (Rowell, 1964) and hamadryas and olive baboons inhabit semidesert (Zinner et al., 2001); two environments in which vervets cannot survive. One subspecies of vervet, the djam-djam, reaches elevations of 3km in the forested Bale mountains of Ethiopia (Mekonnen et al., 2010), as do a population of olive and anubis baboons (Mori and Belay, 1990). Baboons, unlike vervets, are found up to elevations of 3km in the Drakensbergs of South Africa (Whiten et al., 1987). Baboon make greater use of the open savannah than vervets (Struhsaker, 1967b), which range less from tree refuges and sleeping sites.

1.5 FEEDING & DIET

Feeding takes up a significant proportion of the time budget of vervets and baboons. The amount of the vervet time budget spent feeding varies across populations from 20% in a population in Cameroon to 40% in a population Amboseli, Kenya (Harrison, 1985). However, adjacent populations at the same site can vary significantly in time budget as was found at Amboseli for grooming and moving behaviour, though not in this case feeding (Isbell and Young, 1993). In the baboon case foraging time varies. For instance feeding time takes up about 45 - 48% of the day at Amboseli (Bronikowski and Altmann, 1996) but as much as 70 - 85% by chacma baboons in the Kuiseb River Canyon in Namibia (Hamilton III et al., 1978). This is demonstrated to decrease with increasing proportion of fruits and seeds, thought to be high quality, while in contrast decreasing with subterranean foods, low quality and requiring time and effort to manipulate and consume (Hill and Dunbar, 2002).

Both vervets and baboons are eclectic feeders. This generalism is likely to be a major underpinning factor of their wide distribution. Both will eat a variety of leaves, grasses, fruits and seeds (Napier and Napier, 1985). However while both are generalists, a closer examination reveals that baboons appear to exploit a wider spectrum of resources. For instance at Amboseli baboons consume around 200 more foods than sympatric vervets (Altmann, 1998). In particular baboons take more subterranean foods such as corms, rhizomes and tubers (Dominy et al., 2008, van Doorn et al., 2010). These are of special importance during the dry season for many baboon populations (van Doorn et al., 2010, Altmann, 2009). These foods are difficult to acquire, taking up to a minute to dig up (Whiten et al., 1987) and complex manipulation to process (Rhine and Westlund, 1978). Baboons also take small game such as rabbits (Rowell, 1966) or small ungulates (Davies and Cowlishaw, 1996, Hamilton III and Busse, 1978). Baboons are difficult to categorise other than as opportunists, taking a general range of foods, but in a selective manner (Alberts and Altmann, 2006).

Vervets diets consists largely of fruits and flower (Harrison, 1984) doubtless owing to their closer association with trees, and reduced time ranging on the open savannah compared with baboons (Struhsaker, 1967a). This is likely to be related to their small size and correspondingly greater predation risk (Struhsaker, 1967a). Additionally, vervets are too small to dig up subterranean foods, lacking the muscular power (Altmann, 1998). Even if they could access this resource it is likely that they would be unable to eat these tough foods (Dominy et al., 2008) owing to their smaller masticatory muscles. With smaller size and thus a smaller alimentary tract vervets would not be capable of extracting as much energy from such foods as baboons (Demment and van Soest, 1985). While vervets are generalist in the main, they tend to be quite focused on a single food source at any given month in the year, switching as the seasons change time (Barrett, 2005, Chapman and Chapman, 1999). Thus they have dietary breadth at the broad but not narrow temporal scale.

1.6 APPEARANCE & MORPHOLOGY

Perhaps the most striking difference between the baboon and the vervet is size. Baboons, at roughly 10-30kg, are much larger than vervets, at 3-4kg (Bolter and Zihlman, 2003, Fleagle, 1988). This has numerous consequences, chief of which is that the smaller vervets have 16 predators while baboons have only four (Struhsaker, 1967b). In addition, the small size of the vervet means they have less muscular power and shorter limbs limiting the amount of ranging vervets can do relative to baboons (Altmann, 1998).

In addition to its ecological consequences, size has a profound effect on morphology. Morphological proportions typically change over development, such as the dimensions of the head relative to the body in humans, a phenomenon termed anisometric growth (Emerson and Bramble, 1993, Gould, 1971). Often this is thought of as a trajectory which animals trace as they grow (Elton et al., 2010, Collard and O'Higgins, 2001, Ravosa, 1998). The underpinning of this is scaling laws (Schmidt-Nielsen, 1984). If an animal doubles in mass its muscles must do twice as much work. However, under isometric growth the muscle cross sectional area will have increased by $2^{2/3}$. This smaller exponent means the forces the muscles are able to generate is relatively less (Emerson and Bramble, 1993). As such larger animals must have disproportionately large muscles to move larger body parts In terms of skull shape, size increases require extra muscle attachment such as neuchal crests and occipital extensions on the neurocranium and increased facial dimensions (Emerson and Bramble, 1993, Sakka, 1985). This is not just related to biomechanics: the brain and sensory organs grow relatively less after birth than the face, and so the neurocranium tends to be relatively smaller in older animals.

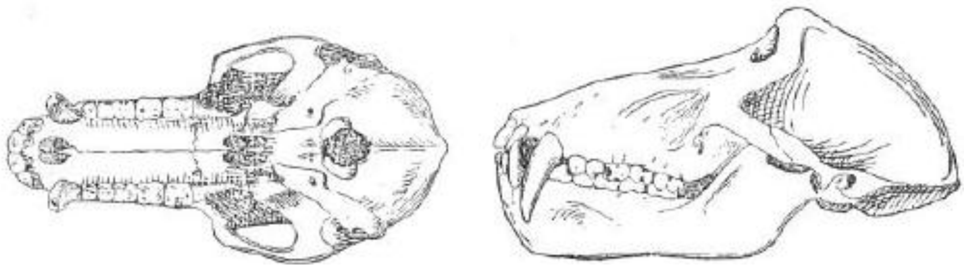


Figure 1.2. Adult baboon skull in norma ventralis *and* norma lateralis. *Taken from Zuckerman. (1926).*

Baboon craniofacial morphology is characterised by extreme prognathism resulting in a dog-like appearance (fig. 1.2). This long rostrum and mandible contains long molars and broad incisors at the anterior (Fleagle, 1988). The maxillary canines are long, and deeply rooted, with the mandibular first premolars serving to hone them (Fleagle and McGraw, 1999). There are maxillary fossae between the tooth row and upper rostrum (Freedman, 1963). Supraorbital tori, and sagittal and maxillary crests are present (Zuckermann, 1926).

Figure 1.3. Adult vervet skull in norma ventralis *and* norma lateralis.

The vervet has a markedly shorter rostrum and dental arcade than the baboon, with no maxillary fossa (fig. 1.3). The canines are shorter, though still prominent and sexually dimorphic, with the lower first premolar acting to hone the upper canine. The orbits and braincase are proportionally larger and sagittal and nuchal crests are absent.

Subspecifically, the vervet and the baboon are diagnosed on the basis of their pelage. Chiefly this is in facial characteristics such as the elongated whiskers of *Chlorocebus* *a. aethiops* or the absence of a frontal band above the eyes in *C. a. sabaeus* (Osman Hill, 1966 pp 533-537). The baboons differ in pelage colour, giving them their common names, although the male hamadryas baboons differ from others in having a mane (Nagel, 1973). These soft-tissue differences in both species correspond to differences in underlying skull form (Elton et al., 2010, Jolly, 2001). A gross pelage difference in baboons is that between the northern forms with wavy hair and the southern sort with straight (Jolly, 2003), corresponding approximately to the major phylogenetic split found by Zinner et al. (2009b).

Interestingly, given their geographic separation (fig. 1.1a) the Guinea baboon has affinities with the hamadryas baboon (Jolly, 2001), in particular its small size and the presence of a mane (Jolly, 1993). It seems likely that these are homologous ancestral features that have been lost to the derived anubis baboon that now separates them (Jolly, 2003). The smallest subspecies is *P. h. kindae*, with males the size of females of the larger subspecies (Jolly, 1993). As baboons are evolved from smaller animals this reflects the retention of the ancestral condition (Singleton, 2005). Aside from its size the Kinda baboon is distinctive in having a white neonatal coat (Jolly and Phillips-Conroy, 2005), and is subsumed by the yellow baboon according to certain authorities (Jolly, 1993). Indeed, it is between the Kinda and yellow baboon proper that a cline was first noted (Freedman, 1963) with Kinda in the west and larger yellow baboons in the east. In spite of its obvious interest to morphologists, information on this subspecies is scarce, though studies are being undertaken in relation to hybridisation between this and the yellow and chacma baboons in Luangwa and Kafue (Jolly and Phillips-Conroy, 2005 , Jolly et al., 2011).

Aside from morphological differences between subspecies, there is evidence of interpopulational differences within subspecies, in particular the olive baboon. Jolly (1993) noted that the specimens in the forests of Uganda and the Congo were larger than those towards hybrid zones and desert: the peripheries of its range. However our knowledge cannot be considered complete: virtually all of the studies on this subspecies have been on East African populations (Kunz and Linsenmair, 2008b, Higham et al., 2009). In West Africa morphological differences have been described (Elliot, 1913) but in an anecdotal rather than statistical sense (see baboon clinal variation Chapter 2).

1.7 SPECIES CONCEPTS AND THE EVOLUTIONARY SIGNIFICANCE OF SUBSPECIES

While extensive subspecific variation has been uncovered so far in the vervet and baboon, the evolutionary significance of this is yet to be discussed. Species and subspecies are terms in Linnean taxonomic classification. Taxonomy is a framework used to reflect the nested pattern of biological descent. Working from kingdom to subspecies, each level denotes more recently shared ancestry. While the relative position of a taxonomic level is objective, the absolute position is not. There is no objective reason to place a particular clade at the family level, other than to denote a level more specific than an arbitrarily chosen order and less specific than a genus. It is arbitrary in the sense that if all taxonomy were lost, when people constructed a new scheme, the relative positions of terms would be the same but the level themselves would probably differ. Species, however, is different in that as well as being a taxonomic level it also has an extra dimension of evolutionary meaning, in which sense it is less arbitrary (Coyne, 1994, Cracraft, 1989, Eldrege, 1993, Dobzhansky, 1951, Hey et al., 2003). This is best explained in terms of a definition give by Ernst Mayr : “species are groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups” (Mayr, 1942: 120). Mayr later specified that this was meant for sympatric taxa (Mayr, 1963). This has become known as the biological species concept. Thus for proponents of the biological species concept the species becomes “a field for gene recombination” (Carson 1957) to the exclusion of other populations in different species.

However, while species are “real” they are difficult to define. Many authors reject the biological species concept on the grounds that a species by this definition might not be monophyletic: there may be some nested clade that is reproductively isolated from the adjacent branches (Velasco, 2008, Cracraft, 1989). For this reason some researchers use the phylogenetic species concept which has monophyly as a criterion rather than reproductive compatibility. At the more behavioural extreme is the species recognition concept (Paterson, 1985), which concerns sexual signalling. According to this view, if the sexual signals of the transmitter are not interpreted by the receiver as indicating a potential mate these populations should be considered separate species, as no reproduction can take place. This is true even if there are no postzygotic barriers such as hybrid infertility.

Discussing species presents an epistemological problem, as consistently defining a species is so challenging. That is not to say that species do not exist, as a lack of definition does not equate to an ontological problem (Jolly, 1993, Eldrege, 1993). However, in practice many authors use a combination of definitions. This variation in standards is important to bear in mind. Scientist are subject to biases (Gippoliti and Amori, 2007, Isaac et al., 2004). Less rare species are more studied (Doherty and Harcourt, 2004), and geography and politics exert an influence on this. Certain clades are more studied because of their “charisma” and the IUCN Red List is highly biased in favour of mammals, birds and reptiles (Stuart et al., 2010). The well studied orders are becoming increasingly split into new species, while others are not: a phenomenon known as “taxonomic inflation” (Padial and De la Riva, 2006, Gippoliti and Amori, 2007). This phenomenon is particularly true in primates, and is driven by the conservation imperative; specific status carries a higher weight in the minds of the public and politicians (Mace, 2004). Ironically however this taxonomic shift, leading to inflation, actually makes it harder to determine how much diversity has already been lost and where the trajectory of extinction lies (Mace, 2004).

Despite difficulties of definition and the existence of taxonomic inflation, the greatest evidence for the existence of species as entities is that biological variation is discrete and not continuous (Coyne and Allen Orr, 1998, Dobzhansky, 1937). This is because reproduction, in the case of sexually reproducing organisms, is the glue that keeps a group of populations cohesive and on the same evolutionary trajectory, while natural selection favours certain discrete traits that confer an adaptation in the environment but not others. The discrete nature of specific form can best be understood in terms of Wright’s (1932) adaptive landscape model. Wright (1932) envisaged a species occupying a position on a topographically varied landscape (fig. 1.4). In this conceptualisation elevated locations equate to adaptive states and depressed areas maladaptive ones. Natural selection is the driving force that pushes a species up the hill in the model, or adapts it to its surroundings in reality. Different species inhabit different adaptive landscapes and these vary with environment. The varied topography of the landscape results in discrete rather than continuous variation, resulting in the discrete species observed in nature, each notionally hovering over some adaptive peak

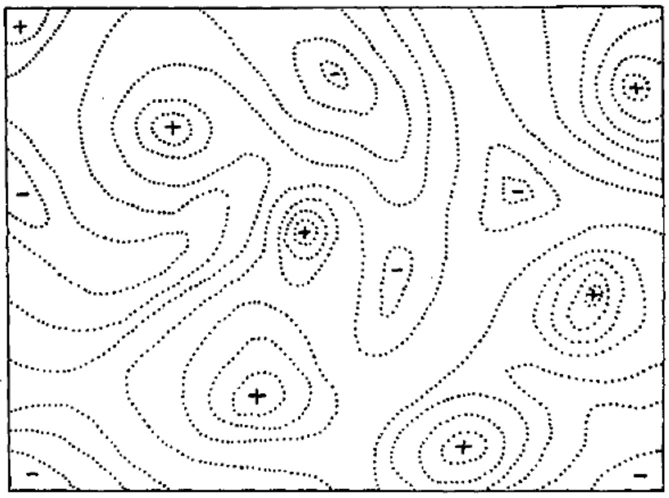


Figure 1.4. Wright's adaptive landscape (taken from Wright 1932). Dotted lines indicate contours, + represent adaptive peaks and – represent maladaptive troughs.

Species are not homogenous, but structured, often spatially (Cracraft, 1989, Thorpe, 1987, Winker, 2010). This fact was recognised taxonomically over a century ago by Sundevall who was first to use trinomial terms for geographic varieties (Winker, 2010). Indeed Mayr and Wright, the originators of the biological species concept, favoured the use of subspecific designations as a useful way of describing diagnosable features of non-reproductively isolated populations (Isaac et al., 2004). Subspecific differentiation is extensive in numerous species (Thorpe, 1987, James, 1970). This may be clinal variation related to a changing environmental variable, such as size in sparrows in America (James, 1991) and Australia (Baker, 1980) and New Zealand opossums (Millien et al., 2006, see Chapter 2). Other variation is categorical or polytypic, as in cases of animals of distinct lineages remeeting at hybrid zones, such as the hooded and carrion crow (Cook, 1975, Saino, 1998, see Chapter 2 for fuller discussion). Indeed true panmixia, the ability of any individual in a population to mate with any other, is rare, usually as a result of distance between individuals across a geographic range (Thorpe, 1987). As such homogeneity is almost nonexistent save for species that only breed in one locality (Thorpe, 1987).

Defining subspecies is even more difficult than defining species (Winker, 2010). Quantitative criteria have been proposed such as the 75% rule (Amadon, 1949), which states that for a group to be considered a subspecies 75% must be correctly diagnosed on the basis of some trait or traits from the other putative subspecies. However, this is not widely employed. Usually some arbitrary level of diagnosable phenotypic differentiation, especially when geographically based, is termed subspecific (Winker, 2010). While objectivity is a difficulty, such a level of categorisation is highly useful. Ceasing to categorise below the species level conflates extensive intraspecific variation and masks biologically significant reductions in gene flow between groups of populations. This is true both in the present and in the past for populations that have been divided and reunited. While the practice of recognising subspecies may lack rigour, focusing on the minutiae of classification detracts from the biology of the system being described (Jolly, 1993) and is thus to be avoided.

The conservation implications of defining subspecies are extensive. The IUCN rarely recognises subspecies for conservation purposes, instead protecting the whole species or not. As such rare subspecies may go unprotected (Gippoliti and Amori, 2007). Additionally, there are considerable biases in the recognition of subspecies: of those recognised by the IUCN most are primates and none are chiropterans or rodents (Gippoliti and Amori, 2007). Even within the primates, rare species can be understudied and thus cryptic variation can be overlooked (Doherty and Harcourt, 2004). *C. aethiops* is extremely well studied and for the most part is far from being endangered. However, such depth of study has revealed the existence of the ecologically distinct djam-djam (Mekonnen et al., 2010); in a less well studied species such diversity could have been overlooked and lost.

The evolutionary importance of subspecific variation can again be best expressed by returning to Wright's adaptive landscape. Wright recognised that species were not homogenous and thus considered a species to be a cloud rather than a point on an adaptive landscape. This has profound evolutionary implications. A species with a wide spread over an adaptive landscape is likely to constitute subspecies occupying different but adjacent peaks. As such the species is less likely to go extinct when certain local conditions change either by stochastic effects such as drought, famine or disease or more long term environmental change. Additionally a wide spread over this landscape increases the catchment area for including a rising adaptive peak as the environment changes. Both these processes offer the possibility of one population essentially dragging another up a rising peak from a falling one (Wright, 1932).

The cohesiveness of a species is maintained by reproduction (Wright, 1932). A reduction in gene flux facilitates divergence both by differential selection as an adaptive response to different environments, and via the accumulation of differences owing to chance effects: genetic drift. Using Wright's model, a breakdown in reproduction leads to a constriction in the species "cloud" on the adaptive landscape. Each may occupy a separate adaptive peak. Over time this results in further constriction and eventual splitting of the groups. For this reason some authors have considered subspecific differentiation as representing incipient speciation. However, low levels of gene flow can impede speciation, which requires divergent selection on several traits (Rice and Hostert, 1993). As such the notion that subspecies are about to become species has been challenged (Johnsen 2006). Jolly (1993) argued that subspecies may be stable and longstanding features of a species rather than on the verge of budding off. While evolutionary trajectories may begin to diverge, secondary contact between recently separated taxa may result in hybrids that happen to be adaptively suited to the environment (Hey et al., 2003). This would change the trajectory of the lineages entirely. Nevertheless, the forces that sculpt subspecies, namely natural selection as a response to local conditions or else neutral genetic drift, are the same as the forces that sculpt species. Indeed Darwin (1859) held that small differences within species could tell us about the process of natural selection. As such the heterogeneity within a species presents an important insight into natural selection (Winker, 2010).

While the biological species concept fulfils certain theoretical expectations, application of this to Old World monkeys is made difficult by the high extent of hybridisation between taxa. The most significant instance of this is the production of fertile hybrids between *Papio* and *Theropithecus* (Dunbar and Dunbar, 1974, Jolly et al., 1997). According to the biological species concept the lack of postzygotic mating barriers makes these the same species: yet conventional taxonomy, reflecting real and profound differences in morphology, ecology and evolutionary history, puts them as separate genera (Fleagle, 1988). Indeed the species recognition concept also fails to distinguish them. While the baboon and gelada have different sexual signalling features male geladas mate with female baboons in spite of absence of gelada-like periovulatory vesicles while male baboon mate with female geladas in spite of their small and nonbaboon-like perineal swelling (Jolly et al., 1997). Of course divergent adaptations and ecologically disparity might select against these hybrids in the wild (Jolly et al., 1997), but the capacity for gene flow remains.

There are extensive guenon instances of hybridisation (de Jong and Butynski, 2010). Many of the sympatric arboreal guenons hybridise as well as terrestrial *Chlorocebus aethiops* and *Chlorocebus patas* (Galat-Luong, 1996, Bolwig, 1978). The impact of such hybridisation in terms of population genetics and evolutionary importance is unknown. It is tempting to dismiss such events as novelties with little evolutionary significance. However, recent genetic advances have discovered numerous lineages exhibit mosaic genomes indicative of past hybridisation, with primate examples including lemurs and apes (Arnold and Meyer, 2006). Indeed a newly described species, *Rungwecebus*, appears to owe its origin to a hybridisation event between baboons and mangabeys according to genetic evidence (Zinner et al., 2009a).

Such findings are the result of very recent analyses on very few taxa, and the overall prevalence of such events in the origin of species is hard to assess. On balance, such events are probably not common with most speciation events arising from allopatric speciation (Turelli et al., 2001, Coyne and Allen Orr, 1998) . Barriers to dispersal, similar to those that form subspecies, arise preventing reproduction and facilitating the divergence of lineages. Crucially with subspecies genetic material can still pass back and forth, and thus there is some degree of interpopulation cohesion on the adaptive landscape.

Baboons exhibit several subspecific hybrid zones. The hamadryas and the olive baboon meet and hybridise in Ethiopia (Phillips-Conroy et al., 1991, Kummer, 1968) producing fertile animals that are intermediate in form (Phillips-Conroy and Jolly, 1981) and behaviour (Bergman et al., 2008). Additionally, there is a well described hybrid zone between olive and yellow baboons (Samuels and Altmann, 1986, Alberts and Altmann, 2001, Charpentier et al., 2008). Hybrids in captive populations have a higher incidence of supernumary teeth (Ackermann et al., 2006). While the hybrids are fully fertile, such features tend to indicate some level of genetic incompatibility and the breaking up of coadapted gene complexes. This suggests a greater genetic division between these subspecies than the others.

A hybrid zone had recently been documented between the chacma and the Kinda baboon (Jolly et al., 2011). This is of considerable interest as these are markedly different in size; the Kinda baboon is the smallest subspecies. Related to this is the one sided nature of reproduction at this hybrid zone, with male Kinda baboons mating with female chacmas (Jolly et al., 2011). Male chacmas appear to regard the smaller female Kinda baboons as immature and not potential sexual partners. This mating structure provides a fascinating insight into genetic introgression (see Chapter 5).

It has been argued that this subspecific variation may be a longstanding feature of the population (Jolly, 1993). This may be the case as even small amounts of gene flow prevent speciation (Rice and Hostert, 1993). However, the subspecies are clearly not without flux in their geographic extent, as both the yellow-olive and the chacma-Kinda zones are moving (Jolly et al., 2011, Samuels and Altmann, 1986). Indeed movement is a common feature of hybrid zones in numerous taxa (Buggs, 2007).

Of course while there are diagnosable subspecies, these groups are not discrete, but variable across their ranges. Intermediates exist at hybrid zones over a range of several miles. However, adjacent populations share morphological affinities beyond these hybrid zones, (Jolly, 2001): the variation is clinal. For instance there is a gradual change in pigmentation variation in face mantle and anal region between East and West Hamadryas (Jolly, 1993, Kummer, 1968, Elliot, 1913). Additionally the chacma subspecies can be further divided into four geographically based populations, the gray-footed, the Kalahari, the Transvaal and the cape chacmas. The gray-footed chacma baboon has affinities with geographically adjacent yellow, that it does not share with the cape chacma, and thus occupies an intermediate position (Jolly, 2003). To understand the evolution of subspecies Jolly (1993) introduced the terms phenostructure, descriptive of the phenotypes and genotypes of a species, and zygostructure, describing the mating pattern. Past zygostructure creates current phenostructure and current zygostructure dictates future phenostructure. The current phenostructure is not truly typological but clinal because of past zygostructure, which has allowed allows hybridisation and gene flow. Thus subspecific forms are diagnosable but blurry entities.

Vervets are similar to baboons in being polytypic but clinal (Grubb et al., 2003). The similarity of contiguous groups makes taxonomic assignment difficult and the status of these geographic populations as species or subspecies is debatable and debated (Grubb et al., 2003). Here the vervet *Chlorocebus aethiops* is treated as a species comprising six subspecies, following the groupings of Kingdon (though not the rank; he considers them separate species in a superspecies (Kingdon, 1997)). Like baboons vervets have hybrid zones between the subspecies. *C. a. pygerythrus* and *C. a. tantalus* hybridise and intergrade in southwest Uganda and Congo-Kinshasa, and the former also hybridises with *C. a. aethiops* in Ethiopia (Grubb et al., 2003). In the absence of major geographic barriers, and with stepped clinal variation it is valid and appropriate to model these species as a single clinally varying population. A study using this paradigm revealed an east to west clinal pattern of increasing facial proportions relative to the neurocranium in vervets (Cardini et al., 2007). The study then asked if the clinal variation was underpinned by environmental gradients, as predicted by biogeographical theory (Mayr, 1956). Morphological variation was correlated with rainfall, suggesting environment is an important factor in clinal variation. Though this size variation is reminiscent of the allometric pattern recent work has revealed that differences between subspecies are not exclusively allometric (Elton et al., 2010).

1.8 SOCIAL SYSTEM & BEHAVIOUR

Like all primates both the vervet and baboon are highly social. Group sizes typically range from 16-50 for the vervet monkey (Struhsaker, 1967a) and 4-40 for the baboon (Dunbar, 1988). Minimising predation risk is argued to be at the heart of group living (Hill and Lee, 1998). Dunbar (1988) surveyed numerous baboon populations revealing lower group size at low versus high predation sites, a finding corroborated by Barton (1996). Vervets have a suite of alarm calls as antipredator behaviours (Seyfarth et al., 1980), an adaptation suggesting that predator defences and group vigilance are important for this species too.

Sociality often results in some degree of hierarchical structure. Baboons (Johnson, 1989, Packer et al., 1995) and vervets (Struhsaker, 1967b) are typically hierarchical with dominant individuals exerting their dominance agonistically via supplanting (taking food off another). Female reproductive success is highly influenced by dominance with high ranking females showing shorter interbirth intervals in baboons (Wasser et al., 2004) and vervets (Fairbanks and McGuire, 1984). For baboon males dominance is physically determined, with larger males able to supplant others (Alberts and Altmann, 1995, Bulger, 1993, Harding, 1980). Males are much larger than females, with female baboons being as small as 50% of male size (Fleagle, 1988) but only 80% of male size in vervets (Fedigan and Fedigan, 1988). However, there is an expectation of greater sexual dimorphism in baboons, as larger species have more sexual size dimorphism as a rule (Rensch, 1950, Leutenegger and Cheverud, 1982). Of course in both species the level of sexual dimorphism varies (Whitten et al., 1998, Jolly and Phillips-Conroy, 2006).

The social forces that cause sexual dimorphism also result in different dispersal strategies. Females are philopatric and males disperse between groups in vervets (Isbell et al., 1993) and baboons (Alberts and Altmann, 1995) with the exception of the hamadryas baboon which herd females and live in single male units (Nagel, 1973). Vervets monkeys are unusual in that they have concealed ovulation (Andelman, 1987) in contrast to the oestrous displays of females in other cercopithecids (Huchard et al., 2009), notably the baboon (Jolly et al., 1997). Adult male baboons of high rank consort more with oestrous females than males of lower rank, thus monopolising them at their most fertile (Gesquiere et al., 2007). Male vervets are unable to tell when a female is ovulating, and this paternity uncertainty may have a role in preventing infanticide (Andelman, 1987).

An impoverished environment has had a profound effect on the social system of the hamadryas baboon. The olive and yellow baboons have multimale societies in which males disperse from their natal group and females remain (Alberts and Altmann, 1995). However, the hamadryas baboon exists in one-male units, where a solitary male dominates a harem of females (Kummer, 1968). Males coercively herd these females and do not tolerate these females to associate with rival males. This arrangement is argued to be a response to their semi desert habitat where high competition for resources disfavours large groups (Kummer, 1968). Females fan out to reduce foraging competition, and so males attempt to herd females to maximise their access to these females and hence increase their fitness. Hamadryas baboons come together for protection on sleeping cliffs and will move to foraging sites as a herd, but the troops soon breaks up on reaching it (Kummer, 1968).

There is evidence for a similar system in the Guinea baboon (Maestripieri et al., 2007). Like the hamadryas the Guinea baboons have one male units that build up into larger association for sleeping and travelling. However, the important difference is the lack of herding females and presence of male-male tolerance (Maestripieri et al., 2007, Galat-Luong et al., 2006). Another social feature unique to this subspecies is the range and frequency of vocalisation (Byrne, 1981). Calls are used to ward off predators by indicating a large group size and to reconvene a group after dispersal, again as a predator defence (Byrne, 1981).

1.9 BEHAVIOURAL FLEXIBILITY

The baboon is the most widespread and abundant nonhuman African primate (Altmann and Altmann, 1970). In an age when anthropogenic effects are threatening all too many species with extinction through climate change and habitat loss the baboon remains largely unthreatened (IUCN, 2010). They owe their cosmopolitan distribution to their adaptability: they are highly opportunistic and will make the most of unusual resources such as swarming locusts (Kummer, 1968) or caterpillars (Altmann, 2009) or taking advantage of encroaching human agriculture (Strum, 1991). Vervets are similarly widespread, nonthreatened aside from the djam-djam (Mekonnen, 2008), and opportunistic, often taking advantage of human foods (Brennan et al., 1985). However, they have a lesser capacity to adapt, direct evidence for which comes from observations of baboons at Amboseli during a prolonged bout of unfavourable conditions. During the 60s and 70s there was a marked changed in the water table in the Amboseli basin where a rise in salinity killed off the fever trees, one of the main food plants of baboons (Altmann et al., 1985). The vervets died out, yet the baboons were able to survive by switching to the remaining less favourable resources (Altmann et al., 1985). Of course, given the sympatry and ecological overlap of these two animals it is possible that the vervets were outcompeted by the baboons. Potentially in isolation the vervets might have been sufficiently flexible to survive. However, the fact remains that the baboons are more resilient, by virtue either of their ability to adapt or their ability to outcompete.

Baboons are clearly better able to track dietary resources than vervets, taking seasonal and interannual variation in their stride (Bercovitch and Harding, 1993). Indeed such is their flexibility that they have broken free from the ancestral condition of seasonal reproduction (Alberts and Altmann, 2006). This means that they can convert unpredictable peaks in resources into reproductive output, rather than being confined to giving birth in a single season and losing a year if conditions prove unfavourable. Baboons respond to environmental variation with interbirth interval correlating with temperature (Hill and Dunbar, 2002). Also, in some populations there is a tendency towards a slight peak in births. Wasser (1996), in a nine year study at Mikumi, Tanzania, found a birth peak in the dry season with mating in the previous wet season. Nevertheless, this was a birth peak and not a birth season, as births continued throughout the year. Nevertheless, the peak is thought to be adaptive in that infants enter a wet season when they are being weaned. It has been shown that rainfall increases conception rates at Gilgil (Bercovitch and Harding, 1993), and hormonal work has shown that progesterone is higher at suboptimal times of the year, i.e. when resources are poor, as well as in low status female, inhibiting conception (Wasser, 1996). The rain-induced increase in conception did not amount to a birth peak however suggesting a facultative reproductive strategy, where conception does not necessarily lead to birth. Similarly ovulation, conception and births are all reduced after drought (Beehner et al., 2006a), with miscarriage twice as likely. The abortion of pregnancy is a facultative response to a resource-limited condition, while rain-induced conception is a facultative response to a environment suddenly rich in resources. This fine control of the life history stages in reproduction gives baboons a “reproductive filter” (Wasser, 1996), enabling them to respond to their changing environment or the social environment in terms of position in the dominance hierarchy (Smuts and Nicolson, 1989).

While vervets are seasonal (Butynski, 1988), they are not so strictly seasonal as many guenons. Indeed Else (1986) described them as being “marginally seasonal” and Fairbanks and McGuire (Fairbanks and McGuire, 1984) noted that captive vervets were capable of breeding throughout the year. However, nutritionally enhanced and less seasonal conditions are likely to be quite different from the situation in the wild making it hard to conclude anything for certain. Indeed, birth seasons have been shown in open air captive groups (Rowell, 1970, Else et al., 1986, Rowell and Richards, 1979) suggesting some seasonal importance to reproduction. Reproduction in the wild is certainly seasonal with births taking place between October and December in Kwazulu-Natal Province, S. Africa, (Baldellou and Adan, 1997) and at Amboseli (Lee, 1984). It seems that females have an internal hormonal clock, modulated by seasonal cues such as temperature and rainfall (Baldellou and Adan, 1997), with little evidence of the facultative, aseasonal variation of the baboon (see Chapter 6).

1.10 GOALS OF THE STUDY

The extensive intraspecific variation has begun to be explained in the vervet and the baboon, but the pattern of baboon morphological variation and how these divergences came about remain unresolved. One goal of the study is to map the morphological variation in the baboon to visualise the pattern, quantify any trends and their relation to environmental variables and see if the pattern is the same as that published for the vervet (Cardini et al., 2007). A second goal of the study is to establish if there are dietary differences between the subspecies for both the vervet and baboon, and to see if there are any affinities between species in this pattern. Hypothetically both species might have a more frugivorous subspecies in the same part of Africa for instance. Additionally this study aims to establish if the dietary differences relate to subtle morphological variation corresponding to biomechanical function.

A third goal of this thesis is to quantify the interrelation of all these effects, diet, environment, size, taxon, on the pattern of subspecific variation in skull morphology for both species. This will determine relative importance in each of these factors and help to make conclusions on the causation of divergences. Finally, these results will be compared to see if both taxa have similar correlations with external variables and hence potentially similar evolutionary pressures, or else totally different patterns.

These questions are divided up and answered in the following manner. In Chapter 2, the craniofacial variation of the baboon skull is mapped for both size and shape.

The chapter also dissects shape into its allometric and nonallometric components, and compares the pattern of the two and their relation to environmental variables with a view to getting at the putative environmental underpinnings of these trends. In Chapter 3 baboon and vervet diet are analysed for subspecific differences. The reliability of inter-study comparison is discussed and the dietary data are presented for baboon and vervet populations. Differences are analysed statistically, and comparisons are made with other Old World monkey species. Chapter 4 discusses food physical properties. Partial least squares is used to assess diet-morphology covariations and lever arm mechanics to assess biomechanical adaptation. Chapter 5 discusses the roles of phylogeny in structuring subspecific variation and tests predictions about the strength of the phylogenetic signal in the two study taxa. Chapter 6 discusses the interrelation between the factors, environmental, spatial, phylogenetic and dietary and the effect these have on morphological variation in the two species. Each relationship is expanded upon and outlier subspecies are excluded to see what overall effect this has on the model. The differences between interrelations for both taxa are discussed. Chapter 7 takes the results from all studies uses them to determine whether the vervet and baboon subspecific radiations are the same or different or not, as well as if they are underpinned by natural selection or stochastic factors.

CHAPTER 2. PATTERNS OF CLINAL VARIATION IN THE BABOON

2.1 INTRODUCTION

2.1.0 Overview

Intraspecific diversity typically shows spatially structured variation (Thorpe, 1987). Between species the axes of spatial structuring or clinal variation tend to be similar (Bergmann, 1847, James, 1970, Millien et al., 2006). Numerous studies have attempted to explain this both by studying a single species and by analysing overall patterns across species (Ashton et al., 2000, Millien et al., 2006, James, 1970) . While many factors have been implicated in clinal variation, such as temperature (Mayr, 1956), moisture (James, 1970), primary productivity and seasonality (Boyce, 1978), generalities across animals remain elusive (Millien et al., 2006). A possible reason for this is that such comparative studies are too broad and disparate taxa are environmentally responsive in different ways. Moreover environments change and adaptations may lag behind this, and themselves be in a state of flux. More fine grained analyses may be able shed light on the role of environmental forces structuring subspecific variation.

The underpinnings of intraspecific diversity are central to this thesis. The study presented in this chapter seeks to understand what causes intraspecific diversity in two widespread, polytypic monkeys, the vervet and the baboon, and to establish if their patterns of variation are driven by similar environmental forces. This chapter therefore describes the pattern of variation in the baboon and quantifies the environmental correlates. Vervets are also reanalysed for the sake of methodological consistency, and compared with baboons. If the two exhibit similar patterns of intraspecific variation and have similar environmental correlates this would be strong evidence for the generality of environmental influences in structuring morphological diversity. If not, it is likely that subtle differences between these broadly similar species are enough to alter the environmental influence and will argue against overarching biogeographical rules.

2.1.1 Patterns of Clinal Variation

Intraspecific geographic variation is a feature of the vast majority of species (Thorpe, 1987) and is a rich seam of biological variation (Winker, 2010). This geographic variation may be morphological (Forsman, 1997), physiological (Tracey and Walsberg, 2000), behavioural (Macedonia and Taylor, 1985, Ryan and Wilczynski, 1991) or related to life history parameters (Ballinger, 1979). Such variability may be categorical, corresponding to differences between a mainland and insular populations or between populations divided by a dispersal barrier (Thorpe, 1987). However, in many cases variation in a trait is continuous, for instance in calls (Ryan and Wilczynski, 1991) and life history parameters such as growth rate (Sand et al., 1995) and litter size (Lord, 1960). However, by far the most prevalent form of clinal variation is in size (Millien et al., 2006, Mayr, 1956, Ashton et al., 2000). Not only is the trend common in species, but it is also consistent in its pattern across species. In particular Bergmann observed that animals with the same body plan (roughly within the same genus or species) tended to get larger with increasing latitude (Mayr, 1963, Bergmann, 1847). Size influences metabolism and dictates energetic requirements and thus has profound ecological effects (Peters, 1983, Schmidt-Nielsen, 1984). As such varying this parameter is a vital adaptive response.

Alongside size clines, Allen (1877, Mayr, 1956) noticed that with increasing altitude animals got stockier, with shorter extremities such as limbs and ears. The latitudinal and hence thermal component of this variation led Allen and Bergman to conclude that these *a posteriori* observations were best explained as thermoregulatory adaptations. By reducing size an animal can increase its surface area to volume ratio which is better for dissipating heat. This is advantageous at the hotter latitudes towards the equator. Elongating the extremities achieves the same effect.

Bergmann’s and Allan’s rule remain a focus of study in the field of biogeography (Ashton et al., 2000, Blanckenhorn et al., 2006, Millien et al., 2006). Evidence for a size decrease with latitude is found in an array of mammals such as woodrats (Brown and Lee, 1969), hares (Baker et al., 1978), bats (Findley and Traut, 1970) and pumas

(Gay and Best, 1996). Meta-analyses confirm that 71% of mammals and 76% of birds (Millien et al., 2006) show this trend, which is greater than the 50% cut-off required for a generalisation. Similarly Allen's rule is found in numerous species such as nonmigratory sea birds (Nudds and Oswald, 2007), jackrabbits (Griffing, 1974) and across three species of geographically contiguous foxes (Millien et al., 2006).

Translocation experiments show that Bergmannian clines emerge quite rapidly. In the case of the domestic sparrow, which was introduced into North America from Britain in the 1850s and spread across the continent, large animals are now found in the north and small ones in the south (James, 1991). This pattern conforms to that of over a dozen other bird species with comparable geographic ranges. Introduced sparrows exhibited the same trend in an independent introduction in New Zealand (Baker, 1980). The introduction of the opossum from Southern Australia to New Zealand again resulted in a clinal pattern corresponding to that on Australia itself (Millien et al., 2006).

2.1.2 Possible Underpinnings of Clinal Variation

The short time span over which clinal variation emerges, as in the sparrow and opossum case, as well as the commonality between species provide strong evidence for adaptation. However, although Bergman's thermoregulatory hypothesis remains a likely explanation for this variation it is difficult to prove causation from correlation. Latitude correlates with variables other than temperature. James (1970) studied six North American birds and discovered that a combination of humidity and temperature was far more powerful at explaining size variation than either factor on its own. Evaporative water loss is greatest not only at low latitudes, but also at altitude and in arid environments. In both cases this can be minimised by increasing body size. The same relationship was found in a study of bobcats (Wigginton and Dobson, 1999). Similarly moisture was found to be a significant size predictor in bats (Burnett, 1983).

While different latitudes have different mean conditions they also have different variation around that mean. With increasing distance from the equator the seasonal pattern of variation is chiefly in temperature with a hot summer or cold winter according to the inclination of the earth. Size of the landmass also dictates this effect with larger landmasses varying more than smaller ones owing to the buffering effect of the sea. The equator in contrast has minimal temperature variation (Legates and Willmott, 1990) but marked variation in rainfall. The meeting of the winds originating in the northern and southern hemispheres creates an area known as the intertropical convergence zone (Ellis and Galvin, 1994). Though situated about the equator this zone drifts throughout the year, reaching its farthest point north of the equator in January and south in July. As it passes over the equator it brings the rains, and so there are two a year, with drier periods in between. This is the situation dominant on the tropical savannah. Latitude is not the only factor determining rainfall however. The Congo basin, which is a rainforest biome, has reduced seasonality in plant primary productivity relative to savannah on similar latitudes (Okecha and Newton-Fisher, 2006). The presence of so many plants and high temperatures result in high evapotranspiration resulting in high humidity rains that vary more within a day than throughout the year. Another related factor is photoperiod, which varies most further from the equator. This compounds the effects of low temperature and low rainfall on primary productivity in the winter months, as less light results in less photosynthesis. Not only is there less vegetation for animals to eat, there is also less time in which to forage (Hill et al., 2003).

Animals and plants exhibit a number of responses to high seasonal variation. Woody plants shed their leaves when sunlight is reduced over the winter, and shrubs grow subterranean storage organs to get them through periods of reduced light and hence photosynthesis (Dominy et al., 2008). Animals cope with seasonal fluctuations of food by storing fat over the summer months and using this to make up for the negative energy balance over the winter (Lindstedt and Boyce, 1985). As stores are proportional to absolute size, some researchers have claimed that the observed pattern of increasing size with latitude is selected for to buffer seasonal food shortages (Millar and Hickling, 1990, Boyce, 1978, Lindstedt and Boyce, 1985), though of course dissociating this from Bergmannian thermal predictions is difficult. Nevertheless, Ferguson and Larivière (2008) in a study on carnivores found too that larger size was predicted by seasonality and primary productivity. However their path analysis model suggested that this was mediated by the effect of home range and population density. They concluded that larger size enables the increased ranging necessary for acquiring resources distributed over a larger unproductive high latitude environment (Ferguson and Larivière, 2008). While this analysis seems plausible, whether this can be generalised to noncarnivores, with diets of more abundant foods is an open question.

While the abiotic components of the environment, such as temperature and photoperiod and seasonal variation therein, may have a direct effect on morphology, they may also have an indirect effect via primary productivity. Primary productivity, the biomass of plant matter, is higher at lower latitudes owing to abiotic factors such as the amount of sunlight for photosynthesis. Greater primary productivity is likely to equate to greater food availability, both for primary consumers directly but also indirectly for secondary consumers. Greater food availability was suggested as another factor in determining size in bats (Burnett, 1983) and an analysis of carnivores found primary productivity, measured by actual annual evapotranspiration, had a greater explanatory power of size variation than latitude or temperature (Rosenzweig, 1968). For a number of middle eastern animals Yom-Tov and Geffen (2006) found that primary productivity was the greater determinant of body size. However, their study was over a very limited range of latitudes and temperatures, raising an interesting question about the mechanism of size variation. As their populations were so close, they are likely to be largely genetically homogenous and differences therefore might be a response rooted exclusively in phenotypic plasticity. More wide scale variation is likely to be genetically fixed as a result of the difficulty of admixture of large continental distances. The role of scale in structuring variation is undetermined. Potentially slight local variation might build up to create global variation or alternatively it might add noise to a general global trend.

Reinig (1939, reported in Scholander, 1955) refuted the existence of Bergmannian clines, stating that size clines were present from the core to the periphery of an animal’s range. This, he argued, was because, peripheral habitat at environmental boundary of an animal’s range may represent sub-prime habitat. A pattern consistent with the “abundant centre hypothesis” is found in European badgers (Virgós et al., 2011), and thought to be underpinned by food availability. Indeed when a range is bounded by a resource poor environment such as desert or mountains, this hypothesis is intuitive. However, this idea has received no support in the case of carnivores (Meiri et al., 2009). Larger animals in temperate zones, which are less productive, would seem to argue against this deterioration in habitat quality. Additionally many species have range expansion arrested by the sea or rivers, rather than a gradual deterioration of habitat quality.

Many researchers]place resource abundance and primary productivity in a central position to ecological and morphological variation within species. Reaching this conclusion has been hampered by the difficulty of quantifying this variable. Measuring primary productivity directly has proved difficult, and often rainfall is used as a proxy (Dunbar, 1990). However, modern remote sensing techniques can determine the gross presence of photosynthetic pigment by analysing reflected light (ADDS, 2005, Willems and Hill, 2010, Willems et al., 2009). This direct measure is likely to revolutionise our understanding of the effect of primary productivity.

2.1.3 Resources & Growth

Primary productivity is argued to act on body size through the presence of food resources. Resources are often less plentiful on islands (Lomolino, 2005, Lomolino, 1985), and this is argued to be causal in the observed patter of size variation between insular and mainland populations, namely the trend for large animals become smaller and small animals become larger on islands (Millien et al., 2006). For large animals fewer resources mean a greater cost to growth, which is reduced. There is argued to be an optimal body size for each animal bauplan (Lomolino, 2005, Jones and Purvis, 1997), that small animals are below in order to escape predators, enabling them to flee down holes. Predation pressure is reduced on islands and so this cap on growth is lifted. This argument was framed in life history terms by Palkovacs (2003) who pointed out that large animals benefitted by bringing forward reproduction relative to their mainland counterparts, thus becoming adult at an earlier stage in ontogeny and ceasing further growth. Conversely, with a reduction in mortality risk for small animals the pay-off for reproducing as early as possible is lifted relative to growth, favouring larger adult sizes.

2.1.4 Covariance of Size and Shape

Size and shape covary tightly (Gould, 1974). The size-shape axis, or allometric trajectory, that a species traces as it grows has therefore has been considered a line of least resistance in evolutionary change (Marroig and Cheverud, 2005). The assumption is that it is easier for a species to adapt up or down this trajectory than orthogonal to it. Body size is assumed to be an ecologically adaptive trait (Schmidt-Nielsen, 1984, Millien et al., 2006) and responds to a number of meaningful ecological effects, such as resource availability and distribution or type, namely diet (Marroig and Cheverud, 2005), predation (Hill and Dunbar, 1998) and social factors. As such size is posited to be the first feature to change in an adaptive radiation, allowing animals to move from one adaptive peak to another (Wright, 1931), while shape is slower to deviate (Marroig and Cheverud, 2005). Indeed, size has been demonstrated to be more plastic to the environment than change as a result of its simpler genetic underpinning in *Drosophila* (Breuker et al., 2006).

2.1.5 Clinal Variation in Primates

Despite a wealth of studies in other orders, clinal variation in primates and its environmental underpinning have gone largely unstudied. A Bergmannian trend, albeit circumscribed, is present in *Macaca fascicularis*. However, This breaks down at 14°N and in the core species area (Schillaci, 2009). At more northerly latitudes it was speculated that a faunal interactions may work against the Bergmannian trend (Fooden and Albrecht, 1993). However, the congeneric *M. nemestrina* did not behave in the same way, deviating from a Bergmannian pattern north of the equator. A clearer pattern of clinal variation was detected in *Saguinus geoffroyi* in craniometric variation from east-west in Central America (Natori and Kondo, 1998) and in Brazilian tufted-eared marmosets (Albrecht, 1982). However, these are not Bergmannian though no explanatory hypothesis was advanced.

In several studies the pattern of clinal variation is mosaic rather than affecting the whole body equally. For instance in *Macaca fuscata* maxillary sinus volume decreased with latitude (Rae et al., 2003). This volume is inversely related to nasal volume. As such the surface area of the nasal mucosa increases with latitude hinting at a thermoregulatory adaptation to warm and moisten the cooler, drier air. While not Bergmannian this is similar to surface area changes described by Allen's rule. A more classical instance of Allen's rule was found in vervets. Tail length was found to reduce with increasing altitude (Turner et al., 1997), reducing surface area and suggesting cold adaption. However, this was not found in other limbs. Similarly in *Macaca* on the Kra peninsula clinal variation is present in crown-rump length and intermembral index but not facial height or tail length (Schillaci, 2009). Rather than being thermoregulatory however, the crown-rump length and intermembral index were more likely to be related to changes in locomotor strategy owing to changing habitat (Hamada et al., 2008), undermining the case for thermal variation causing subspecific variation.

Primates are subject to the island rules, with large ones getting smaller and small ones getting larger relative to mainland forms (Bromham and Cardillo, 2007, Welch, 2009, Nowak et al., 2008). This argues for body size variation being responsive to the same factors as other orders, in particular life history trade-offs relating to resource abundance and predation. However, that primates do respond in this way does not mean that this is what underpins clinal variation. Indeed correlational nature of the examples of clinal variation given makes proving causation challenging. Experimental manipulation is the most unambiguous method of establishing causation, though in the case of size-temperature variation it is of course impracticable and unethical. Nevertheless, instances of translocation provide evidence that environments do modulate body size with temperature. A population of macaques were translocated from Japan to two locations in the USA (Paterson, 1996). The macaques at the colder Oregon site were heavier than those at the warmer Texas site. This corresponded to a decrease in surface area to body mass of about 10%, consistent with metabolic heat loss argument. The time depth was only two generations, suggesting phenotypic plasticity (Paterson, 1996). A comparison of china-born and Louisiana-born macaques displayed a comparable trend with those from the latter warmer climate exhibiting lower mass and longer limbs than the cold-climate oriental specimens (Clarke and O'Neil, 1999). Both studies seem to suggest temperature determines body size and proportions. However, caution must be used when making conclusions from populations *in vivo* as these non-natural surroundings can be different from nature in numerous ways as well as the fact that captive animals develop aberrantly (O'Regan and Kitchener, 2005).

A more consistent and comparable set of studies reveal strong clinal variation in three African primates. Blue monkeys (Cardini et al., 2010), vervets (Cardini et al., 2007) and red colobus monkeys (Cardini and Elton, 2009) have all been found to exhibit a decreasing size cline from Central to East Africa. The pattern is not entirely the same and there are differences in other parts of Africa: blue monkey and red colobus get smaller in West Africa whereas vervets get larger (Cardini et al., 2007, Cardini et al., 2010, Cardini and Elton, 2009), but the Central-East African trend remains. This trend was found to be highly correlated with average annual rainfall in vervets arguing for a resource-based underpinning (Cardini et al., 2007), although this relationship was less strong for red colobus (Cardini and Elton, 2009), and in baboons, while Dunbar (1990) found a relationship between rainfall and body mass, recent analysis with fuller data show this is not the case across *P. hamadryas* (Jolly, 2011) though may be the case within its subspecies (Jolly, 2011).

Owing to the idiosyncrasies of these findings are partly because of a lack of study, as with meta analyses across orders, there is no definitive answer as to what causes clinal variation in primates. Indeed this may be because an array of environmental factors is involved such as rainfall, moisture, and productivity (Millien et al., 2006, Meiri et al., 2007). However, this uncertainty begs further study to dissociate these variables.

2.1.6 Clinal Variation in the Baboon

Table 2.1. Approximate body mass values for the baboon subspecies (taken from Fleagle, 1988, with P. h. kindae *data from Jolly, et al. 2011).*

Subspecies	**Body Mass (kg)**	
	F	**M**
P. h. anubis	13.3	21.8
P. h. cynocephalus	12.3	29.8
P. h. hamadryas	9.9	16.9
P. h. papio	12.1	25.1
P. h. kindae	10.0	16.0
P. h. ursinus	14.8	29.8

Describing the subspecific variation within *Papio hamadryas* as discrete or continuous clinal has been at the heart of the study of this species since the beginning (Osman Hill, 1971, Zuckermann, 1926, Goldblatt, 1926, Elliot, 1913). While there are discontinuities, modelling baboon morphological variation as continuous revealed that geographic position explained 60% of shape variation (Frost et al., 2003). Across Africa Frost et al. (2003) found evidence of a stepped cline in a north south direction, with the greatest step between northern and southern taxa. Northern forms had wider skulls and less ventrally flexed rostra than southern forms. However, the size correction used by Frost et al. (2003) renders comparison with vervet monkeys difficult, as for this species size was the major part of morphological variation. Indeed it is likely to be the most important ecological aspect (Peters, 1983). Size variation has been documented (table 2.1) for the subspecies. Additionally Jolly (1993) observed that among the olive baboon the forest-dwelling populations in Uganda and the Congo were larger, as did Elliot(1909), while those animals at the periphery of the range were smaller. Also chacma baboons are large bodied (table 1, Anderson, 1982) while hamadryas and Guinea baboons are small (Jolly and Phillips-Conroy, 2003, Jolly and Phillips-Conroy, 2006). While there are diagnosable and discrete characteristics that can be used to identify baboon subspecies, such as pelage, baboon variation does have a continuous component in morphology and size. The best example of this is the size cline running from Zambia to the east African coast from Kinda to yellow baboons (Freedman, 1963).

While baboon morphology is undoubtedly spatially variable, it is not clear whether this variation has arisen in response to the environment, as is the suggestion in so many other cases of clinal variation. Primate instances of biogeographic rules seem lacking. However baboons are extremely responsive to the environment in numerous ways (Chapter 1). This is well documented in the case of changes to group size (Byrne et al., 1993), composition (Hamilton III and Bulger, 1992) and hierarchy (Barton et al., 1996) between populations. Similarly behavioural time budget is affected by day length (Hill et al., 2003), rainfall (Bronikowski and Altmann, 1996) and temperature (Hill, 2006). Of course this behavioural and social plasticity and responsiveness might buffer the morphology from the effects of natural selection. Examining the correlation between environmental and craniofacial variation will help answer this question.

Environmental variation over the baboon range is extensive. Rainfall and temperature have a clear relationship with primary productivity and thus affect the availability of resources. Additionally the seasonal photoperiodic reduction with latitude reduces foraging time and compounds the effects of food shortage over the winter months (Hill et al., 2003). Resource availability influences infant growth in baboons and provisioned specimens grow faster and reach a higher weight than unprovisioned animals (Strum, 1991). The effects of infant provisioning continue into adulthood (Strum, 1991). As has been mentioned, early work showing a size-rainfall relationship has been refuted by fuller data, although it cannot be ruled out that within subspecies size is structured by rainfall mediated resource ability (Jolly, 2011). Of course rainfall is only one crude proxy for primary productivity and environmental variation, and there is still much to uncover in both the pattern of baboon size and shape variation and its interrelation with environmental variables. As this species has such a great geographic extent and wide range of environmental variation it is an excellent candidate for the study of clinal variation and is likely to add considerably to the growing body of knowledge on this subject.

2.1.7 Aims, Hypotheses and Assumptions

The first aim of this chapter is to describe and quantify the geographic variation in baboon size and shape variation in order to test the hypothesis that baboons are subject to Bergmann’s rule, as is the case for certain other mammalian species. Indeed Frost et al (2003) found north-south shape variation, and thus such a rule may be in operation. Alternatively it may be expected that given the absence of such a rule in vervets (Cardini et al., 2007) that there would not be a latitudinal pattern of size variation. Consequently, the second hypothesis to test is that vervets and baboon have affinities in the pattern of subspecific size and shape variation across their broadly similar geographic ranges. In order to be confident in the comparison, vervet data are reanalysed to address some methodological differences between published vervet work (Cardini et al., 2007, Elton et al., 2010) and the adapted method employed here. This will shed light on the extent to which the two taxa have been moulded by the same environmental forces, versus disparate stochastic effects.

The second aim of this chapter is to dissociate size dependent and size independent baboon shape. Size is evolutionarily labile and much of shape variation is size-dependent or allometric, often with larger animals exhibiting proportionally smaller crania but larger faces (Gould, 1971, Emerson and Bramble, 1993). As such it has been assumed that differences in size independent shape reflect greater divergences between taxa (Marroig and Cheverud, 2005); in other words translations along a size-shape trajectory require little genetic drift or selection whereas deviations from this trajectory do. This assumption will be used to test the null hypothesis that the shape variation in baboons is chiefly the result of allometric scaling. Visualisation of the clinal pattern of size-independent shape will thus display differences most related to phylogenetic distance, and will thus enable interpretation of baboon morphology in a context of past environmental variation and population structure.

2.2 METHOD

2.2.1 Sample

Table 2.2. The morphological sample broken down by subspecies and sex.

Subspecies	Sex	N
P. h. Anubis	Male	120
	Female	56
P. h. cynocephalus	Male	63
	Female	11
P. h. hamadryas	Male	17
	Female	4
P. h. kindae	Male	11
	Female	11
P. h. papio	Male	13
	Female	1
P. h. ursinus	Male	45
	Female	9
	Total	361

Anatomical landmark data for 361 *Papio hamadryas* spp. (table 2.2) were extracted from the Leverhulme Old World monkey database (Elton and Cardini, 2008) . Each specimen was described by 86 craniofacial landmark coordinates (table 2.3). This morphological dataset was originally taken from museum skulls, by a previous researcher, and only well provenanced specimens, namely those with latitude and longitude data or a place name for which they could be found, were included. To avoid the inaccuracies and archaic terminologies inherent in museum catalogues, for this analysis taxonomic assignment was carried out on the basis of specimen location. This involved plotting point localities for all specimens using ArcGIS (ESRI, 2009) and assigning a taxon to each on the basis of which of the six subspecific geographic range it fell in (see Chapter 1 for subspecific ranges). The advantage of this method was that if no subspecific taxon was given but the specimen was well provenanced, as was occasionally the case, this method saved us from disregarding the specimen for analysis. If a taxon was given it typically agreed with the corresponding geographic range designation. While the time period over which specimens collected adds some uncertain in the face of moving geographic ranges, such changes, are likely to be on the scale of tens of miles, are likely to be negligible compared with the pan-continental resolution considered here. Subspecies taxon GPAs were carried out, enabling the identification of any outliers resulting from misclassification.

Table 2.3. Descriptions of the landmarks digitised used to capture shape in the Leverhulme Database and this study (taken from Cardini et al., 2007).

No	Description
1	Prosthion: antero-inferior point on projection of pre-maxilla between central incisors
2	Prosthion2: antero-inferior-most point on pre-maxilla, equivalent to prosthion but between central and lateral incisors
3	Posterior-most point of lateral incisor alveolus
4	Anterior-most point of canine alveolus
5	Mesial P3: most mesial point on P3 alveolus, projected onto alveolar margin
6-9	Contact points between adjacent pre-molars/molars, projected labially onto alveolar margin
10	Posterior midpoint onto alveolar margin of M3
11-14	Contact points between adjacent pre-molars/molars, projected lingually onto alveolar margin
15	Posterior-most point of incisive foramen
16	Meeting point of maxilla and palatine along midline
17	Greater palatine foramen
18	Point of maximum curvature on the posterior edge of the palatine
19	Tip of posterior nasal spine
20	Meeting point between the basisphenoid and basioccipital along midline
21	Meeting point between the basisphenoid, basioccipital and petrous part of temporal bone
22	Most medial point on the petrous part of temporal bone
23	Most medial point of the foramen lacerum
24	Meeting point of petrous part of temporal bone, alisphenoid and base of zygomatic process of temporal bone
25-26	Anterior and posterior tip of the external auditory meatus
27	Stylomastoid foramen
28,30	Distal and medial extremities of jugular foramen
29	Carotid foramen
31	Basion: anterior-most point of foramen magnum
32,35	Anterior and posterior extremities of occipital condyle along margin of foramen magnum
33	Hypoglossal canal
34	Centre of condylar fossa
36	Opisthion: posterior-most point of foramen magnum
37	Inion: most posterior point of the cranium
38	Most lateral meeting point of mastoid part of temporal bone and supraoccipital
39	Nasospinale: inferior-most midline point of piriform aperture
40	Point corresponding to largest width of piriform aperture
41	Meeting point of nasal and pre-maxilla on margin of piriform aperture
42	Rhinion: most anterior midline point on nasals
43	Nasion: midline point on fronto-nasal suture
44	Glabella: most forward projecting midline point of frontals at the level of the supraorbital ridges
45	Supraorbital notch
46	Frontomalare orbitale: where frontozygomatic suture crosses inner orbital rim
47	Zygo-max superior: antero-superior point of zygomaticomaxillary suture taken at orbit rim
48	Centre of nasolacrimal foramen (fossa for lacrimal duct)

49	Centre of optic foramen
50	Uppermost posterior point of maxilla (visible through pterygomaxillary fissure)
51	Frontomalare temporale: where frontozygomatic suture crosses lateral edge of zygoma
52	Maximum curvature of anterior upper margin of zygomatic arch
53	Zygo-max inferior: antero-inferior point of zygomaticomaxillary suture
54	Zygo-temp superior: superior point of zygomaticotemporal suture on lateral face of zygomatic arch
55	Zygo-temp inferior: infero-lateral point of zygomaticotemporal suture on lateral face of zygomatic arch
56	Posterior-most point on curvature of anterior margin of zygomatic process of temporal bone
57	Articular tubercule
58	Distal-most point on post-glenoid process
59	Posterior-most point of zygomatic process of temporal bone
60	Foramen ovale (posterior inferior margin of pterygoid plate)
61	Meeting point of zygomatic arch and alisphenoid on superior margin of pterygomaxillary fissure
62	Meeting point of zygomatic arch, alisphenoid and frontal bone
63	Bregma: junction of coronal and sagittal sutures
64	Lambda: junction of sagittal and lamboid sutures
65	Antero-superior point of mandible between central incisors
66	Antero-superior point of mandible between lateral incisors
67	Posterior-most point of lateral incisor alveolus
68	Anterior-most point of canine alveolus
69	Mesial P3: most mesial point on P3 alveolus, projected onto alveolar margin
70-73	Contact points between adjacent pre-molars/molars, projected labially onto alveolar margin
74	Posterior midpoint onto alveolar margin of M3
75-78	Contact points between adjacent pre-molars/molars, projected lingually onto alveolar margin
79	Superior tip of coronoid process
80-81	Most lateral and most medial points on mandible condylar surfaces
82	Anterior-most point on roughening for attachment of masseter on inferior margin of the angle of mandible
83	Mandibular foramen
84	Posterior-most point on superior area of insertion of medial pterygoid
85	Region of insertion of genioglossus muscles (midline posterior-most point on upper ‘ridge behind incisors’)
86	Region of insertion of geniohyoid muscles (midline posterior-most point on lower ‘ridge behind incisors’)

The original dataset only contained landmark data for the left half of the baboon and vervet skulls. Also not all of the specimens were complete. For this analysis these problems were addressed using the method outlined fully in Cardini et al. (2010). Briefly, a GPA (Zelditch et al., 2004, Slice, 2007, Rohlf and Slice, 1990), was carried out, superimposing the landmark configurations and removing differences in size and orientation. However, this superimposition was carried out only on the midline landmarks. The *impute* function of Morpheus et al. (Slice, 1999) was used to fill in missing landmarks on the basis of other specimens of the same taxon and sex. Skulls were reflected in Morpheus et al. to create right sides. These were superimposed and the new shape co-ordinates were paired with the corresponding left. The left and right midline landmarks were averaged for each specimen (the skulls were not perfectly symmetrical) and the two halves were united in a single configuration. Size was added back at all stages, post GPA.

2.2.2 Capturing Shape

The major axes of shape variance of the coordinate data are summarised by principal components (Adams et al., 2004, Slice, 2007). These vectors are orthogonal axes that maximise the variance explained, analogous to best fit lines, but in multiple dimensions. The first PC describes the most variance and the last the least. PCA produces as many principal components as there are coordinates. However, in a regression there is a trade-off between the number of variables used and the accuracy of the model (Cardini et al., 2010). Thus to work out the optimal number of PCs to use, i.e. the fewest that describe most of the total variance, the following method was used: the Euclidean distance matrix (ED), based on the PCs, is correlated with the Procrustes distances matrix (PD). When all PCs are included the ED matrix correlates perfectly with the PD matrix. Reducing the number of PCs reduces the correlation between ED and PD matrices. This drop-off is not linear but has a turning point. This point represents a trade-off between accuracy and economy of PC inclusion (Cardini et al., 2010).

Variation in specimen morphology within groups was then visualised and outliers were identified using UPGMA cluster analysis of the PCs, and various biplots of PCs. Morphological outliers that were the result of incorrect grouping or those with specimens aberrant landmarks were assumed to be the result of measurement mistakes and were excluded from the analysis.

2.2.3 Sex-Correction

The sample size of female baboons is small (table 2.2). Rather than attempt to make nonrobust conclusions about the two sexes separately, it was decided to boost the male sample by converting the female morphologies to males (Cardini et al., 2010), thereby increasing the variation for analysis. This was achieved by adding the difference between the mean male and mean female size and shape to the mean female size (univariate) and shape (multivariate: differences per coordinate). This was done for each subspecies separately to allow for differences in subspecific differences in sexual dimorphism. This method thus added female variation around the mean to male variation, increasing the chances of detecting an environmental signal. An assumption here is that females have a similar geographic pattern to males. Provisional analyses suggest that both exhibit corresponding spatial variation in size. To check that this produced genuine male phenotypes, cluster analysis was used on the PCs to show grouping was not on the basis of former sex. Discriminant function analysis was used to check that males and transformed females were not different in size and shape.

2.2.4 Geographical Averaging

Specimen localities were far from evenly distributed. Certain localities had single skulls while other had up to ten. The Lake Victoria area was particularly densely sampled. Such local clustering is likely to skew the results of an overall trend, as regressions minimise variance and much of the variance in concentrated in a particular regions. By averaging localities the variance is more evenly weighted. 50km buffers were calculated in ArcGIS (ESRI, 2009) around each locality and were used work out which specimens should be averaged. Microsoft Excel (2007) was used for averaging. Different taxa were not averaged because of our *a priori* expectation of a difference in morphology.

2.2.5 Environmental Variable Selection

Raw environmental data for 0.5 decimal degree points for precipitation, moisture index, and temperature were taken from the Wilmott & Matsuura database (Willmott et al., 1998, Willmott et al., 2001, Willmott and Matsuura, 2001). An extrapolated surface was created from this. Normalised difference vegetation index (NDVI) (Zinner et al., 2001, Willems et al., 2009) is a remotely detected measure of photosynthetic activity and was downloaded for each month from the Africa Data Dissemination Service (ADDS, 2005). Altitude was acquired from the Earth Resource and Information Center (USGS, EROS). Using ArcMap the specimen localities were plotted and using Spatial Analystand the Extract to Points function values for each of the above variables was obtained for each specimen. Then monthly means, standard deviations and ranges were calculated as well as other indices that have been found to be important factors in other studies such as P2T (the number of months where precipitation (mm) is twice the temperature ($°C$)), seasonality index (SI) and Shannon Rainfall index (D) (Bronikowski and Webb, 1996, Korstjens and Dunbar, 2007), calculated thus:

$$D = -\frac{\sum(\, \mathrm{p}_i . \ln(\mathrm{p}_i)}{\ln(12)}$$

Where p_i is the proportion of the total rainfall in a given month.

$$\mathrm{SI} = \frac{\mathrm{Prec}_{\mathrm{Max}} - \mathrm{Prec}_{\mathrm{Min}}}{\mathrm{Prec}_{\mathrm{Mean}}}$$

Where $\mathrm{Prec}_{\mathrm{Max}}$, $\mathrm{Prec}_{\mathrm{Min}}$ and $\mathrm{Prec}_{\mathrm{Mean}}$are the maximum, minimum and mean precipitation value.

2.2.6 Regressing Size and Shape on Geography

The spatial variation in morphology was investigated using trend surface analysis (Legendre and Legendre, 1998). This technique was employed because it is a highly effective way of modelling spatially structured variation and has been employed for other African primates, enabling comparability of results. However, the model is best employed for continuous variation. While there is hybridisation, some gene flow and consequent character affinities on both sides of baboon subspecific division, gene flux reductions are present and have been more extensive in the past, leaving their stamp on subspecific variation (Jolly, 1993, see Chapter 5, Zinner et al., 2009b). The model therefore becomes inaccurate at these divisions, smoothing over these sharper discontinuities and providing a distorted picture. However, local distortions aside, the general geographic pattern of variation is expected to be representative, and is appropriate for answering the hypotheses, namely determining if the existing biogeographic rules have shaped subspecific variation, and if the overarching pattern is similar to that of other vervets. Indeed a quantification of the total variance explained by the TSA gives an insight into how far the model can be trusted, and it is of interest to compare this with vervets. More localised information about where the slopes are steepest can be gleaned from the discriminant function analysis, where higher misclassification rates denote greater dissimilarity. Interpreted together these two methods can give a less biased view.

Trend surface analysis modelling works best with continuous variation, although variation in the baboon case contains discontinuities in the form of a stepped cline. The Kinda baboon is an outlier for size, and forms a sharper discontinuity with the other taxa. It could be hypothesised that because it is so small this discretely different subspecies is not responsive to the environment in quite the same way; it is on the other side of an adaptive watershed. If this is so it would reduce a covariation between environment and morphology in the other baboon taxa. An additional consideration is that the sharp change between this taxon and its neighbour presents a difficulty to modelling using this method, as discussed above. For these reasons the analyses are carried out with and without this outlying taxon to see what effect it has on the TSA and partial regression analysis

There are two isolated populations over which there is no gene transfer of any sort. These are those of the Saharan massifs, cut-off by the Sahara, and the Southern Saudi Arabian populations isolated by the Red Sea (Masset and Bruner, 2009). Morphological characters of these geographical outliers are unlikely to be the result of the forces driving the main interconnected population, as they are more likely to be at the result of drift and founder effects. Additionally their position at the periphery of the spatial range makes them particularly powerful with regard to distorting a trend. For these reasons these outliers were removed.

The trend surface analysis method for multivariate data involves regressing the principal components (PCs) of shape onto spatial variables; longitude (x) and latitude (y) in the linear case or a cubic expansions of this in the polynomial case. This study regressed PCs onto the linear case (xy) and the full cubic case (x y x^2 xy y^2 x^3 x^2y xy^2 y^3) but also onto the significant cubic case i.e. where nonsignificant terms were removed. To compare the quality of the models the variance explained by each regression was calculated. The predicted values of these bi- or polynomial terms were then plotted directly on the map. Size can be plotted directly on a map but shape, which is multivariate, cannot. In the case of shape a PCA of the predicted PCs was carried out using NTSys (Rohlf, 2008), resulting in geospatial PCs (gsPCs) (*sensu* Cardini and Elton, 2009). These were plotted on a map and contours displayed using ArcGIS (ESRI, 2009).

In order to test the robustness of the geospatial PCs to the removal of some of the data, and hence the strength of the trend, the analysis was carried out on a dataset comprising a random two thirds of the full dataset. Similarity in the pattern on a reduced dataset attests to the robustness of the trend. To get an idea of the quality of each holdout the variance of the held out sample explained by the holdout model was calculated.

2.2.7 Partitioning Spatial and Environmental Terms

Spatial terms and environmental terms are not independent but correlated. Partial regression (Legendre and Legendre, 1998) is a method to quantify the variance explained by certain factors exclusively as well as the shared or overlapping component of correlated factors. Practically this procedure involved regressing size and shape (separately) onto the spatial components, latitude and longitude, and environmental terms, such as rainfall and temperature. The variance explained by this overall model was quantified. The same analysis was carried out for the environmental component alone and then for the spatial component alone. Because the first spatial-environmental regression represents the variance explained by both the two separately and the overlap, the exclusive component of each can be calculated by simple subtraction and algebraic substitution (see Legendre and Legendre, 1998).

2.2.8 Size Correction

Size has a profound effect on shape. Removal of the size-dependent component of shape was achieved by regressing shape onto size and saving residuals in SPSS (SPSS Inc., 2009). Because the subspecies were found here to have different allometric trajectories a code representing taxon was used as a covariate. This model keeps allometric size-shape slopes of equal gradient but allows them to differ (Elton et al., 2010).

2.2.9 Subspecific Differences

Discriminant function analysis was used to assess the degree of similarity of subspecies (Elton et al., 2010). The ratio of misclassified individuals to correctly classified individuals, after cross-validation, gives a measure of similarity. For instance if two subspecies are always correctly classified they are clearly different, while if they are misclassified into the other group more than 50% there cannot be said to be a difference between them. This was used before and after the size-correction establishing the importance of size in subspecies distinctiveness.

2.3 RESULTS

2.3.1 Baboon Size

Actual baboon centroid sizes for the specimens were plotted.

Figure 2.1. The location of baboon specimens for all taxa (n=112), where point size is scaled according to the centroid size of the skull.

The existing variation was modelled using a trend surface analysis approach. The same analyses were carried out on two thirds to the datasets creating holdouts in order to test the robustness of the trend.

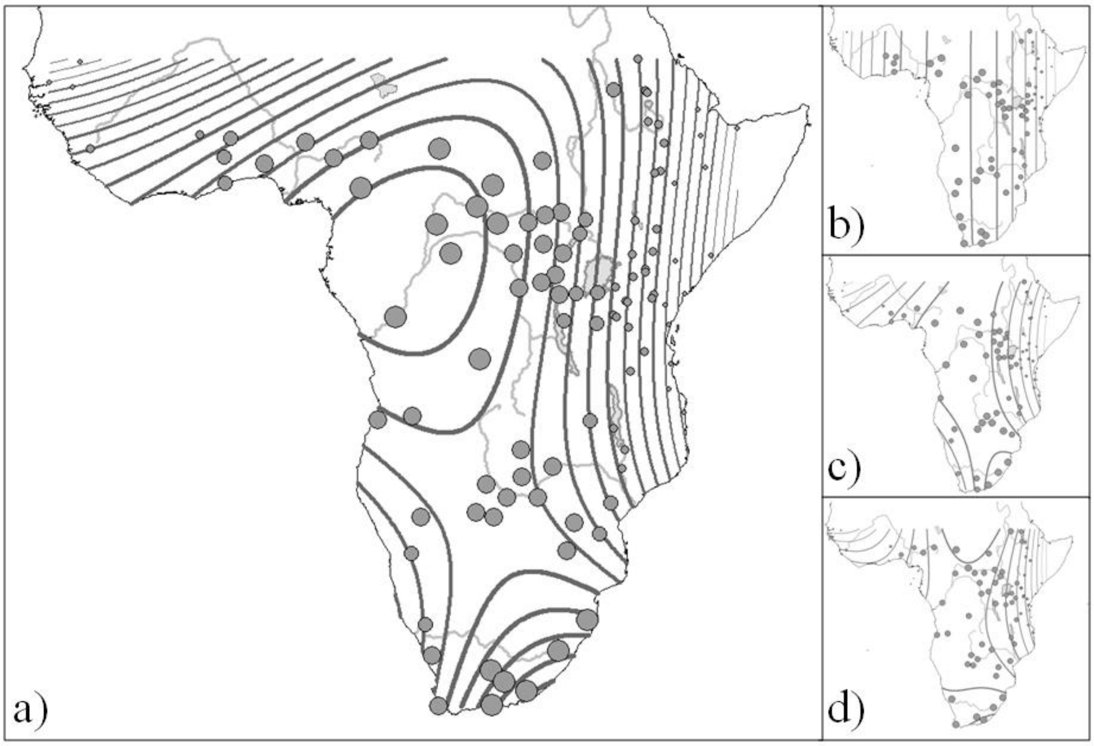


Figure 2.2. The baboon size trend surface analysis for a) all taxa minus P. h. kindae *and b-d) the three holdouts. Terms in regression* ***a)*** *were x y^2 x^3 xy^2, variance explained 55.9%. n =106. Variances explained for the holdouts are* ***b)*** *33.0,* ***c)*** *72.3 and* ***d)*** *22.4% of the held-out third.*

There is considerable size variation in the baboon subspecies (fig. 2.1). The Kinda baboon in particular is much smaller than the other subspecies. One of the assumptions here is that subspecific variation is environmentally structured. If one taxon is so different from the others it is unlikely to respond to the environment in the same way, just as species may respond to a common environment disparately. For this reason the trend surface analysis is first carried out excluding this subspecies. The nonKinda TSA reveals a strong east-west cline of increasing then decreasing size (fig. 2.2 a). This trend explains 55.9% of the size variance. This pattern is borne out in the holdouts (fig. 2.2, b, c, d). The TSA shows a north-south cline slightly less pronounced than the east-west one with a peak around central Africa, rising again in South Africa. This trend is weaker in the two of the holdouts (fig. 2.2b, 2c) and not present in one (fig. 2.2d).

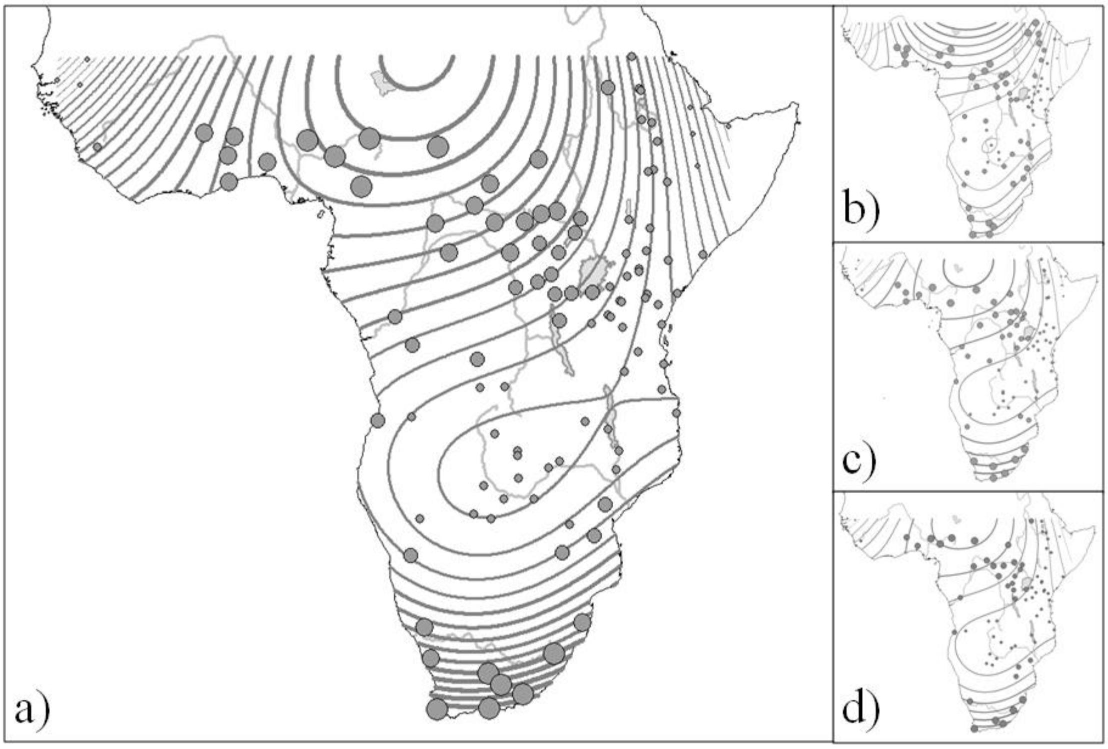


Figure 2.3. The baboon size trend surface analysis for a) all baboon taxa b-d) the three holdouts. Terms in regression a) were xy x^3 x^2y y^3*, variance explained 24.7%, n =106. Variances explained for the holdouts are b) 9.7, c) 29.5 and d) 18.2% of the held-out third.*

The TSA when the Kinda baboon is included has a much lower explanatory power: 24.7% compared with 55.9% when this taxon is excluded (fig. 2.3a). The clinal pattern of increasing and then decreasing size from east to west is present (fig. 2.3a) as with the *P. h. kindae* excluded TSA (fig. 2.2a). The with- and without -*P. h. kindae* TSAs are mainly different in the range of and adjacent to this taxon. The three holdouts corroborate the pattern (fig. 2.3b, c, d).

2.3.2 Vervet Size

While vervet clinal variation has been mapped (Cardini et al., 2007) methodological differences between this study and that that might create artefactual differences. For consistency of comparison therefore the same analysis was carried out for vervet size.

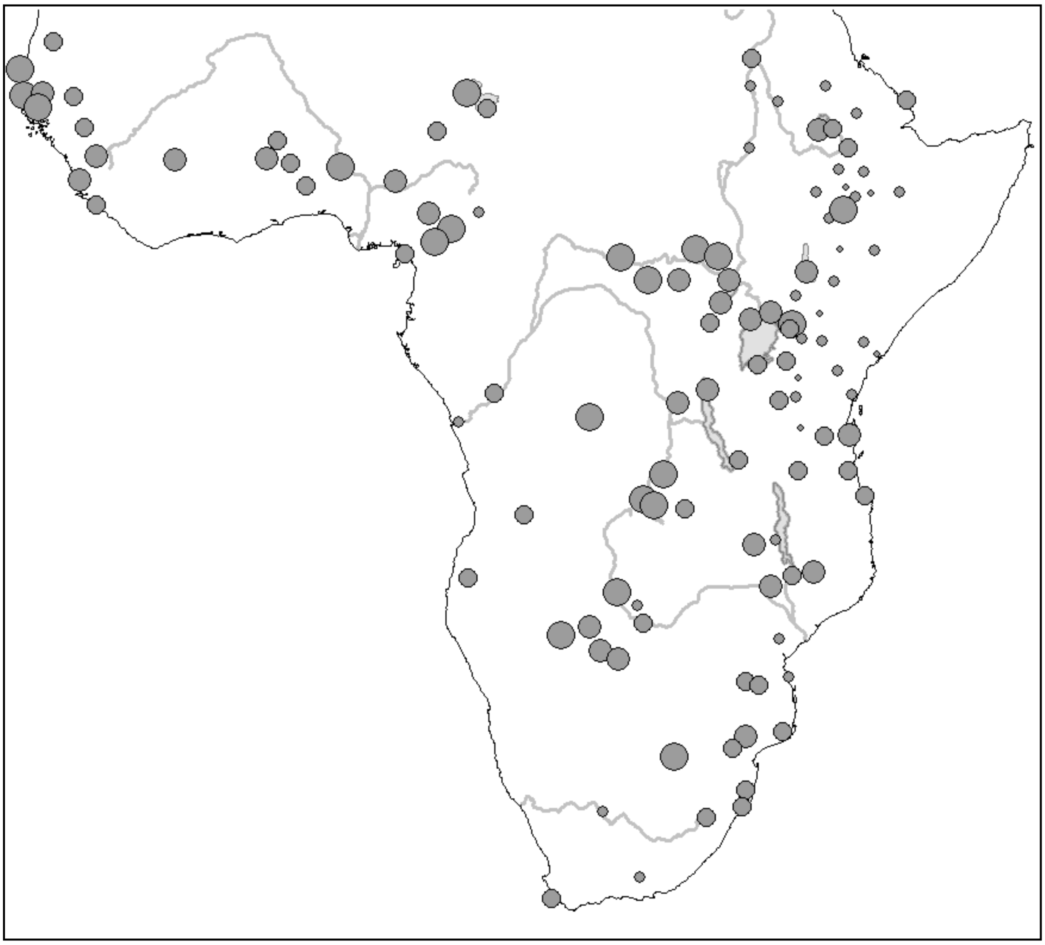


Figure 2.4. The location of specimens for all vervet taxa (n=117), where size of the dot is proportional to centroid size of the skull.

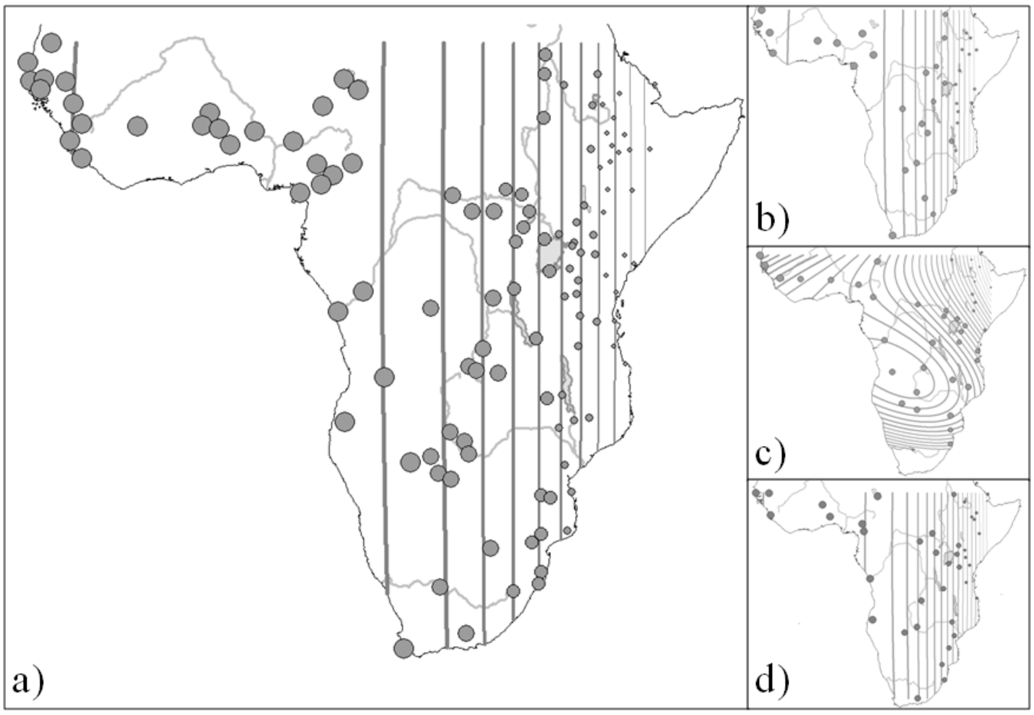


Figure 2.5. The vervet size trend surface analysis for a) all vervet taxa b-d) the three holdouts. Terms in regression a) were x^3 *alone, which explained 29.5% of the variance, n =117. Variances explained for the holdouts are b) 19.8, c) 57.8 and d) 29.6% of the held-out third.*

Vervets are variable in size across their geographic range (fig. 2.4). Trend surface analysis of this variance reveals a strong east-west axis of variation (fig. 2.5). This is robust as the three holdout samples demonstrate the same trend, exactly for holdout 1 and 3 (fig. 2.5 b, d), and approximately with a small amount of north south variation for holdout 2 (fig. 2.5c).

2.3.3 Baboon Shape

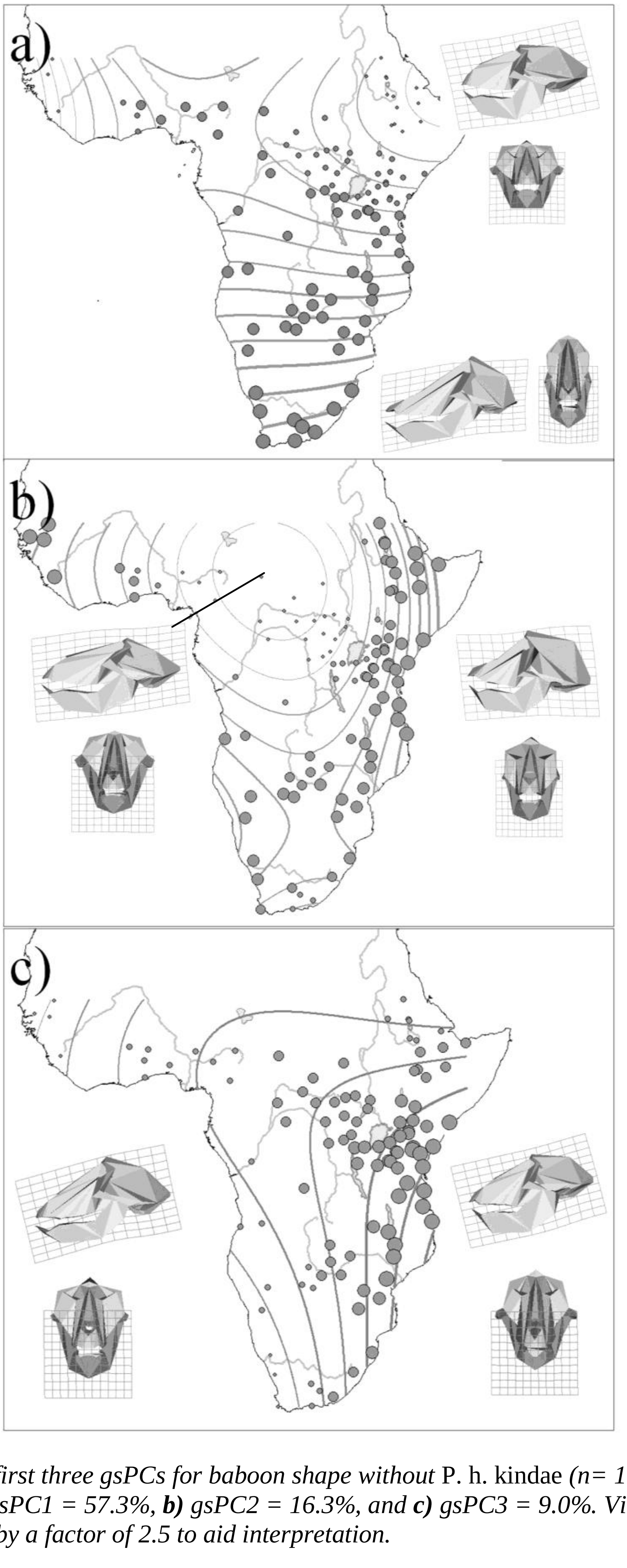


Figure 2.6. The first three gsPCs for baboon shape without P. h. kindae *(n= 106). Variance explained by* ***a)*** *gsPC1 = 57.3%,* ***b)*** *gsPC2 = 16.3%, and* ***c)*** *gsPC3 = 9.0%. Visualisations are exaggerated by a factor of 2.5 to aid interpretation.*

The first geospatial PC of baboon shape, which explains most variation, shows a minimum in west Africa and north east Africa with central Africa intermediate and South Africa at a maximum (fig. 2.6a). Morphologically this minimum corresponds to a short rostrum and mandible, large neurocranium and wide face compared with the maximum. Also, the face is convex rather than concave and the anterior part of the neurocranium is elevated relative to the occiput in the minimum relative to the maximum extremes of shape.

The second gsPC (fig. 2.6b) has a similar spatial pattern to gsPC1 with minima located in West and north-east Africa, but maxima in Central Africa and a slight drop and rise down to South Africa. The minimum corresponds to a small face, large neurocranium and wide face relative to the maximum. The rostrum of the minimum is concave while the larger is convex in contrast to gsPC1. The third gsPC (fig. 2.6c) which accounts for a smaller amount of variance shows a maximum along the coast of East Africa decreasing north and west. The maximum exhibits a deep while the minimum has a shallow jaw and flared zygomatic arches. The shape pattern (fig. 2.6a) is similar to that of size (fig. 2.2a) and indeed the first and second gsPCs but not the third are correlated with size (table 2.4).

Table 2.4. Results of regression of gsPCs onto centroid size.

Sample size	**Geospatial PC**	**F**	**P value**
112	1	11.72	0.001
	2	14.171	0.000
	3	1.24	0.268
106	1	27.207	0.000
	2	49.067	0.000
	3	1.087	0.300

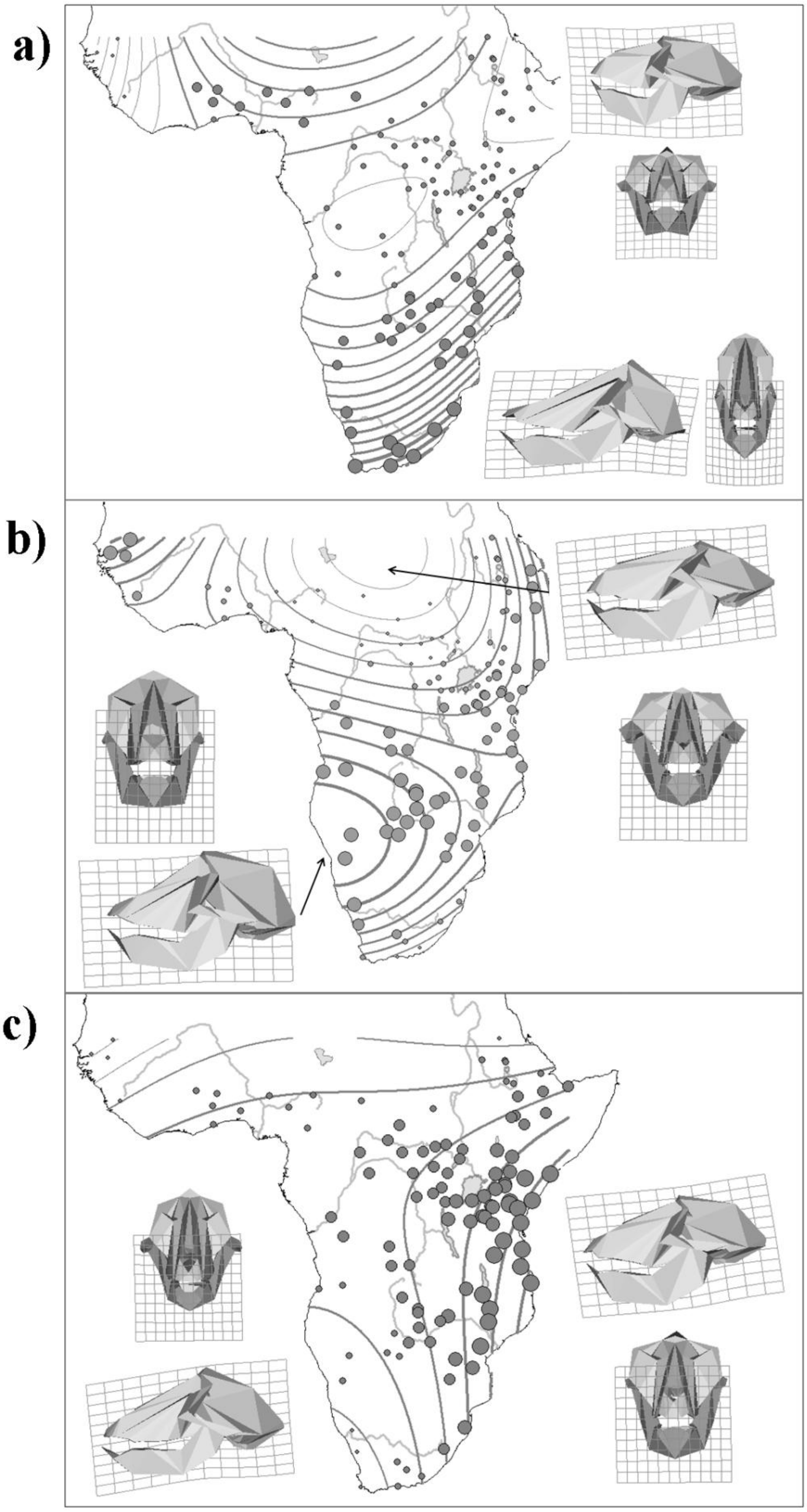


Figure 2.7. The first three gsPC for baboon shape including P. h. kindae *(n= 112). Variance explained by a) gsPC1 = 57.3%, b) gsPC2 = 16.3%, and c) gsPC3 = 9.0%. Visualisations are exaggerated by a factor of 2.5 to aid interpretation.*

2.3.4 Size-Controlled Shape

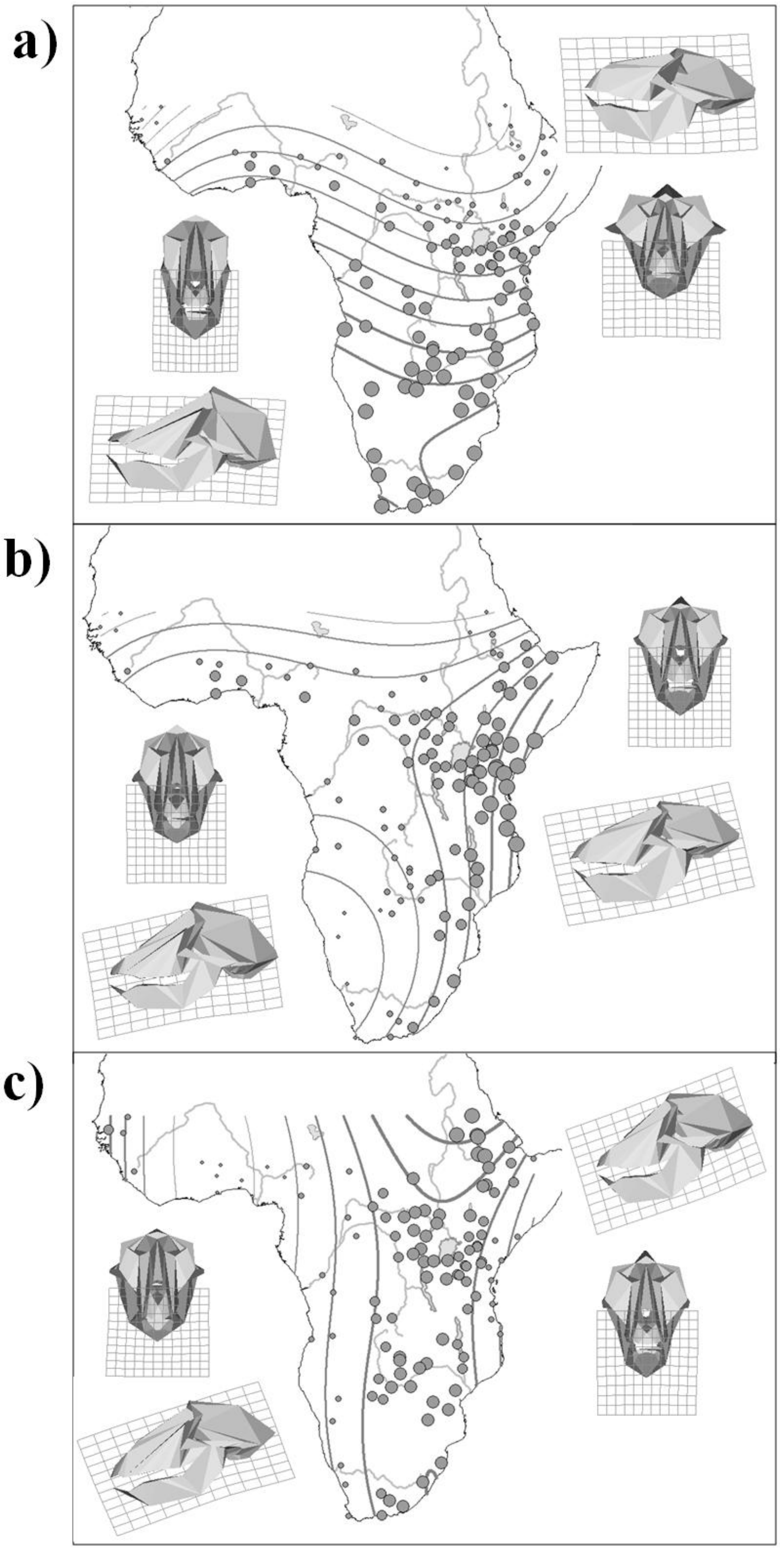


Figure 2.8. Size-controlled geospatial PCs for the full dataset (n=112). Percentage of variance explained by ***a)*** *SCgsPC1 is 61.0%* ***b)*** *SCgsPC2 is 14.5%* ***c)*** *SCgsPC3 is 8.7%. Visualisations exaggerated by a factor of 2.5 to aid interpretation.*

The first size-controlled gsPC reveals a north-south clinal trend (fig. 2.8). The northern morphology corresponds to shorter rostrum (i.e. decreasing nostril to glabella distance) and a change from a concave to a convex rostrum, as well as a slightly shallower mandible and a shorter narrower head relative to the north. The second size controlled gsPC explains only a quarter as much of the variance as gsPC1. It displays an east-west trend with a maximum on the coast of East Africa dropping off to the west and north. The third size-controlled gsPC describes a complex clinal pattern. In West Africa the morphological differentiation is rather subtle accounting 8.7% of the total variation. This subtle anatomical differentiation seems to relate mainly to the depth of the mandibular corpus, which is deeper in West Africa.

2.3.5 Subspecific Differences

Table 2.5. Discriminant analyses showing the cross validated classification rates for the six subspecies.

	P. h. papio	*P. h. hamadryas*	*P. h. anubis*	*P. h. cynocephalus*	*P. h. ursinus*	*P. h. kindae*
P. h. papio	100	0	0	0	0	0
P. h. hamadryas	0	77.78	11.11	11.11	0	0
P. h. anubis	2.04	4.08	75.51	12.24	6.12	0
P. h. cynocephalus	0	0	25	65	10	0
P. h. ursinus	0	0	0	12	88	0
P. kindae	0	0	0	0	0	100

The discriminant function scores (table 2.5) reveal that *P. h. papio* and *P. h. kindae* are never misclassified while *P. h. hamadryas*, *P. h. ursinus* and *P. h. anubis* are misclassified.

Table 2.6. Discriminant analysis showing the cross-validated classification rates for the groups subspecies with size controlled.

	P. h. papio	*P. h. hamadryas*	*P. h. anubis*	*P. h. cynocephalus*	*P. h. ursinus*	*P. h. kindae*
P. h. papio	100	0	0	0	0	0
P. h. hamadryas	0	44.44	55.56	0	0	0
P. h. anubis	4.08	4.08	75.51	14.29	2.04	0
P. h. cynocephalus	0	0	35	55	10	0
P. h. ursinus	0	0	0	4	68	28
P. h. kindae	0	0	0	0	66.67	33.33

The size-controlled cross validated discriminant function scores change for all but the Guinea baboon (table 2.6). The *P. h. hamadryas* is misclassified more as *P. h. anubis* and *P. h. cynocephalus*. Additionally P. *h. anubis* is misclassified more as *P. h. papio* and *P. h. cynocephalus* and less like *P. h. ursinus*. *P. h. cynocephalus* is misclassified more as *P. h anubis* and less like itself , while *P. h. ursinus* becomes misclassified more as *P. h kindae* and less as *P. h. cynocephalus*. *P. h. kindae* is misclassified more as *P. h ursinus*.

2.3.6 Environmental and Spatial Correlates

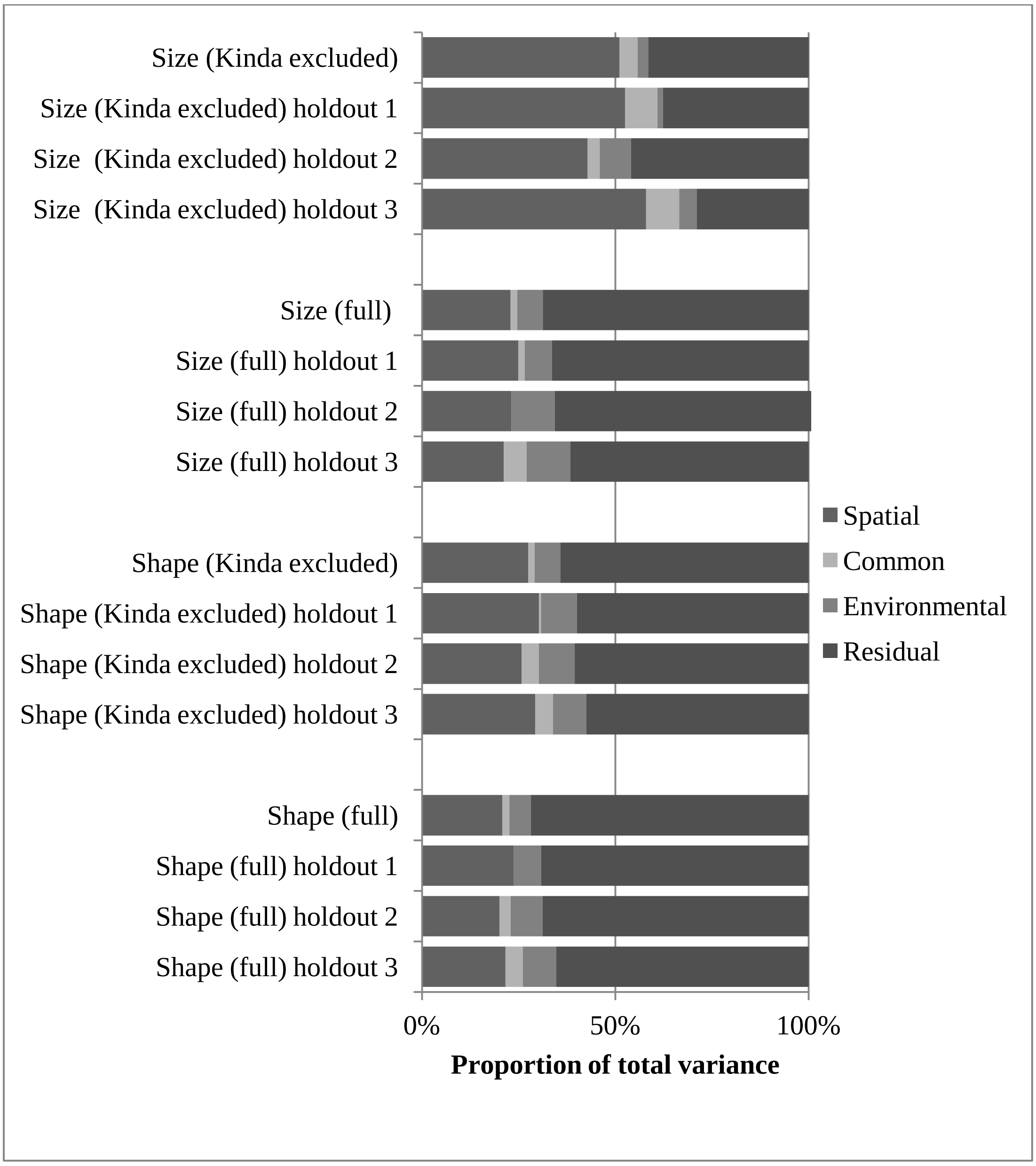


Figure 2.9. Partial Regression results showing the percentages of variance explained by significant spatial terms (x, y, x^2 *...), and environmental terms (mean temperature, rainfall etc.) and their overlap for size and shape and all the holdout with and without the Kinda baboon sample.*

In all partial regressions the spatial terms dominates, with typically a small overlap and low exclusively environmental component. Spatial terms account for a larger proportion of the variance in size than when the Kinda baboon is removed (fig. 2.9). When this subspecies is included the TSA accounts for much less of the size variance. There is a slight increase in the environmental component when the Kinda baboon is included. For shape, exclusion of the Kinda baboon makes little difference with a slight decrease in the dominant spatial component.

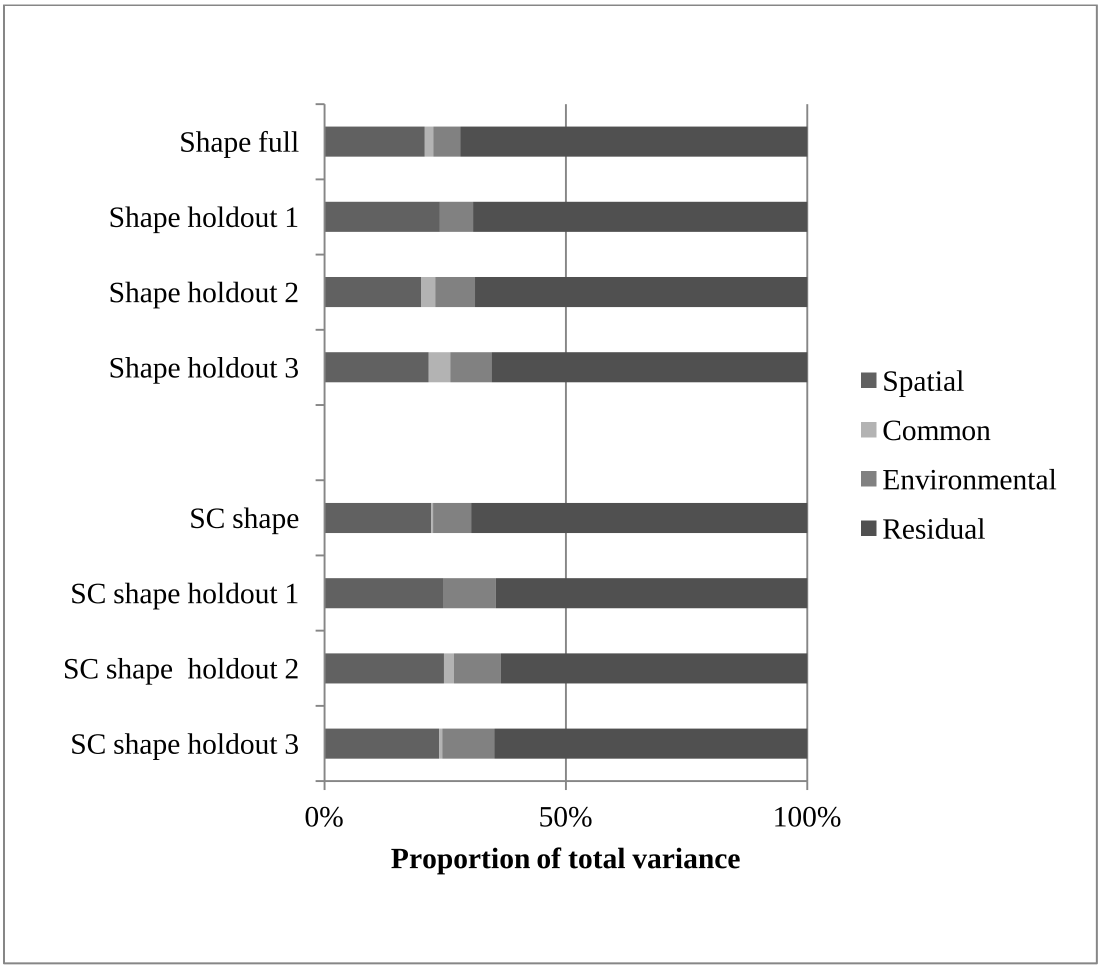


Figure 2.10. Partial regression results showing the percentages of variance explained by significant spatial terms (x, y, x2 ...) and environmental terms (mean temperature, rainfall etc.) for shape and size-controlled shape.

There is little difference between the partial regression for full shape and the partial regression for allometrically controlled shape (fig. 2.10), with size dominating as with the other partial regressions (fig. 2.9).

2.4 DISCUSSION

2.4.1 Clinal Patterns of Size

A well supported east-west pattern of size variation was found with small-sized animals in the east and west with large animals in central Africa. This instantly rules out Bergmannian thermoregulatory explanations (Millien et al., 2006) or those based on seasonality buffering over periods of food shortage (Boyce, 1978). Nevertheless, this finding is not unexpected on the basis of described baboon size variation. The eastern- and westernmost subspecies, the hamadryas and Guinea baboon respectively, are reported to be small bodied (Fleagle, 1988, Jolly and Phillips-Conroy, 2006). As the baboon arose in southern Africa (Newman et al., 2004) these two subspecies are on the furthest fringes of the baboon's current range. This is consistent with the edge effect explanation (Reinig 1939, reported in Scholander, 1955), as with the pattern found in European badgers (Virgós et al., 2011). The theoretical underpinning for smaller size at the edge of a specific geographic range is hypothesised to be decreasing habitat quality. However, while the hamadryas baboon lives in a resource poor environment (Schreier and Swedell, 2009, Kummer, 1968), the Guinea baboon lives in a very productive environment with high levels of rainfall, primary productivity and fruit abundance (Culot, 2003, Anderson and McGrew, 1984). However, the similarity in small stature (Fleagle, 1988), pelage (Jolly, 1993), and social arrangement, namely a form of one male group (Maestripieri et al., 2007, Galat-Luong et al., 2006), of these subspecies makes it more parsimonious to regard these traits as ancestral, present when the two radiated into the north-eastern and -western corners of sub-Saharan Africa. A subsequent expansion of the larger bodied olive baboon into the range between these subspecies might account for this small-large-small pattern (Jolly, 2003).

Of particular interest is the lack of north south variation in size. This is not in line with expectations, as the chacma is classically regarded as the largest subspecies (Fleagle, 1988, Anderson, 1982). Indeed this has been explained as being adaptive for its more temperate environment, requiring larger mass for heat conservation, and potentially starvation resistance (Anderson, 1982). Nevertheless, the central African baboons appear to occupy broadly the same contours as the chacma baboon in the size trend surface analysis. Larger size in forest baboons has been reported, but these Central African populations are not well studies. Elliot (1909) claimed that slight differences in pelage and morphology were diagnosable and designated them *Papio tessellatum* (Elliot, 1909, 1999), though taxonomic splitting at this time was extensive. Nevertheless, Gautier-Hion et al. refer to this “species” as penetrating all the way to Kisangani in the Democratic Republic of the Congo, hundreds of miles from the rainforest edge. Rowell (1964, 1966) described an extensive suite of ecological and behavioural differences between what may correspond to Elliot’s *P. tessellatum* (although found in the patchy forest of Queen Elizabeth National Park, rather than true rainforest) and the savannah baboons in the east. The most salient feature was the proportion of time spent in the forest, reaching as much as 60% with and indeed baboons were described as competent climbers in the canopy. Resources were described as “superabundant” (Rowell, 1966), with baboons eating fruits, flowers, and barks of this environment. The environment was seasonal but food was described as consistently available over the year. Moreover it was speculated that this food, which was largely leguminous, was highly rich in protein.

The variation from central Africa to East Africa passes through the Northeastern Congolian lowland forests, the Abertine Rift montane forest and East African Acacia Savannah biomes. It seems likely that this transect exhibits a marked drop in primary productivity. The savannah in east Africa is xeric and unproductive and highly seasonal in the presence of resources (Alberts and Altmann, 2006) in contrast to the environment described by Rowell (1966). Savannah baboons are forced to eat poor quality, high fibre foods such as roots and tubers (Harding, 1976, Rhine et al., 1989, Norton et al., 1987). The relaxation of limiting resources therefore is likely to result in less energy exerted on ranging and foraging and promote greater investment in somatic growth, accounting for the larger size of baboons in Uganda (Rowell, 1966). However, the abundance of food resources causing large size cannot be acting in the case of the small Guinea baboons and or the large Chacma baboons. In the former case as has been suggested evolutionary history is more likely to be at play, with this taxon retaining a smaller body size than the derived olive baboon. That said, West African olive baboons are smaller than their central African counterparts, though whether they form a continuous trend of size reduction to the Guinea baboon is unknown as this subspecies is understudied in West Africa (Kunz and Linsenmair, 2008b). For the chacma however, perhaps the large size, in common with the central olive baboons, represents a similarity in outcome to a different process. The partial regression analyses can shed some light on this. Environmental terms explained a small proportion of the total size and shape variance. As this block encapsulated primary productivity in the form of NDVI, this is at odds with a resource based underpinning to clinal variation. However, a poor relationship would indeed be expected if some populations are large because increased resources permit extra growth, such as the Congo basin olive baboons, and some are large because their temperate/seasonal environment selects against small size, such as the temperate-dwelling chacma (see Chapter 6).

Of course the low explanatory power of the environmental terms in the partial regression could be because NDVI, though being a good measure of primary productivity (i.e. photosynthesis), does not distinguish primary productivity in terms type. Not all biomass is edible to baboons: plant material can range from grasses to trees, and one would only expect an increase in the edible proportion of vegetation to result in a size increase. Still this is puzzling given the importance of rainfall in vervet clinal variation (Cardini et al., 2007). Additionally it cannot be ruled out that the environmental variables included in this study do not encapsulate all those relevant to baboon physiology, life history, and thus morphological variation. Future analyses might be augmented with additional data. High wind speed, for instance, causes heat loss generally (Rogowitz and Gessaman, 1990), and has been implicated as a driver of size in baboon (Barrett and Henzi, 1997). Additionally it is possible that the behavioural adaptations in baboons are sufficient to buffer them from environmental effects. For instance *P. hamadryas* are able to chose cool microhabitats to lower thermoregulatory costs (Stelzner, 1988).

While the above points are difficult to rule out, the fact that environmental variation does not linearly explain clinal variation is not totally unexpected, given Jolly’s (2011) findings that rainfall was not a strong predictor of size across baboon subspecies. Baboon responsiveness to current environmental variation cannot be ruled out completely, as conceivably high primary productivity in one population might result in large size because of increased resources, low primary productivity in another might necessitate large size for buffering during seasonal food shortages.

2.4.2 Clinal Patterns of Shape

The clinal pattern of shape variation largely mirrors that of size. Small animals have a skull shape exhibiting a relatively small face and relatively large neurocranium; a pattern seen in vervets (Cardini et al., 2007) and red colobus morphology (Cardini and Elton, 2009), and is indeed a standard mammalian pattern (Emerson and Bramble, 1993). However, the pattern of clinal shape change contained an additional north-south component of variation. Owing to the allometric nature of growth, shape information contains size-dependent and size-independent components. Removal of the former confirmed that the east-west trend in shape was underpinned by size variation while the north-south cline was not.

The discriminant functions analyses corroborate the hypothesis that size is the major, but not exclusive, part of subspecific shape variation. Comparison of the size-controlled and non-size-controlled DFAs reveal an erosion of size related differences. *P. h. anubis* becomes less distinct from neighbouring *P. h. cynocephalus* and *P. h. papio.* However this large-bodied subspecies become less like *P. h. ursinus* with size correction demonstrating a real size-controlled shape differences. As the specimens are all adults the size-shape relationship reflects static allometry, which is distinct from ontogenetic allometry (Cock, 1966, Cheverud, 2005). The latter reflects the shape change with increasing size over growth common to a species or subspecies. However, the former is not unrelated to the latter and has a gradient in the same direction, though often steeper or shallower. If smaller subspecies are scaled down versions of larger subspecies this would suggest a truncation of a common static allometric relationship (Freedman, 1962). This agrees with the visualised shape change from the paedomorphic morphology of these smaller bodied animals, characterised by a relatively shorter rostrum and smaller face to the neurocranium. Extrapolating from this to an ontogenetic mechanism is harder however, because of the difference between ontogenetic and static allometry. However, it has been shown that hamadryas baboons have a truncated growth trajectory relative to the olive baboon (Jolly and Phillips-Conroy, 2003) and the yellow relative to the olive (Jolly and Phillips-Conroy, 2006). It seems likely therefore that static and ontogenetic allometry are linked and that differences extension or truncation of growth account for these subspecific differences in shape.

Interestingly *P. h. papio* was never misclassified arguing for distinctness of shape and size-corrected shape. This might represent a real difference reflecting its isolated and peripheral geographic range in West Africa relative to other subspecies. Alternatively it might reflect the low sampling effort for this less studied subspecies, or the fact that the olive baboon, its neighbour, is sampled mostly in east Africa. If it does intergrade our data are unable to demonstrate this fully. Further work will have to be done to establish clinal patterns in West Africa. However, this case reflects the importance of modelling the variation as continuous, such as the TSA, as well as discontinuously, in the DFA case, as biological reality lies somewhere in-between.

The north-south pattern of size-corrected shape variation is not unexpected. First, this matches the finding of Frost et al. (2003), in a similar study on size corrected baboon morphologies. Our visualisation exhibits low bizygomatic breadths and ventrally flex rostra for southern species concordant with their findings. Second, size-controlled shape is more likely to reflect the phylogenetic history. The high genetic integration of a complex structure such as the skull means moving along the existing shape-size trajectory is easier than deviating from it, as less genetic change is required. Size can thus be said to be a path of least resistance in evolutionary changes (Marroig and Cheverud, 2005, Elton et al., 2010). Large deviation from an allometric trajectory are likely to involve high selective pressures or reflect deeper evolutionary time. Baboons are thought to have arisen in south Africa and thence radiated north (Newman et al., 2004). Adjacent populations in the East and West Africa share a size-shape trajectory reflecting more recent ancestry. The deepest split and thus the greatest size-shape trajectory disparity lies between northern (i.e. East and West) and southern populations; a finding concordant with the axis of genetic variation (Zinner et al., 2009b).

2.4.3 The Kinda Baboon

The Kinda baboon is a notable outlier for size, and even though it is known to grade into the larger yellow baboon to the east (Freedman, 1963). This cline is sufficiently steep that it could not be well represented by a polynomial expansion in the trend surface analysis. Inclusion of this subspecies revealed an extensive trough in size and shape, placing adjacent large taxa at low size contours. This deficiency of the model to deal with so steep a cline is demonstrated by the lower explanatory power of spatial terms in the partial regression with the inclusion of the Kinda baboon.

While the Kinda baboon was found to be an outlier in size, this was not so for size-controlled shape. This suggests that, though this animal has a distinctive paedomorphic morphology, it is distinct only insofar as it is allometrically scaled down relative to its neighbouring subspecies. Interestingly the Kinda baboon becomes more mutually similar with the chacma. This is a finding of intense interest as the Kinda baboon has always been held to be a member of the yellow baboon subspecies, and most authors subsume this population within *P. h. cynocephalus*. Thus the discriminant function analysis suggests that the clinal slope is steepest between the Kinda-chacma group and the other subspecies. The greater chacma-Kinda affinity could be an artefact of the greater sampling of more eastern than southern, Kinda-adjacent yellow baboons, and so is a finding that should be taken with caution. Certainly the phylogenetic split within baboons is between the three northern taxa and the chacma, Kinda and yellow baboon. However, the complex history of introgression may have resulted in yellow baboons acquiring a more northern skull morphology.

The ecological causes, assuming this is the result of natural selection rather than drift, and consequent implications of Kinda size are unknown, as this is an understudied subspecies. It has a markedly smaller size and reduced sexual dimorphism (Leigh, 2006, Jolly et al., 2011) and preliminary behavioural observations have found females exhibiting male-like vigilance and alarm behaviours, and males showing greater interest in nonoestrous females than exhibited by males of other subspecies (Phillips-Conroy et al., 2009). Once again, given the lack of an obvious ecotone between this and other subspecies it seem unlikely that the small size of this subspecies is a response to present day environmental variation, perhaps suggesting a neutrally adaptive cause for this small size. It is highly possible that the morphology has changed in response to the social system, rather than to the environment directly. This is a pattern seen in the hamadryas baboon, where the single male units reduce the need for large male size in agonistic encounters (Jolly and Phillips-Conroy, 2003). The social system arises out of the dispersal of resources which causes females to disperse and requires males to try to herd females to increases their own reproductive success. Such socioecological mediation between the environment itself and morphology as a result of sexual selection reduces the link between environment and morphology, perhaps resulting in lower correlational values. Some of the morphological patterns seen, such as prognathism may be related to canine size for display and agonistic encounters (Leutenegger and Cheverud, 1982, Plavcan et al., 1995), and not reflect the prognathism associated with allometric scaling and large size. Without a complete matrix of values for sociological variation such as groups sizes, sexual compositions, and dispersal these links are impossible to establish, and are beyond the scope of this study.

Overall the finding that the outlying nature of *P. h.* kindae morphology is the result of its small size, is of interest to the study of this taxon in particular and to the study of morphological variation in general. Jolly (1993) points out that future palaeontologists might diagnose only two species of baboon: the Kinda and a taxon comprising the other subspecies. The finding that its deviation in in shape is chiefly related to its change in size is therefore an important lesson in understanding fossil phenotypic variation.

2.4.4 Morphological Variation and the Effects of Evolutionary History

So far we have been able to dismiss overarching biogeographic rules as determinants of baboon size and shape variation. Similarly limited support has been found for an association between baboon environmental and morphological variation. Clinal models have been hampered by discrete rather than continuous variation, or else very steep continuous variation, proving baboon variation does not neatly align with an ecotone, and thus does not arise as a direct response to the environment. While potentially some clinal variation, in particular the Central-East African cline, might be explicable in terms of environmental variation, it is worth considering the other factors that may be at play. Baboons have been around for at least two million years (see Chapter 5), and modern environmental variation thus accounts for a relatively small part of their evolutionary history, and thus reflects only a fraction of the selective pressures they have been subject to. Pleistocene environment fluctuations resulted in periods of increasing and decreasing aridification resulting in periodic barriers to gene flux (Zinner et al., 2009b). These barriers promote adaptation to regional conditions, rather than a mixing of genes across a range of disparate regions, thwarting specialisation. They also facilitate the effects of genetic drift, in causing isolated populations to diverge. While these barriers are now relaxed this has left a legacy in genetic structure (Zinner et al., 2009b) and hence phenotype (Jolly and Phillips-Conroy, 2003, Charpentier et al., 2008). Hamadryas baboons cease growing at an earlier stage than anubis baboons (Jolly and Phillips-Conroy, 2003), a pattern that is clearly genetically fixed. Additionally the olive baboon matures faster than the yellow baboon, an ontogenetic feature under strict genetic control rather than as the result of phenotypic plasticity (Charpentier et al., 2008). The chacma baboon also has a later peak testosterone level than the yellow baboon, and again this is not the result of plasticity (Beehner et al., 2009). While these features are potentially ecologically adaptive the genetic fixity makes them less plastic and hence less likely to vary with an ecotone. The spread of these less labile genetic features is likely to be related to population history or zygostructure (Jolly, 1993).

Baboons are not unique in being structured by past-environment mediated population history. Numerous African animals are not only polytypic but have similarities in the crude positioning of subspecific borders such as the Eland (Lorenzen et al., 2010), giraffe (Brown et al., 2007) and numerous others (Hewitt, 2004). Such overlapping hybrid zones are referred to as suture zones, and represent points where fauna have reunified after being isolated in refugia (Swenson and Howard, 2004). While these phylogenetic differences may have some adaptive signal there is likely to be a lag in response to this. Additionally this isolation may cut-off subspecies on the adaptive landscape (Wright, 1932). At this point stochastic effect might alter their phenotype and thereafter similar environmental pressures might push them up different adaptive peaks (Chapter 7).

2.4.5 Comparison with the Vervet and Other Taxa

A Central Africa-East Africa trend was found in the vervet monkey (this study, Cardini et al., 2007), the blue monkey (Cardini et al., 2010) and the red colobus monkey (Cardini and Elton, 2009). This is a robust trend in baboons as it appears in the Kinda baboon included and excluded trend surface analysis, and in the holdout samples. This would superficially suggest that baboons, along with blue monkeys, vervets and red colobus monkeys, are subject to an ecogeographical rule in equatorial Africa, though without a mechanism it is hard to rule out that this similarity is spurious. Indeed the trends are not entirely the same. Baboons were found to get smaller in West Africa which was the pattern with blue monkey and red colobus, though not the vervet. This is unexpected as the baboon and vervet are ecologically comparable, both being more terrestrial and inhabiting the savannah. In contrast the blue monkey and red colobus monkey are both arboreal. The small size of the red colobus in West Africa was explained in terms of forest fragmentation leading to a tendency to small size, in order to limit competition (Cardini and Elton, 2009). Given that the baboon is not restricted to forests but rather avoids them this hypothesis is unsubstantiated as an explanation for this species.

Like vervets, baboon subspecies are most similar to adjacent ones. However, an important difference between baboons and vervet monkeys is the allometric component of shape variation between subspecies. For baboons this was a major component, in particular between the hamadryas, olive and yellow baboon. However, for the vervets allometry though underpinning some of the clinal variation was less a factor (Elton et al., 2010). Quite distinct subspecies remained after size-correction, whereas with baboons this procedure eroded subspecific differences considerably, in particular between the northern taxa. For instance in vervets *C. a. pygerythrus*, though small, exhibited morphological affinities with the large *C. a. cynosuros*, and was not a scaled down version. In the baboons for example the removal of static allometric differences saw the smaller hamadryas baboon appear to be more similar to the adjacent olive baboons (in terms of a reduced gradient on the size-controlled TSA) demonstrating size to be a major differentiator between subspecies.

Partial regression reveals a high spatial component to baboon clinal variation in both size and shape. For vervets size variation is 25% for females and 10 % in males. Both these figures are much smaller than the 55% found in this study for size variation. Similarly for shape females and males have 6 and 7% of variance explained by the spatial component compared with between 20 and 25% in this study. The suggestion populations are more smoothly differentiated and more clinal than vervets. An explanation for this might be related to dispersal and gene flow.

Larger animals generally have larger home ranges, and animals with larger home ranges have greater dispersal (Bowman et al., 2002). Baboons are much larger than vervets and certainly range further. One would expect greater gene flow and a greater spread and thus smoothing out of characters in baboons relative to vervets. The good fit of baboon morphological variation to a trend surface model demonstrates such an effect.

2.4.6 Conclusion

Both baboons and vervets exhibit extensive subspecific variation. In the case of baboons this is clinal but stepped, with zones of sharp change corresponding to subspecific differences as found in other studies (Frost et al., 2003, Jolly, 1993). There is little evidence for an overall biogeographic rule: environmental predictors are low, and shape gradients do not seem to correspond to environmental ecotones. This falsifies the hypothesis that this is the major determinant of morphological variation. Subspecific differences appear to be genetically fixed (Beehner et al., 2009, Charpentier et al., 2008) and may have arisen through selection to past rather than present environmental conditions, as modern conditions reflect only the most superficial level of the history of this species. Such factors are likely to have altered socioecology and investment in somatic growth, and thus morphology. Additionally changes may have accumulated through genetic drift owing to reduced gene flow as a result of population separation in the Pleistocene (Zinner et al., 2009b, Keller et al., 2010).

Interestingly much of baboon shape variation, in contrast to vervets, is size-related. Adjacent taxa appear to be largely scaled up or down according to a static allometric trajectory, as sharp TSA contours disappear when size is controlled. Indeed the Kinda baboon, though small, is an allometrically scaled down version of its neighbours rather than a morphologically distinct subspecies. These static allometric differences potentially reflect differing amounts or rates of ontogenetic growth. However, the hypothesis that subspecific differences are exclusively down to scaling is falsified in that differences remain when size is controlled for. Indeed the size-free shape variation gives the greatest insight into genetic divergence (Marroig and Cheverud, 2005), and corresponds to the axis between southern and east and west central Africa found to the the major phylogenetic split in genetic analyses (Zinner et al., 2009b). This is likely to reflect the baboon’s origin in southern Africa and expansion north, again implicating phylogenetic history as a major determinant of baboon subspecific variation.

CHAPTER 3. DIETARY SPECIALISATION OF THE BABOON AND VERVET SUBSPECIES

3.1 INTRODUCTION

3.1.0 Overview

Survival is underpinned by foraging success. For the vervet and baboon feeding efficiency is maximised by being flexible and making the most of available resources (Alberts and Altmann, 2006, Barrett, 2005). However, environments are disparate in the foods available. For instance forested habitats contains more fruits and seeds than the savannah (Rowell, 1966), which contains more subterranean foods (Dominy et al., 2008). Data for numerous baboon and vervet populations exist, yet remarkably there has been little intraspecific comparison (Barton et al., 1992). Yet it is likely that these environmental differences and associated dietary differences exert divergent selection pressures on the subspecies. Consequently it is probable that there is some dietary specialism in the face of the overall generalism of the study taxa. It is important to establish ecological differences as these are likely to be the first step in the genetic and morphological diversification that leads ultimately to speciation (Schluter, 2000). Consequently this study will compare the degree of subspecific dietary divergence within the vervet and baboons and identify any similarities. A similar pattern of subspecific divergence between the two species would suggest a common environmental response. Alternatively, differences in the subspecific divergences would suggest unique environmental responses, perhaps related to unique features of the vervet or baboon. This comparison is therefore of enormous value in understanding how the environment acts on primate diversifications.

3.1.1 Foraging Ecology

Diet is a major determinant of behaviour, socioecology and ultimately survival in primates. In most populations of baboon foraging takes up a major part of an animal's day and is the highest priority (Hill et al., 2003). Baboons were recorded to spend just under half the daylight hours at both Amboseli, Kenya (Bronikowski and Altmann, 1996) and the Drakensbergs, Mountains of South Africa (Whiten et al., 1987) foraging. Foraging is performed to the exclusion of other activities meaning baboons must fit the other nonfeeding behaviours into the remaining time. The major categories of a time budget are usually resting, moving, foraging and socialising in the form of grooming (Dunbar, 1988). Time budget and associated behaviours are driven by the necessity to forage and feed efficiently. As foods become limited foraging must increase relative to other activities. For instance during the dry season at Amboseli baboon foraging increases while resting time decreases (Alberts et al., 2005, Bronikowski and Altmann, 1996). Indeed Hill (2003) reported that chacma baboons spent 36% of the time foraging in summer and 50% in winter. This increase is underpinned by a reduction in food quality in the dry season. Between populations, foraging time is also related to the quality of the diet. Foraging time decreased with increasing proportion of fruits and seeds in the diet (Hill and Dunbar, 2002). These are nutritionally high quality items, full of easily digestible carbohydrates, that are relatively easy to access and consume. In contrast foraging increases with the proportion of hard to digest fibrous, subterranean foods, which are low in quality and require time and effort to manipulate and consume.

The vervet, like the baboon, spends much of its time budget foraging. Vervets at Mt Assirik, Senegal, spent an average of 45% of their time foraging (Harrison, 1985) reaching 55% in some months. Time spent foraging was 39% at Blydeburg, (Barrett, 2005) and 35% at Windy Ridge, South Africa, (Baldellou and Adan, 1997). In Amboseli during the well-documented fever tree die-off, the vervets spent more time foraging and ranging as fever trees became more and more depleted (Lee and Hauser, 1998), demonstrating, as with baboons, that this is a priority behaviour modulated by ecological circumstances.

As with the baboon, vervet foraging time is related to food quality. A value of 20% feeding time was recorded at a site where the vervets had access to human, i.e. rich, food (Brennan et al., 1985). Indeed high fibre diets resulted more often in maternal rejections of offspring (Fairbanks et al., 2010), demonstrating the fitness costs of poor diet.

3.1.2 Baboon Diet

The baboon is an outstanding dietary generalist. In the words of DeVore and Hall (1965, p. 43) "...it is almost easier to list the items which they do not eat than to describe the items which they do." Similarly Rowell (1966) suggested that a list of foods eaten by baboons is equivalent to a botanical list of the area. Baboon diet includes fruits, such as figs, and baobab and *Acacia* fruits, as well as their seeds and berries (Altmann and Altmann, 1970, Culot, 2003, Kunz and Linsenmair, 2008b). Leaves and grasses are eaten as well as grass seeds (Altmann and Altmann, 1970). Subterranean foods or geophytes such as roots, tubers and corms are an important dietary constituent (Norton et al., 1987, Whiten et al., 1987). Baboons also eat flower blossoms, exudates and rotten bark. Arthropods, molluscs and small invertebrates are common (Altmann and Altmann, 1970). However, this apparent breadth mischaracterises the baboons which, though eating from a wide range of plants, select only certain parts from each. For instance the fresh shoots of grasses, as they emerge after the rains, are consumed (Altmann and Altmann, 1970), tamarind seeds are dehusked to remove the less nutritious and indigestible parts (Rhine and Westlund, 1978) and underground sedge corms are stripped and peeled and wiped free of earth and grit (Rhine and Westlund, 1978). Similarly at Laikipia *Acacia* pods are torn open with the teeth and the seeds removed with the tongue. The coats of these seeds are then removed in the mouth (Whiten et al., 1991a). This manipulation, dexterity and selectivity is highly beneficial. For instance the fruit of *Acacia tortilis* is rich in protein but also contains trypsin inhibitor: a toxin. Baboons first select seed pods from trees that express less of this toxin. Next they remove the seeds from the pods and the seedcases from the seeds (Altmann, 2009). This has two advantages. First, the overall trypsin inhibitor content of the foods has reduced by 91%. Second the nutritional profile of the food item is greatly increased: protein is increased by 160%, as is carbohydrate at 111%, with fibre reduced to 7%. Evidently, this time consuming behaviour confers a real nutritional advantage.

Aside from picking the choicest part of a plant, baboons also track resources, such as seasonal fruits and berries, as they appear throughout the year (Altmann and Altmann, 1970). They are also able to switch to less favourable foods when the environment demands it, such as sedge corms. This is termed handoff foraging (Alberts and Altmann, 2006).

Local knowledge is of great help to survival. Indeed, adults have been observed breaking off from the main group to inspect a tree they know is about to fruit on the basis of past experience (Rowell, 1966). However, stochastic events are not missed. Occasional foods are taken huge advantage of such as swarms of caterpillars (Altmann, 2009) or locusts (the less nutritious wings of which are selectively discarded (Kummer, 1968)). Baboons have also opportunistically taken advantage of recent anthropogenic changes such as the refuse created by tourism (Bronikowski and Altmann, 1996) and livestock supplements such as ostrich pellets (van Doorn et al., 2010).

Faunivory is another important aspect of baboon diet. Low level cases of invertebrate eating, chiefly arthropods or molluscs, are widespread. Indeed animal matter has been termed the preferred food source (Hamilton III et al., 1978) which agrees with the conclusions of Whiten et al. (1991b) that protein is most preferable feature in food selection. However faunivory is not restricted to invertebrates. The hamadryas baboon is recorded as eating *Madoqua* (dik dik) and species of guinea fowl (Swedell et al., 2008) while "small game" is consumed by olive baboons, bringing them into competition with humans in Tanzania (Marlowe and Berbesque, 2009). In South Africa vervets are eaten by chacma baboons (Willems and Hill, 2009), while one hare was taken by a member of the troop every 30 hours in Uganda (Rowell, 1966). However, predation of vertebrates by baboon would appear to be an occasional activity in terms of time budget (Butynski, 1982) and is therefore far from a staple food however preferable it may be.

A major factor in determining what food resources are available is season. In the more seasonal habitats, such as the savannah, characterised by wet and dry seasons, periods of food shortage occur. At this time preferred foods are absent requiring species to "fall back" on other less desirable foods (Marshall and Wrangham, 2007, Altmann, 2009). The proof that they are true fall back foods is demonstrated by the fact that they are present in the vicinity all year round but only resorted to when other foods are absent (Altmann, 2009). Fallback foods are often difficult to acquire such as subterranean plant storage organs, also termed "geophytes" (Hill et al., 2003). These roots, tubers and corms that exist below the surface are laborious and time-consuming to dig up (Whiten et al., 1987) and then subsequently must be cleaned of grit. They are estimated to be of low nutrient quality and as they must be dug up in the open, without cover or shade, they represent a minimal gain for considerable work and risk. Yet in the dry season baboons face little choice. In the winter at Drakensburg where temperature and precipitation are low these hard to process underground storage organs are eaten significantly more by the inhabitant chacma baboons (Byrne et al., 1993, Whiten et al., 1987) as is the case at the Cape (van Doorn et al., 2010). This is similar in Mikumi, Tanzania, for corms (Rhine and Westlund, 1978) which have been termed an “undepletable resource” though they are largely ignored in the wet season.

3.1.3 Vervet Diet

Vervets, like baboons, are generalist and opportunistic feeders (Fedigan and Fedigan, 1988, Barrett et al., 2006). Fruits and flowers have been shown to be the preferred foods for this species (Harrison, 1984) and indeed most populations eat more fruit than anything else (Barrett, 2005, Harrison, 1982, Willems, 2008, Moreno-Black and Maples, 1977). Major food constituents include fruits, seeds and seed pods, flowers, young leaves, and saps as well as insects and eggs (Kingdon, 1997, Klein, 1978, Whitten, 1982). Fruits are processed extensively, for instance *Acacia xanthophloea* pods are bitten into, and dehusked in the mouth using the tongue and then consumed (Klein, 1978). Before consumption fruits may be sniffed or bitten into. For instance fruits of *Garcinia huillensis* are bitten to penetrate the skin and on the basis of olfactory cues they are accepted or rejected and dropped to the ground (Gartlan, 1966). For many smaller fruits, foraging consists largely of filling up the cheek pouches and then using muscular action, or fingers, to move these into the mouth to be masticated later (Gartlan, 1966). Theses pouches are quite capacious. Gartlan (1966) found that they could hold almost 250g worth of peanuts.

Flowers, the other preferred food (Harrison, 1984), feature in the diet of most populations. Indeed Whitten (1982) found flowers, mostly from *Acacia tortilis*, to be the dominant dietary component in Kenya, though typical foraging time values are mostly between 10 and 20% (Harrison, 1982, Wrangham and Waterman, 1981, Dunbar and Dunbar, 1974).

Vervets are folivorous with a preferences for young leaves and shoots over mature leaves (Harrison, 1984). Indeed the most folivorous subspecies of vervet, the djam-djam, which feeds primarily on the leaves of bamboo (*Arundinaria alpine)*, was recorded as having only 1.1% of its diet composed of mature leaves (Mekonnen, 2008). Young leaves and shoots are richer in protein and contain less tannin, which underpins this preference (Wrangham and Waterman, 1981).

As with leaves and fruits, sap is another arboreal food component making up to 18% and 6% of the diet in two populations at Amboseli (Klein, 1978). These gums or exudates may flow from the bark naturally, or if not they can be accessed by chewing tree bark with the incisors and licking the area exposed (Klein, 1978).

By far most of the foods eaten by vervets are vegetation. However, most populations show instances of faunivory, often invertebrates but occasionally small reptiles such as skinks and chameleons as well as eggs (Harrison, 1984). However, this is done opportunistically, for instance taking advantage of seasonal swarms of grasshoppers (Gartlan, 1966). Insects are taken if they are in view: they are not sought out (Barrett, 2005). This is in contrast with fruits, for which vervets exhibit evidence of a mental map. Vervets have been observed moving to trees about to fruit that are out of sight: specific goal-directed movement (Barrett, 2005).

Variation in fruiting and flowering is largely seasonal. Even at the equator, where temperature fluctuates little relative to higher and lower latitudes, there is seasonality in food availability related to the rains (Gartlan, 1966). Fruits are less prevalent in the dry season across vervet sites, for instance in South Africa (Barrett, 2005), Senegal (Harrison, 1982) and Kenya (Wrangham and Waterman, 1981). This variation by month may be as marked as 20% fruit in December and 75% fruit in May (Harrison, 1982), or by season 42% fruit in the wet and 8% in the dry (Galat and Galat-Luong, 1977). In the dry season fallback foods such as tree leaves and grasses are consumed more in the reduced presence of fruits and flower (Galat and Galat-Luong, 1977). Fruiting is of particular importance as birthing is timed to occur just before this (Butynski, 1988).

3.1.4 Dietary Comparison of the Study Taxa

While vervets exhibit a high dietary similarity with baboons, they have a much reduced range of dietary items. Altmann (1998) suggests that baboons eat between two and three times the variety of foods. Indeed, vervets are recorded as eating as many as 65 plant species by Harrison in Senegal (Harrison, 1982), 46 by Lee and Hauser at Amboseli (Lee and Hauser, 1998) and a mere 26 by Agmen in Nigeria (Agmen et al., 2010). For baboons this figure is typically over 150. Moreover, this relatively more restricted diet (though still broad by comparison with other primates) is compounded by the fact that though vervets eat a range of foods they specialise on relatively few at any given point in time (Barrett, 2005). For instance *Acacia* spp. is one such type, where 50% of feeding is on these plants (Wrangham and Waterman, 1981). Other studies have found it to be a staple at same site (Lee and Hauser, 1998) and in South Africa (Barrett et al., 2010). In the Sahelian zone of Senegal *Pterocarpus* (Harrison, 1982) is the staple food rather than acacia.

Perhaps one reason for the reduced diet of vervets relative to baboons is that the vervet, though savannah dwelling, travels less distance from the trees they use as refuges (Altmann and Altmann, 1970, Struhsaker, 1967b) than baboons.
Possibly this is because vervets have significantly more predators and are thus at a higher risk of predation at any given time (Dunbar, 1988). Consequently they spend more time foraging in the trees eating fruits and leaves. Partly this may be down to the smaller size of vervets. According to metabolic scaling, larger animals have relatively slower metabolisms (Schmidt-Nielsen, 1984) and thus need relatively less energy enabling them to eat relatively less food or food of lesser quality. Additionally, larger animals have longer guts and hence retention times and can extract more energy from food. (Demment, 1983), known as the Jarman-Bell principle (Geist, 1974). Vervets as a result of their proportionally higher metabolism and shorter food retention time must consume a more calorific diet, while baboons can subsist on less energetic fibrous foods. These physiological constraints must partly dictate the vervets' diet constraining them to eat more carbohydrate rich foods such as fruits. This fits in with Harrison's (1985) observation that vervets are energy maximisers in their foraging strategies. Another constraint of body form is strength. The conclusions of Altmann's (1998) observations in East Africa was that vervets were comparable in diet to yearling baboons in but without the strong subterranean

foods component because they do not have the strength to dig these foods up (also noted by Struhsaker, 1967a). This finding was corroborated by Barrett (2005) in a South African population.

3.1.4 Aim

In spite of the baboons and vervet being two of the most well-studied primates (Altmann and Altmann, 1970, Fedigan and Fedigan, 1988, Struhsaker, 1967a) , little work has been done to assess the intraspecific variation in diet. Given the extensive environmental and ecological variation present across the geographic ranges of these two taxa it seems implausible that foods can be homogenous in their availability and proportions consumed. As such, some subspecific variation in the proportions of foods eaten might be expected to reflect this environmental heterogeneity (Dominy et al., 2008, Rowell, 1966, Chapman et al., 2004). Alternatively, the generalist dietary strategies of both these taxa (Alberts and Altmann, 2006, Barrett, 2005) might result in no dietary differences between subspecies whatever, i.e. the regional variation does not align with taxonomy. This chapter tests the null hypothesis that there are no differences between subspecific diets in the vervet and baboon. This is done by statistically assessing differences in the dietary proportions of the subspecies for differences food categories. This analysis is based on the assumption is that quantitative data from the literature are accurate and representative, which is discussed. This chapter will also test the hypothesis that that are there affinities between the two taxa in dietary differences, and relate this, if they exist, to their common environment. To answer this, the two patterns of subspecific dietary differentiation, if present, will be compared and similarities explored.

3.2 METHODS

3.2.1 Baboon Sample

Dietary data was found for 20 sites (table 3.1). Of studies nine used the scan method and six used the focal animal method (table 3.1). Information for the remaining six sites is unavailable because the entry is a report of a personal communication, or because the thesis is inaccessible or because no sampling is given. However, studies are very likely to use one or the other method

Observation of the dietary data (table 3.1) reveals Gaynor's study has considerably higher proportions of fruit eating. At 90% this was wildly higher than any other value for a dietary proportion. Consequently this study site was excluded from the analysis.

Table 3.1. Baboon dietary data showing the proportions of foods in the diet by time budget. Details of the site (n=20), method of data collection and study period are given. Studies used in the full year analysis are marked in bold. Abbreviated dietary headings are: F&S = Fruit and seeds, S = seeds, L = leaves, Fl = flowers, A = animal, O = other. Proportions are in %, duration is in months. PC = personal communication.

Subspecies	Site	No	Method	Duration	F&S	S	L	Fl	A	O	Reference
P. h. anubis	Bole	1	Unspecified	5[†]	54.9	1.6	32.9	7.4	0	3.2	(Dunbar and Dunbar, 1974)
P. h. anubis	Comoe	2	Scan	20	47.2	0	33.9	6	0.8	12.7	(Kunz and Linsenmair, 2008b)
P. h. anubis	Gilgil	3	Focal	13	7	27	52.9	5.1	1.9	6.1	(Harding, 1976)
P. h. anubis	Budongo	4	Scan & ad lib.	5	47	1	17	0	0	35	(Okecha and Newton-Fisher, 2006)
P. h. anubis	Gombe	5	Scan (Dunbar PC)	**12***	49	7	14	2	13	15	(Olive PC, cited in Hill and Dunbar, 2002)
P. h. anubis	Masai Mara	6	?		46	8	44	1	1	0	(Popp 1978, cited in Hill and Dunbar, 2002)
P. h. anubis	Shai Hills	7	?	>12*	59	17	8	5	0	11	(DePew 1983, cited in Hill and Dunbar, 2002)
P. h. anubis	Cholo	8	Focal	12	23.2	15	27.3	21	0.9	12.6	(Barton, 1989)
P. h. cynocephalus	Amboseli	9	?	?	27	33	15	5	1	19	(Post 1978, cited in Hill and Dunbar, 2002)
P. h. cynocephalus	Mikumi	10	Focal	60	43	12	14	20	0	11	(Norton et al., 1987)
P. h. cynocephalus	Ruaha	11	Scan (Dunbar PC)	**12***	16	52	19	1	9	3	(Rasmussen, 1978)
P. h. cynocephalus	Ruaha	12	Focal	6 (dry season)	38.8	44	17.2	0	0	0	(Pochron, 2000)
P. h. cynocephalus	Tana River	13	Scan	60	51	24	21	2	0	2	(Bentley-Condit, 2009)
P. h. hamadryas	Erer-Gota	14	Unspecified[‡]	12	42	4	53	0	0	1	(Kummer, 1968)
P. h. papio	Mt Assirik	15	Scan (Dunbar PC)	**12***	74	3	9	9	1	4	(Sharman, 1981)
P. h. ursinus	Cape Point	16	Scan	12	42	16	25	12	4	1	(Davidge, 1978)
P. h. ursinus	Drakensberg	17	Focal	8 (May-Dec)	3	53	26	14	4	0	(Whiten et al., 1987)
P. h. ursinus	Giant's Castle	18	Focal	6 (Jul-Jan)	3	52	24	15	4	2	(Byrne et al., 1993)
P. h. ursinus	Mkuzi	19	Unspecified	?	90	1	6	2	1	0	(Gaynor, 1994)
P. h. ursinus	Suikerbosrand	20	Scan - Dunbar PC	**12***	43	39	8	7	3	0	(Anderson PC, cited in Hill and Dunbar, 2002)

[‡] “on certain days, Kurt recorded the food eaten by each baboon he could observe at the moment he spotted the animal”

[†] May, 1971, May to June and September to October 1972. *Dunbar PC.

3.2.2 Baboon Dietary Categories

For baboons this study uses the following dietary categories: fruits, subterranean foods, leaves, flowers, animal matter and other. These standard categories are well used (Norton et al., 1987, Barton, 1989, Dunbar and Dunbar, 1974) and are based on ecology rather than food physical properties or nutrition, as the aim of this chapter is limited to establishing a differences in feeding ecology (see Chapter 4 for morphology and food physical properties). Though dietary categorisation varies according to the study these groups are extractible from all studies. This is because though these are sometimes split, for instance leaves into mature and young, they are never lumped.

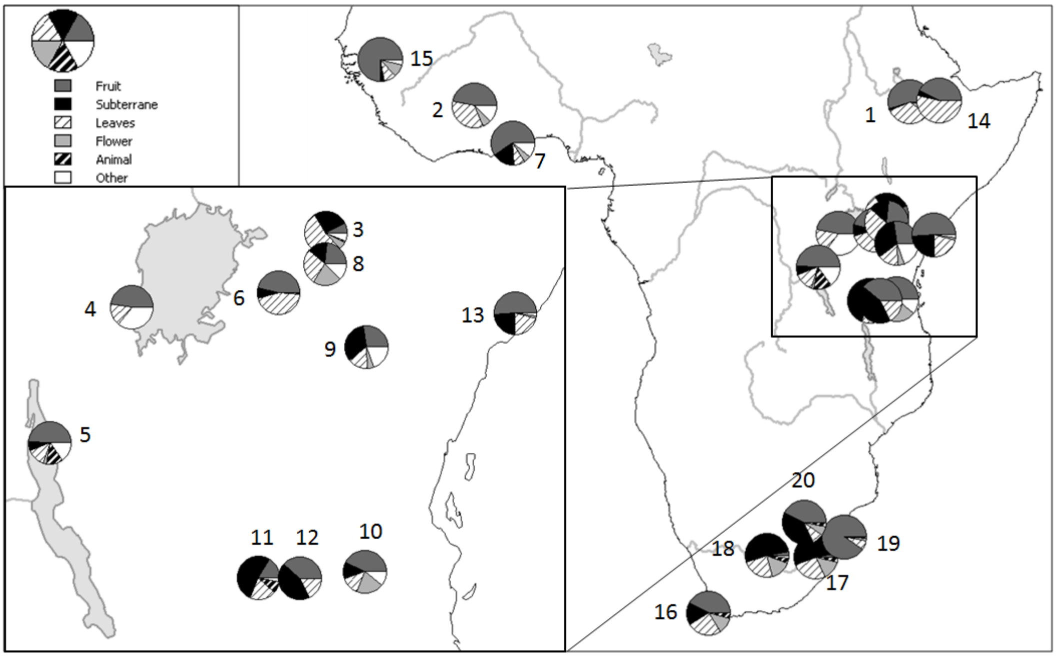


Figure 3.1. Pie charts showing the geographic position of the study site and the food proportions that make up the total diet for baboons. Numbers correspond to those in table 3.1, n = 20.

3.2.3 Quality and Comparability of Baboon Studies

To address the comparability of the published dietary data the methods of observation must be detailed. Field observations of primate activity are usually instantaneous/scan or focal animal sampling (Altmann 1974). The instantaneous method records states at particular time points; the same for more than one animal is called the scan method (Altmann 1974). Consequently, behaviours of brief duration relative to the scanning interval are more likely to be missed, introducing a bias. For instance, if the average fruit-feeding bout is five minutes and the scan interval is ten minutes such behaviour is more likely to be missed than behaviours of longer duration, assuming equal bout frequency; this would be offset somewhat if shorter bouts are more frequent. Nevertheless, the quality of this method depends on the scan interval relative to the duration of behaviours: it is a question of resolution. The range scan interval for scan sample studies varies greatly from one hour (Bentley-Condit, 2009) to two minutes (Kunz 2008). This is clearly quite disparate and one might expect the study by Bentley-Condit to be biased against short feeding behaviours. However, though feeding bouts tend to be briefer than an hour (Post et al., 1980) there is no evidence that feeding bouts are of different length for different foods. As such a lower time resolution should not introduce a bias in the proportion of feeding on one food versus another. The other method, focal animal sampling, is not biased against short behaviours as the animal is followed and all behaviours are recorded from onset to offset (Altmann, 1974). Thus neither should have consistent biases against a particular feeding observation.

Another bias of the focal method is that the behaviour of inconspicuous members of a troop may be missed. However this is also a difficulty with scan sampling. Additionally losing sight of a focal animal means information is lost. Biases in sampling behaviour are probably overcome by sampling lots of individuals over long periods of time, getting closer to what is truly representative of the diets of these animals.

Probably the most serious obstacle for comparing studies is differences in study length. Those lasting less than a year will yield results skewed by seasonality, while full year studies will average across seasons. Five year studies such as Bentley-Condit's (2009) should capture inter- and intra-annual variation, while a study such as Okecha and Newton-Fisher's (2006) of a mere 20 weeks should not. Though the latter was a least divided into wet and dry season study periods it fails to capture the complete annual variation, and the study confesses lower sampling in the wet season owing to the heavy rains. All studies of duration of a year or more are labelled to highlight the studies about which there can be most confidence (table 3.1). These were analysed alone as well as with the remaining dataset. Potentially a study of shorter duration than a year could be valid if it is spread across the year. However, aside from Okecha and Newton-Fisher's (2006) study, already discussed, and Dunbar and Dunbar's (1974) study all studies shorter than a year than looked at consecutive months adding a seasonal bias. Dunbar and Dunbar's (1974) study looked at May in one year, May to June and September to October in the next year, showing poor annual dispersal.

For the Ruaha site two studies were carried out at different times (table 3.1). This provides a window into interannual variation. Pochron's (2000) study was of a duration of six months covering the dry season. However, Rasmussen's (1978) study covered the whole year. The major difference is in the amount of fruit eaten which is much higher in Pochron's study, while subterranean foods are marginally higher in Rasmussen's. This is precisely the opposite of what we would expect based on subterranean foods as a fallback food, more likely to be exploited in the dry season (Altmann, 2009). It is possible that Rasmussen's year was a bad one overall. However different they may be, the two studies are not independent and cannot both be used in the same analysis. Rasmussen's (1978) study, as the more complete is used in the analysis.

Baboon dietary studies are relatively few and do not systematically describe dietary variation across the full geographic extent of this species (fig. 3.1). Certain locations such as East and South Africa are better studied, leaving us with considerable geographic blind spots. Nevertheless, even these adjacent localities have considerable variation in dietary proportions. It is difficult to be certain of how accurate these observations are, and if accurate, how representative they are. While most sites encapsulate all or some intra-annual variation, we have no information interannual variation. There has been extensive climatic fluctuations at sites such as Amboseli, where there has been a persistent drying tend that has had an severe impact on local vegetation and baboon diet (Altmann et al., 1985). Our data come from 1978 before this period, though are perhaps no more representative of this changeable habitat. However, this chapter looks at differences in subspecific diets, using inter-site variation to determine if there are any such differences. Indeed with such limited data it is only the most salient global trends that will be detected. Subtle regional variation cannot be assessed without at least quadrupling baboon dietary studies. The geographic variation, which is taken over various years, therefore gives some broad indication of the dietary variation of the subspecies as a whole. Additionally while the absent of temporal variation is an omission it is unlikely to bias the conclusion in any particular direction.

3.2.4 Vervet Sample

Dietary data were found for 16 populations at 13 sites (table 3.2). Of the 13 study sites four specifically cited Altmann's (1974) focal sampling method while two more described a methodology corresponding to this. Six cited Altmann's (1974) scan sampling method. Information on the study method by Willems (2008) could not be found but it is unlikely to be different from these two predominant methods.

Data were averaged for studies of multiple groups at the same site. This is not expected to introduce bias as all methods and study times were the same. In the case of groups 2 and 3 in Lee's (1981) study the dietary proportions are very similar (table 3.2). Group 1 however is different from the other two being much more folivorous than frugivorous (table 3.2). However, this is assumed to be part of the natural variability at this locality and so it is averaged. This loses some information, but given that most sites have only a single study this intrasite variability cannot used to compare sites. Likewise data for Whitten (1982) are averaged, and both populations appear to have very similar values for the dietary proportions.

Vervets too are present in sites where there is extensive interannual variation (Altmann et al., 1985). Once again, the lack of temporal variation at the same site is an omission, but between site variation at adjacent sites might give some indication of the variability of the same habitat. Once again the data only allow a very broad brush analysis of subspecific differences.

Table 3.2. Vervet dietary data showing the proportions of foods in the diet by time budget. Details of the site (n=16), method of data collection and study period are given. The observed sex is also given. Titles: F&S = Fruit and seeds (together), F = fruit, S = Seeds, Lf = leaves (young), Fl = flower, A = Animal, S = Seeds, O = other.

CHAPTER 4. **Subspecies**	**CHAPTER 5.** **ite**	**No**	**Group**	**F & S**	**F**	**S**	**Lf**	**Fl**	**A**	**S**	**O**	**Author**
C. a. aethiops	Bole Valley	1		50.6	0	0	18.7	17.6	7.4	0	5.7	(Dunbar and Dunbar, 1974)
C. a. djamdjamensis	Oldoyo	2		9.6	9.6	0	80.2	3.1	2.3	0	0	(Mekonnen et al., 2010)
C. a. pygerythrus	Blydeburg	3		70	56	7	8	2	4	0.5	24.0*	(Barrett, 2005)
C. a. pygerythrus	Amboseli	4	1	18	18	0	43	9	3	27	0	(Lee, 1981)
C. a. pygerythrus	Amboseli		2	24	24	0	28	16	2	30	0	(Lee, 1981)
C. a. pygerythrus	Amboseli		3	30	30	0	26	22	3	19	0	(Lee, 1981)
C. a. pygerythrus	Samburu-Isiolo	5	RR	32.9	6.8	26.1	15.7	43.3	0.5	0	7.7	(Whitten, 1982)
C. a. pygerythrus	Samburu-Isiolo		LM	28.2	7.9	20.3	16	51.3	0.4	0	4.1	(Whitten, 1982)
C. a. pygerythrus	Lajuma	6		80.6	0	0	6.4	1.5	0	9.9	1.6	(Willems, 2008)
C. a. pygerythrus	Diani Beach	7		76.6	55.3	21.3	10.6	6.4	0	0	6.5	(Moreno-Black and Maples, 1977)
C. a. pygerythrus	Amboseli	8		20.2	11.7	8.4	19.7	15.3	9.2	28.5	7.2	(Wrangham and Waterman, 1981)
C. a. sabaeus	Mt Assirik	9		63	50.2	12.8	7.4	13	13.1	2.4	1.3	(Harrison, 1982)
C. a. sabaeus	N'Dioum	10		26.6	26.6	0	42.6	4.2	13.1	11.2	1.3	(Galat and Galat-Luong, 1977)
C. a. tantalus	Buffle Noir	11		27.4	26.4	1	5.1	34.3	29	2.2	1.6	(Kavanagh, 1977)
C. a. tantalus	Kalamaloue	12		63	61	2	16.8	11.2	7.2	1.3	0	(Kavanagh, 1977)

C. a. tantalus	Ngel Nyaki	13		49.2	49.2	0	20.5	5.3	25	0	0	(Agmen et al., 2010)

Table 3.2 continued.

Author	**Duration**	**Method**	**Scan interval (min)**	**Sex**
(Dunbar and Dunbar, 1974)	5[1]	Focal	10	Both
(Mekonnen et al., 2010)	10[2]	Scan)	15	Both
(Barrett, 2005)	12	Scan	30	Both
(Lee, 1981)	12	Focal	?	Both
(Lee, 1981)	12	Focal	?	Both
(Lee, 1981)	12	Focal	?	Both
(Whitten, 1982)	12	Focal	30	Females
(Whitten, 1982)	12	Focal	30	Females
(Willems, 2008)	12	Focal	10	Both
(Moreno-Black and Maples, 1977)	6[3]	Scan	-	Both
(Wrangham and Waterman, 1981)	8[4]	Focal	5	Females
(Harrison, 1982)	12	Scan	15	Both
(Galat and Galat-Luong, 1977)	12	Focal	15	Both
(Kavanagh, 1977)	5[5]	Scan	15	Both
(Kavanagh, 1977)	7[6]	Scan	15	Both
(Agmen et al., 2010)	12	Focal	15	Both

[1] May ‘71, May – Jun. & Sept. – Oct. ’72.

[2] Aug. ’07 – May ’08.

[3] Oct. ‘72 – Mar. ’73.

[4] Jul. – Oct '78, Nov. '78 – Jan. ‘79, Aug. – Sep. ’79.

[5] Jan. – Feb, Apr. – Jun ‘75.

[6] May – Jun., ‘74, Mar, Jul. – Oct ’75.

3.2.5 Vervet Dietary Categories

Vervet dietary categories in this study are fruit and seeds, leaves, flower, animal, sap and a grouping called "other" for foods not included in these. These are standard categories used in vervet dietary studies (Harrison, 1982, Whitten, 1982). Because some studies do not consider fruits and seeds as a separate category the resolution of this study has to be at that crude level, as we have no information about how to split these values. For all analyses fruit and seeds are lumped. Leaf in this case means young leaf, and excludes mature leaves: some studies separate these on the basis of their different nutritional components, i.e. they are higher in proteins and contain less deleterious secondary compounds. Animal is almost always invertebrate or else bird's eggs. Sap refers to any exudate or gum from tree bark.

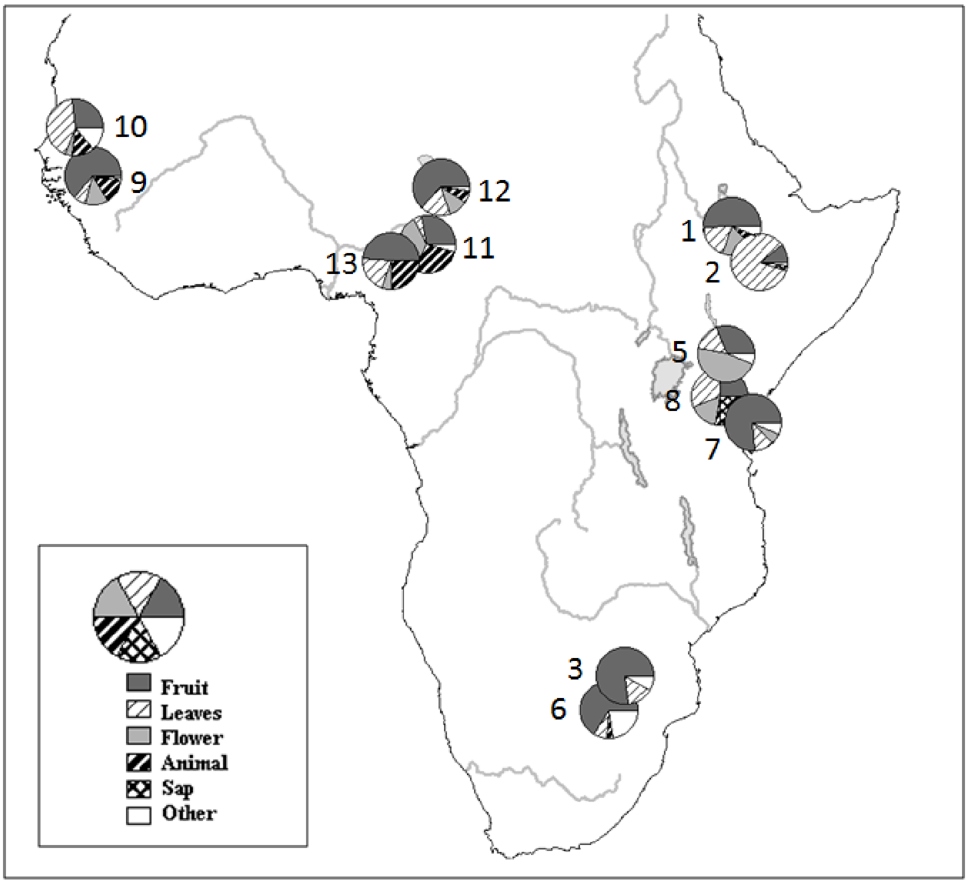


Figure 3.2. Pie charts showing the geographic position of the study sites and the food proportions that make up the total diet for vervet monkeys, as presented in table 3.2. Numbers correspond to those in table 3.2, n = 12.

3.2.6 Comparability of Vervet Studies

As discussed for the baboon studies (3.2.3), variation in sampling between focal and scan methods (Altmann, 1974) ought not to be problematical as any biases should not be systematic. Nine of the vervet studies lasted for a full year and are therefore expected to encapsulate full seasonal variation. Wrangham and Waterman’s (1981) study took place at Amboseli for which full year data were already provided by Lee (1981). Consequently only the latter was used as this was assumed to be more representative of the site. Mekonen's (2008) study fails to capture the year by two months. However, data are presented for both a wet season and a dry season suggesting that major extremes of seasonal variation are captured and that observations are not hugely biased for any one season. Though the dietary proportions for this site are markedly different, in terms of the high proportion of leaves consumed, this is far more likely to be a real biological difference relating to the unique feeding behaviour of this ecologically distinct subspecies of vervet, the djam-djam, than the result of an artefact of biased sampling.

The study by Moreno-Black and Maples (1977) lasted for only half of the year. However, they argue that this captures one wet and one dry season, so even though the full year is not sampled its seasonal extremes are. Dunbar and Dunbar’s (1974) study looked at May in one year, May to June and September to October in the next year, showing poor annual dispersal. However, this is the only published study for *C. a. aethiops* and so it is cautiously included in the analysis.

Kavanagh (1978) gives data for two sites: Buffle Noir and Kalamaloue, both in Cameroon. The former study period was from January to June, save for March, i.e. five months’ worth of sampling across six months of the year. Vervets in Kalamaloue were observed in May and June of one year and March, and July to October in the next. This is seven months of study across eight months, but spread over two years. Again, as the studies span a wet season and a dry season the seasonal biases are likely to be minimised, even if a full year is not observed. Monthly variation in frugivory ranged from 97.1% of observation time in August to 8.8% in March at the Kalamaloue site demonstrating that seasonal variation in food availability has been recorded.

Another potential source of bias is that not all studies observed both sexes (table 3.2) Whitten (1982) and Wrangham and Whitten (1981) observed only females. There is evidence for differences between the sexes in terms of food proportions (Harrison, 1983), but the difference is slight. For instance in Harrison's study of sexual variation in foraging males consumed 62% fruit in the dry season compared to 63% for females without infants and 59% for this with infants. The wet season values were 61%, 57% and 61% respectively. Evidently then the presence or absence of an infant is more of a skewing factor that sex *per se*. The slight differences between the sexes without infants was explained by (Wrangham and Waterman, 1981) in terms of adult males being the better competitors for resources such as fruits. However, the magnitude of these differences is really quite small and so it is concluded that these studies are not incomparable with the others.

3.6.7 Statistical Comparison of the Dietary Data

The logistic regression was used to test for differences in dietary data using R (R Development Core Team, 2008). This method is employed in studies across a range of taxa comprising macaques (Majolo and Ventura, 2004) alligators (Gabrey et al., 2008) and perch (Parker et al., 1999). This method is appropriate as categorical data have statistical properties that violate the assumptions of ANOVAs and linear models. Using ANOVAs on categorical data results in variances and confidence intervals that are inflated beyond the zero to one range (Jaeger, 2008) and the variance is higher when proportions are more equal than if they are very unequal (Crawley 2007). The logistic regression accounts for this by log transforming the data for better comparison of categorical data. This method uses a baseline group as a comparator for which the largest group was chosen: *P. h. anubis* and *C. a. pygerythrus* for the baboon and vervet analysis respectively.

3.2.8 Quantifying Dietary Generalism and Niche Width

To quantify and contextualise the generalism of the study taxa, dietary data were collected for two other taxa to serve as trophic outgroups (tables 3 and 4). These outgroups constituted the red colobus, *Piliocolobus* sp., chosen as it is a specialist folivore (Struhsaker, 2010), and the blue monkey, *Cercopithecus mitis*, chosen for being broadly frugivorous, although exhibiting interpopulation variation in its diet (Twinomugisha et al., 2006). Additionally these taxa were chosen for being widespread and are polytypic (Cardini et al., 2010, Cardini and Elton, 2009), although occupying forest habitats rather than the open environments of the study taxa. The analysis used the dietary data in tables 1, 2, 3 and 4. Because the djam-djam is a vervet subspecies with a highly distinctive diet from the other subspecies analyses were carried out with and without this taxon.

Interspecific dietary comparisons were made in two ways:

I. Generalism versus Specialism

Dietary generalists must necessarily consume more even proportions of foods as no single category can dominate by definition (Aumann, 2001, Magurran, 1988). Specialists conversely must have a diet skewed in favour of one particular resource on which they specialist. To quantify the position of the two study species and the two dietary outgroups on this generalism-specialism axis, the Shannon diversity index was used. This method calculates the evenness of dietary categories (Agostini et al., 2010, Magurran, 1988, Ross et al., 2010), high values indicate equal food proportions and thus dietary generalism. Low values suggest highly unequal proportions suggestive of a single food being the dominant dietary component. As well as calculating the Shannon Index of dietary evenness, to visualise the dietary proportions, data for all four subspecies were averaged and displayed as pie charts.

II. Niche Width

Though species have an average point on the generalism-specialism axis, each population is bound to exhibit differences in dietary proportion. To quantify this intraspecific spread, Roughgarden's method of niche width calculation was used (Roughgarden, 1979, Bolnick et al., 2002, Ebenman and Nilsson, 1982). This method calculates the between population variance, and expresses it as a proportion of the total variance. Species with populations that vary between specialism and generalism will have a wide niche, while those compelled to be specialist or generalist will have a low width.

A matrix (n_{ij}) of *i* populations and *j* diet categories was compiled for the four species. The components of the total dietary variance were calculated for each species thus:

Within population = $\sum_i p_{i\bullet} \left\{ -\sum_j p_{ij} \ln p_{ij} \right\}$

Between population = $-\sum_i p_{i\bullet} \ln\left(p_{i\bullet}\right) - \left\{ \sum_j q_j \left\{ -\sum_i \gamma_{ij} \ln\, \gamma_{ij} \right\} \right\}$

Total variation = $-\sum_j q_j \ln q_j$

Where:

$$p_{ij} = \frac{n_{ij}}{\sum_j n_{ij}} \qquad q_j = \frac{\sum_i n_{ij}}{\sum_i \sum_j n_{ij}}$$

$$p_{i\bullet} = \frac{\sum_j n_{ij}}{\sum_i \sum_j n_{ij}} \qquad \gamma_{ij} = \frac{n_{ij}}{\sum_i n_{ij}}$$

Niche width is given by expressing the between component as a proportion of the total component. All calculations were performed in R (2011).

Table 3.3. Blue monkey dietary data showing the percentages of foods in the diet by time budget.

Study Site	Leaves	Fruit	Flowers	Insects	Other	Reference
Kakamega, Kenya	18.9	57.1	3.7	16.8	3.5	(Cords, 1986)
Nyungwe Forest, Rwanda	6.2	56.7	6.2	24.9	6	(Kaplin and Moermond, 2000)
Cape Vidal, South Africa	26	57	13	4	0	(Lawes, 1991)
Zomba Plateau	32.6	53.5	10.2	1	2.7	(Beeson et al., 1996)
Ngoye Forest. South Africa	3	91	2	0	4	(Lawes et al., 1990)
Kanwayara, Kibale	33	27.7	6.9	37.7	0.6	(Butynski, 1990)
Ngogo, Kibale	22.8	30.1	9.8	35.9	1.4	(Butynski, 1990)
Budongo Forest Reserve, Uganda	33.15	50.8	6.2	0.21	0.2	(Fairgrieve and Muhumuza, 2003)
Mgahinga, Uganda	39.1	26.3	12.4	16.4	6	(Twinomugisha et al., 2006)
Lake Kivu, DRC	32	37	20	11	0	(Schlichte, 1978 cited in Twinomugisha et al., 2006)
Cyprus, South Africa	59.4	23.9	5	5	6	(Scorer, 1980 cited in Twinomugisha et al., 2006)

Table 3.4. Red colobus dietary data showing the percentages of foods in the diet by time budget.

Study Site	**Taxon**	**Leaves**	**Fruit**	**Flowers**	**Other**	**Reference**
Sierra Leone	*P. badius*	51.9	31.2	16.1	0.8	Davies 1977
Kibale, Uganda	*P. tephrosceles*	81.5	7.9	6	4.6	Chapman 1999*
Tiwai, Sierra Leone	*P. badius*	52	31	16	1	Davies et al., 1999
Tana River, Kenya	*P. rufomitratas*	55.4	23.7	20	0.9	Decker 1933*
Fathala Forest, Senegal	*P. temminckii*	48	35.9	8.7	7.4	Gatinot 1977
Zanzibar	*P. kirkii*	60.2	28.8	8	2.9	Mturi 1993*
Kibale, Uganda	*P. tephrosceles*	73.2	6	19.4	1.5	Struhsaker 1975*
Korup National Park, Cameroon	*P. preussi*	89	1	10	0	Usongo & Amubode
Kibale, Uganda	*P. badius*	87.1	7.1	2	3.8	Wasserman & Chapman 2003*
Tana River, Kenya	*P. rufomitratas*	63.9	25	6.2	4.9	March 1981.
Kibale, Uganda	*P. tephrosceles*	78.2	11.3	9	1.5	Clutton-Brock 1975*
Botsima, Salonga, DR Congo	*P. tholloni*	60.7	37.9	1.4	0	Maisels et al. 1994
Kibale, Uganda	*P. tephrosceles*	80	10	7	3	Chapman & Chapman1999

*averaged data.

3.3 RESULTS

3.3. 1 Baboon Dietary Differences

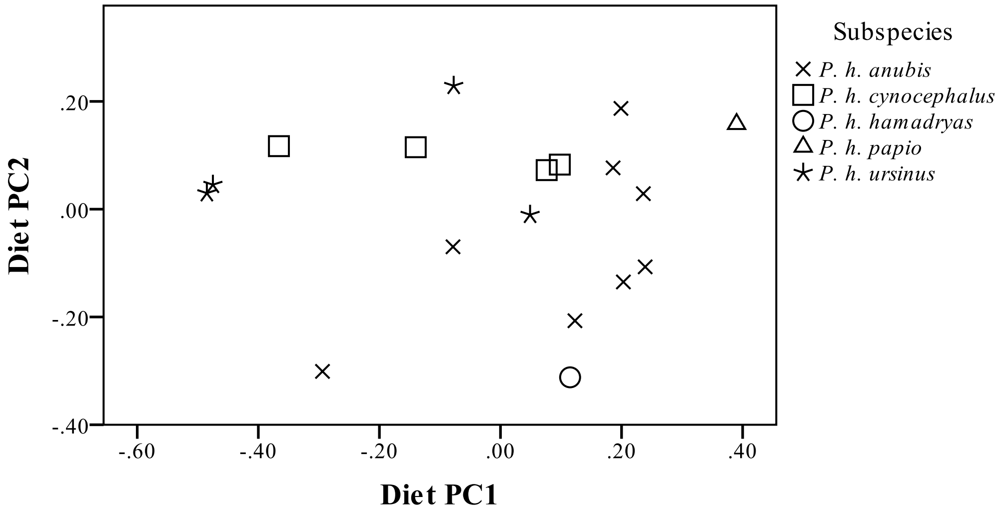


Figure 3.3. A scatter plot of dietary PC1 (62.1% variance) against PC2 (23.2%) for the five subspecies. Loadings are given in table 3.

Table 3.5. The loadings for the dietary PCs.

	PC1	**PC2**
Fruit	0.74	0.26
Subterranean	-0.65	0.41
Leaves	-0.08	-0.87
Flowers	-0.07	0.06
Animal	-0.04	0.05
Other	0.11	0.08

The major axis of dietary variation, accounting for 62.1% of the variation, is between high levels of frugivory versus subterranean food eating (table 3.5). The scatter shows the Guinea baboon as the most frugivorous, followed by dispersed scatter of olive baboons and other taxa, with the chacma baboon emerging at the subterranean food end. The second axis accounts for just under a quarter of the variance and describes high subterranean food eating versus folivory and fruvigory. PC 2 reveals the hamadryas baboon to be the most folivorous subspecies, with a few olive baboons populations. The yellow and chacma appear at the top of this plot indicating greater subterranean food eating on this axis as well.

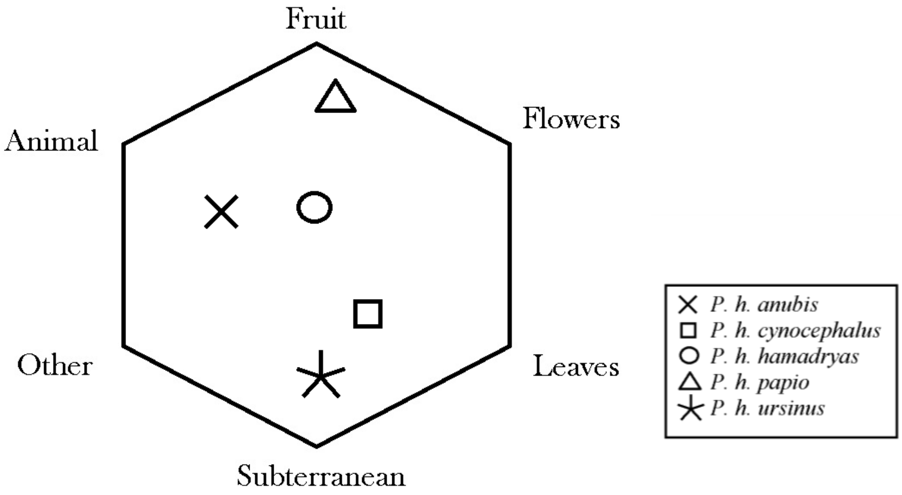


Figure 3.4 A schematic of the showing the differences between the baboon subspecies.

The data from table 3.5 and fig. 3.3 are summarised schematically in fig. 3.4.

Table 3.6. Multinomial logistic regression results for the food proportions for the sites in table 1 excluding the results of Gaynor (1994) and Pochron (2000). Comparisons use P. h. anubis *as a reference. Significant results are shown in bold.*

Factor	**Comparison**	**Estimate**	**Std.**	**Error**	**t-value**
Subterranean foods	*P. h. anubis-P. h. cynocephalus*	0.13854	0.07832	1.7688	0.077
	P. h. anubis- P. h. hamadryas	-0.1407	0.22921	-0.6139	0.539
	P. h. anubis- P. h. papio	-0.2018	0.29158	-0.6921	0.489
	P. h. anubis- P. h. ursinus	0.18059	0.08674	2.082	**0.037**
Fruit and seeds	*P. h. anubis- P. h. cynocephalus*	-0.0284	0.03806	-0.7467	0.455
	P. h. anubis- P. h. hamadryas	0.0017	0.07573	0.0224	0.982
	P. h. anubis- P. h. papio	2.1755	349.25	0.0062	0.995
	P. h. anubis- P. h. ursinus	-0.0616	0.03869	-1.5916	0.112
Leaves	*P. h. anubis- P. h. cynocephalus*	-0.0284	0.03806	-0.7467	0.455
	P. h. anubis- P. h. hamadryas	0.0017	0.07573	0.0224	0.982
	P. h. anubis- P. h. papio	2.1755	349.25	0.0062	0.995
	P. h. anubis- P. h.	-0.0616	0.03869	-1.5916	0.112

	ursinus				
Animal	*P. h. anubis- P. h. cynocephalus*	0.02952	0.18984	0.1555	0.876
	P. h. anubis- P. h. hamadryas	-16.926	2072.04	-0.0082	0.994
	P. h. anubis- P. h. papio	-0.2587	0.69467	-0.3724	0.71
	P. h. anubis- P. h. ursinus	0.11512	0.16768	0.6865	0.492
Other	*P. h. anubis- P. h. cynocephalus*	-0.044	0.07838	-0.561	0.575
	P. h. anubis- P. h. hamadryas	-1.0239	1.01379	-1.01	0.312
	P. h. anubis- P. h. papio	-0.206	0.26819	-0.7681	0.442
	P. h. anubis- P. h. ursinus	-1.2523	0.74501	-1.6809	0.093

Table 3.7 Multinomial logistic regression results for the food proportions for the sites in table 1 of greater than 1 year. Comparisons use P. h. anubis *baboon as a reference. Significant results are shown in bold.*

Factor	Comparison	Estimate	Std.	Error	t-value
Subterranean foods	*P. h. anubis- P. h. cynocephalus*	0.11	0.084	1.317	0.188
	P. h. anubis- P. h. hamadryas	-0.208	0.268	-0.776	0.438
	P. h. anubis- P. h. papio	-0.281	0.34	-0.826	0.409
	P. h. anubis- P. h. ursinus	0.102	0.087	1.179	0.239
Fruit and seeds	*P. h. anubis- P. h. cynocephalus*	0.022	0.052	0.43	0.667
	P. h. anubis- P. h. hamadryas	0.058	0.103	0.559	0.576
	P. h. anubis- P. h. papio	1.423	177.95	0.008	0.994
	P. h. anubis- P. h. ursinus	0.063	0.081	0.778	0.437
Leaves	*P. h. anubis- P. h. cynocephalus*	-0.145	0.123	-1.178	0.239
	P. h. anubis- P. h. hamadryas	0.312	0.99	0.315	0.753
	P. h. anubis- P. h. papio	-0.654	0.6	-1.091	0.276
	P. h. anubis- P. h. ursinus	-0.177	0.149	-1.184	0.236

Animal	*P. h. anubis- P. h. cynocephalus*	-0.067	0.19	-0.352	0.725
	P. h. anubis- P. h. hamadryas	-18.28	2281.41	-0.008	0.994
	P. h. anubis- P. h. papio	-0.43	0.803	-0.535	0.593
	P. h. anubis- P. h. ursinus	-0.035	0.204	-0.17	0.865
Other	*P. h. anubis- P. h. cynocephalus*	-0.368	0.24	-1.531	0.126
	P. h. anubis- P. h. hamadryas	-32.996	4949.86	-0.007	0.995
	P. h. anubis- P. h. papio	-0.505	0.445	-1.134	0.257
	P. h. anubis- P. h. ursinus	-49.566	6341.53	-0.008	0.994

None of the food proportions was significant predictors of taxon apart from subterranean foods (table 3.6). The chacma baboon diet contains significantly more subterranean foods in its diet relative to olive baboon (table 3.6). Another way of interpreting this is to say that for any given subterranean food proportions the odds of the subspecies being *P. h. ursinus* versus *P. h. anubis* olive is 1.20. This is slight but significant. Using only the data for sites that were studied for more than a year reveals no significant differences for any subspecies (table 3.7).

3.3.2 Vervet Dietary Differences

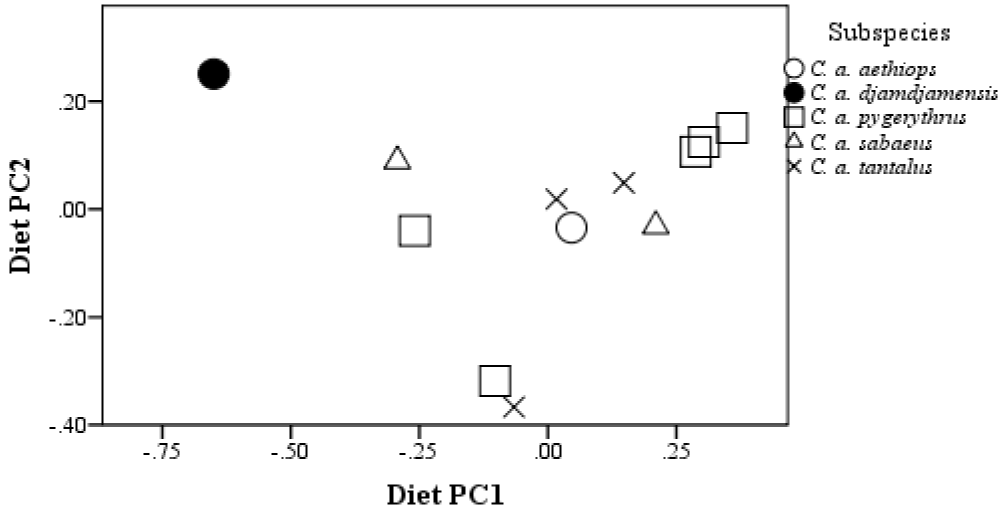


Figure 3.5. A scatter plot of dietary PC1 (62.1% variance) against PC2 (23.5%) for the five subspecies for which dietary information was available. Loadings for the interpretation of the PCs are given in table.6.

Table 3.8. The loadings for the dietary PCs.

	PC01	**PC02**
Fruit	0.76	0.38
Leaves	-0.64	0.53
Flower	-0.07	-0.72
Animal	-0.02	-0.23
Sap	-0.06	0.02
Other	0.1	0.03

The major axis of dietary variation, accounting for 62.1% of the variance, is between high levels of fruit and seed eating versus leaf eating (table 3.8). The second axis accounts for 23.5% of the variance and chiefly describes high folivory and frugivory versus high flower-eating. The scatter reveals *C. a. tantalus* and *C. a. pygerythrus* are at the more frugivorous extreme, with *C. a. djamdjamensis* as the highly folivorous extreme. One population of *C. a. pygerythrus* and one population of *C. a tantalus* appear strongly towards the flower-eating extreme of PC 2, while the other populations are intermediate.

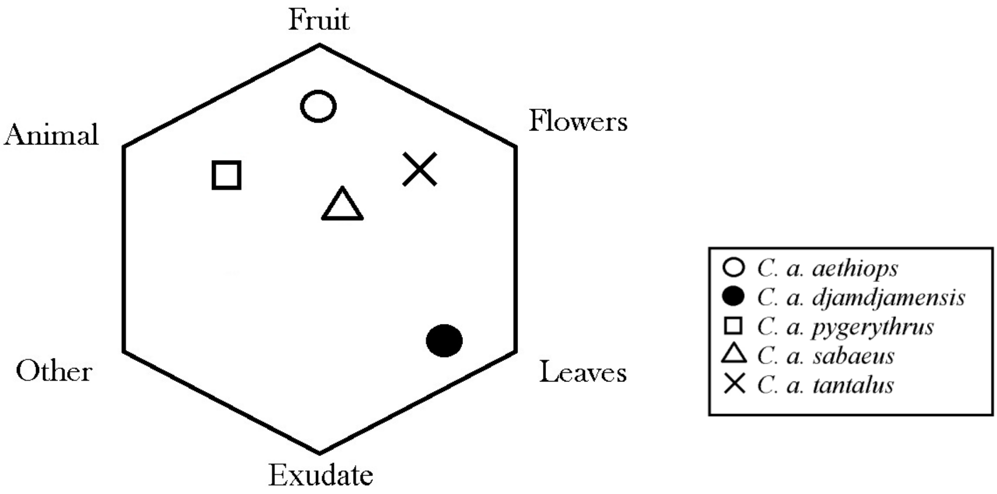


Figure 3.6. A dietary schematic showing the differences between the vervet subspecies.

The data from table 3.8 and fig. 3.5 are summarised schematically in fig. 3.6.

Table 3.9. Multinomial logistic regression results for the food proportions for the sites in table 2. Comparisons use C. a. pygerythrus *as a reference. Significant results are shown in bold.*

Factor	**Comparison**	**Estimate**	**Std.**	**Error**	**t-value**
Fruit	*C. a. pygerythrus- C. a. sabaeus*	-2.87	4.47	-0.6429	0.5203
	C. a. pygerythrus- C. a. tantalus	-2.42	3.87	-0.6241	0.5326
	C. a. pygerythrus- C. a. aethiops	-1.26	5.70	-0.2214	0.8248
	C. a. pygerythrus- C. a. djamdjamensis	-227.74	28096.66	-0.0081	0.9935
Leaf	*C. a. pygerythrus- C. a. sabaeus*	6.50	7.49	0.8672	0.3858
	C. a. pygerythrus- C. a. tantalus	-2.54	8.38	-0.3032	0.7617
	C. a. pygerythrus- C. a. aethiops	2.40	10.15	0.236	0.8135
	C. a. pygerythrus- C. a. djamdjamensis	90.67	10966.38	0.0083	0.9934
Flower	*C. a. pygerythrus- C. a. sabaeus*	-4.24	8.51	-0.4986	0.6181
	C. a. pygerythrus- C. a. tantalus	1.29	5.05	0.2549	0.7988
	C. a. pygerythrus- C. a. aethiops	1.85	7.20	0.2571	0.7971
	C. a. pygerythrus- C. a. djamdjamensis	-1510.00	186000.00	-0.0081	0.9935
Animal	*C. a. pygerythrus- C. a. sabaeus*	1352.24	158651.20	0.0085	0.9932

	C. a. pygerythrus- C. a. tantalus	1364.86	158651.20	0.0086	0.9931
	C. a. pygerythrus- C. a. aethiops	1063.68	137655.80	0.0077	0.9938
	C. a. pygerythrus- C. a. djamdjamensis	-511.13	122702.10	-0.0042	0.9967
Sap	*C. a. pygerythrus- C. a. sabaeus*	-9.01	19.40	-0.4643	0.6424
	C. a. pygerythrus- C. a. tantalus	-1640.00	252000.00	-0.0065	0.9948
	C. a. pygerythrus- C. a. aethiops	-1600.00	355000.00	-0.0045	0.9964
	C. a. pygerythrus- C. a. djamdjamensis	-3.49	15.70	-0.2224	0.8240
Other	*C. a. pygerythrus- C. a. sabaeus*	-3.06	12.41	-0.2467	0.8051
	C. a. pygerythrus- C. a. tantalus	-41.49	30.74	-1.3497	0.1771
	C. a. pygerythrus- C. a. aethiops	-7.27	19.71	-0.3691	0.7121
	C. a. pygerythrus- C. a. djamdjamensis	-41.49	46.82	-0.8862	0.3755

None of the food proportions was significant predictors of taxon (table 3.9).

3.3.3 Comparison of the Study Taxa with Two Trophic Outgroups

To contextualise intraspecific dietary variation in the study taxa, two trophic outgroups were examined.

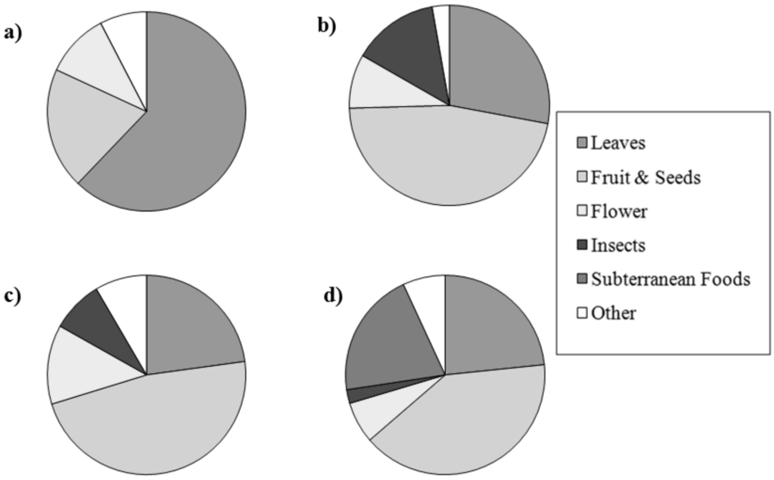


*Figure 3.7. Pie charts showing the average dietary proportion s for **a**) red colobus (n = 13) **b**) blue monkeys (n = 11) **c**) vervets (n = 12) and **d**) baboons (n = 21).*

Table 3.10. Dietary variation for the four taxa is divided into the within population component, the Shannon Index showing dietary evenness, and dietary variance between intraspecific populations, indicating the niche width of the species as a whole.

Taxon	Sample Size	Within Population Variance	Between Population Variance	Total
Baboon	20	1.19	0.3	1.48
Vervet (full)	12	1.1	0.33	1.43
Vervet (djam-djam excluded)	11	1.15	0.27	1.42
Red Colobus	13	0.92	0.13	1.05
Blue Monkey	11	1.12	0.18	1.3

The baboon has the highest Shannon index showing greatest evenness of dietary categories (table 3.10), demonstrated by the more even proportions and the inclusion of an additional category, subterranean foods, relative to the other taxa (fig. 3.9). Exclusion of the djam-djam increases the dietary diversity for the vervets giving it a higher Shannon index than the blue monkey (table 3.10). The red colobus has a low dietary evenness (table 3.10) borne out by the dominance of leaves in its diet (fig. 3.9).

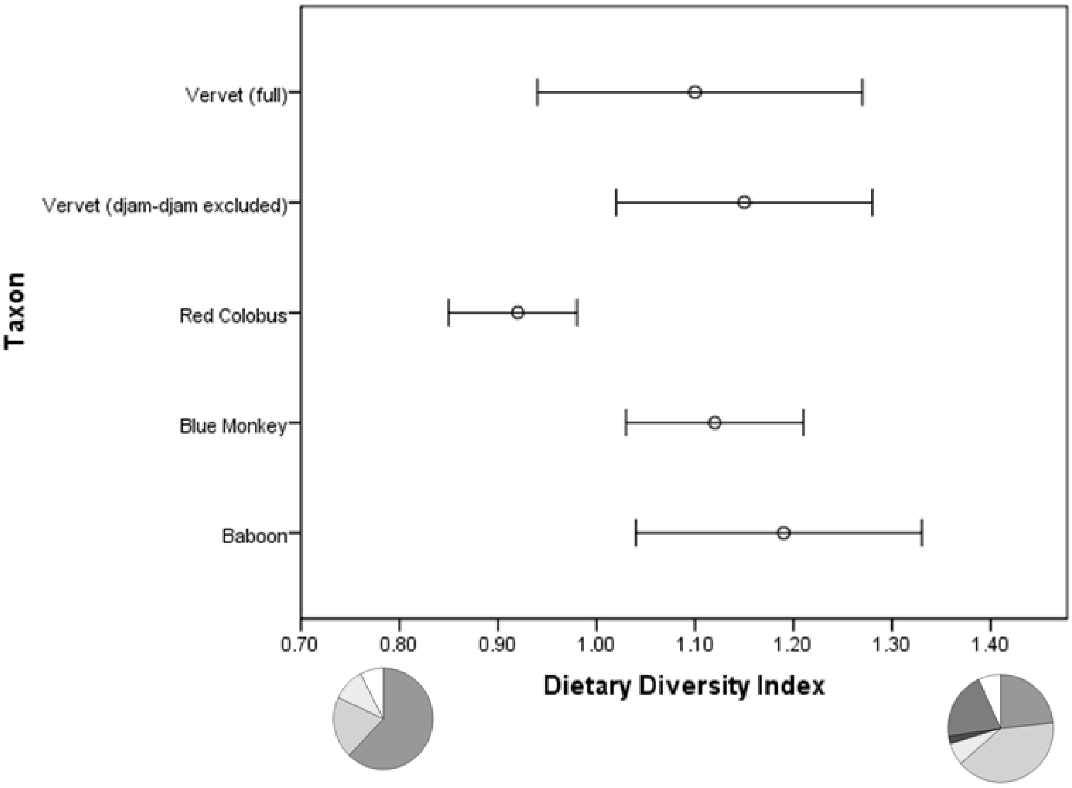


Figure 3.8. A plot showing the mean values of dietary evenness (Shannon Index) for each of the four taxa (circles) with bars denoting the extent of intraspecific variation (niche width).

The vervet monkey has the largest niche width in terms of variation between even and uneven diet (table 3.10, fig. 3.9). Removal of the dietarily distinct djam-djam reduces this niche width and shifts the range and average in the more generalist direction. When the djam-djam is removed the baboon has the highest niche width. The blue monkey has a smaller niche width than the two study taxa, and the red colobus exhibits the lowest niche width indicating, with its low Shannon index, little deviation from dietary specialism.

3.4 DISCUSSION

3.4.1 Comparing Baboon and Vervet Subspecific Dietary Variation

Baboons exhibit a significant difference between two subspecies in the proportion of subterranean food items in the diet. That a difference is detectible when the number of studies is so few suggests that the difference is significant and reflects biological reality. Again, though there is a lack of interannual variation in the data it is hard to see how this would bias the result in on particular direction and result in a type I error. In contrast, for vervets no subspecific dietary differences were detected, potentially reflecting reality but also potentially reflecting a poorer dataset, resulting in a type II error. For baboons the differences centred on subterranean foods; a food item absent from the diets of vervets. There are several potential reasons for this difference between the study taxa, chief of which is that the vervets' small size renders them too weak to dig up these difficult to extract foods (Altmann, 1998, Barrett, 2005). Additionally their shorter digestive tract and concomitantly short retention time means they are capable of extracting less energy from such highly fibrous food than a larger animal, such as a baboon, would be able to (Demment, 1983). This is of great importance as vervets, being smaller, have proportionally higher metabolic rates as a result of scaling laws (Schmidt-Nielsen, 1984). The also have more riparian and arboreal habitat preference than baboons (Kingdon, 1997, Struhsaker, 1967a) within the savannah, resulting in their spending less on the part of the savannah where subterranean food items grows (Dominy et al., 2008). Again, this probably has a size element: the open savannah is relatively more dangerous to vervets, which as a result of their smaller size have more predators than the larger baboons (Dunbar, 1988). This higher predation risk makes them less likely to venture from refugial trees and rules out spending considerable time extracting roots and tubers. Baboons in contrast are only tied to sleeping at these sites and may spend more time foraging over the full extent of the open savannah. It is possible therefore that if vervets were not constrained by their small size they would take advantage of subterranean foods and significant dietary differences would emerge as with baboons. Potentially therefore the lack of significant dietary splits among the vervet subspecies is the result of insufficient range of foods. Certainly this is backed up by the smaller niche width. All vervets eat broadly the same thing. Of course the djam-djam is an exception to this (Mekonnen, 2008, Mekonnen et al., 2010), although we lack sufficient data to prove it statistically, and again the null hypothesis may falsely be being accepted. Were there a significant difference between the djam-djam and other ververt subspecies this would represent a totally different ecological expansion and evolutionarily divergent trajectory of subspecific radiation in the vervet versus the baboon.

3.4.2 Baboon Diet

This study is concordant with the findings of Hill & Dunbar (2002) that subterranean foods, fruits and leaves are the major dietary items by time budget (table 3.1). A weakness of the data is that studies are poorly dispersed geographically and lack interannual variation (fig. 3.1). The poor sampling reflects observational and fieldwork biases and is beyond the scope of this thesis to rectify. For instance it is evidently easier to carry out studies at certain sites for political and historical reasons. Certain countries in which the baboons are unsampled are highly unstable politically, such as Angola and formerly Namibia. Moreover, once a study site is established it is easier to carry out long term studies than begin a new study at another site. East Africa in particular is well represented as is South Africa with something of a gulf in between. Identification of this bias enables a more realistic interpretation of the results.

The finding of the logistic regression on the full data set was of a difference in the proportion of subterranean foods being eaten between the chacma and olive baboons. No such difference was found when the number of studies was reduced to only the full year ones. Though the data for subyear studies contain seasonality biases and therefore lack some reliability the data do not appear in any case to be very different from full year studies (table 3.1). The full year studies, though lacking any seasonal biases, number only eleven and there are five subspecies. It seems likely therefore that the lack of a difference for the full year studies owes more to a low sample size than to the absence of any difference. Indeed the fuller dataset with only Gaynor (1994) and Pochron (2000) excluded consists of only 18 studies, and so the finding is unlikely to be a false positive arising by chance.

This significant difference between the olive and chacma baboon would appear to be fairly well founded and agrees with the qualitative data (Hill and Dunbar, 2002). The chacma baboon has populations inhabiting southern Africa, as well as the tropics, and thus contains the most temperate-living of the baboons (Anderson, 1982). Seasonality is greater here than in the rest of Africa, resulting in colder and darker winter than the other subspecies must face. The shorter day length in winter means there is less time for foraging (Hill et al., 2003, van Doorn et al., 2010) and fallback foods are of greater importance. This subspecies has populations living in mountainous habitats (Whiten et al., 1991a). At such highland sites corms and bases are even more prevalent than at adjacent lowland sites (Whiten et al., 1987) and at both the availability of fruits is very low. Geophytes are by definition plant storage organs which are clearly favoured by a severe winter climate when nutrients must be stored over a period of drought (Whiten et al., 1987). These are more diverse here than in any other part of Africa (Dominy et al., 2008), and it is unsurprising therefore that chacma baboons exploit them to such a high degree. However, our sample is skewed in favour of temperate chacma baboon sites, so this findings must be taken with some caution.

The olive baboon is the generalist within the generalists. Though it inhabits dry savannah, where there is a dry season and a significant fallback to subterranean foods eating (Harding, 1976), it is also found in central Africa in the more forested habitats of Ugand (Rowell, 1966) as well as in West Africa (Kunz and Linsenmair, 2008b, Higham et al., 2009). These habitats are much wetter and lack the seasonal dryness of the East African savannah, and as a result plants do not require underground storage organs and fruits are in greater supply. Indeed fruits were highly abundant in the rainforest fringes of Ugandan and made up a large proportion of the baboon diet (Rowell, 1964). Many of these were leguminous and high in protein and eaten when unripe (Rowell, 1966). Unlike the tough dry fruits of acacia found on the savannah, this environment contains softer fruit such as figs. Another area where fruvigory is particularly high is in West Africa. At the Comoé National Park, northern Ivory Coast, 54% of feeding is of fruits and seeds. Typically immature fruit were selected on the basis that seeds are still digestible and contain more protein (Kunz and Linsenmair, 2008a). Olive baboons in Nigeria also have a access to a higher fruit availability (Higham et al., 2009).

Overall it would seem that the significant dietary difference between olive baboons and chacma baboons are rooted in environmental variation and the consequent foods available. This raises an interesting question as to whether this is incidental, with the animals simply eating what is to hand, or if the subspecies constrained to their respective diets. Could the olive not survive on a diet with a significantly higher proportion of subterranean foods? Given the plasticity of the species, and this subspecies in particular this would not seem very likely. Nevertheless, longstanding ecological differences are likely to put a premium on even subtle adaptations. There are certainly differences between the subspecies that are genetically fixed and not plastic, the most obvious of which are pelage (Chapter 1) and morphology (Chapter 2). Hybrids of olive and yellow baboons mature at a rate proportional to how much ancestry of each they have: the yellow baboon is slow maturing and the olive baboon fast, proving this trait is under strict genetic control (Charpentier et al., 2008). Another genetically fixed, nonplastic difference, can be found in peak testosterone level timing and pattern between the chacma and yellow baboon (Beehner et al., 2009). Olive and chacma baboons are likely to be have genetically fixed life history differences. These features might be ecologically related, perhaps being related to resource abundance. Conceivably the faster maturation of olive baboons might be maladaptive in a more seasonal environment with periods of resource constriction. Physiological adaptations may exist with regard adaptation, and it is possible that craniofacial differences are related to biomechanics (Chapter 4).

The absence of a significant difference between the olive and yellow baboons is somewhat unexpected. Like the chacma the yellow baboons relies heavily on subterranean foods. Sedge corms (Cyperacaea family), found in the yellow baboon’s savannah and savannah woodland habitat, are a staple resource for this subspecies (Rhine et al., 1989). The baboons spend a high proportion of their time budget spent searching for, digging up and processing the subterranean sedge corms (Rhine et al., 1989). This is particularly true in the dry season (Pochron, 2000). Unripe tamarind fruits were also a major food source for a few months of the year (Rhine et al., 1989) as are baobab fruit (Pochron, 2000). It is surprising then that the analysis does not reveal it to be significantly different from the olive. It is worth noting that the t-value is low at 0.077 (table 3.1) but not making the 5% significance level. It is conceivable that a low sample size is responsible for this.

A lack of significant difference between the olive baboon, our baseline, and the Guinea baboon is undoubtedly the result of there being only one quantitative study. It seems likely the Guinea baboon is truly more frugivorous than other subspecies. This subspecies inhabits the westernmost point of West Africa where it lives in savannah woodland (Dunbar and Nathan, 1972) and dry and gallery forest (Culot, 2003). Though studies on this species are sparse, fruits and seeds made up 55.7% of the total diet in the dry season (Culot, 2003) and 74% for the year (Sharman, 1981) suggesting fairly extensive frugivory. The shoots of grasses are consumed in the rainy season but subterranean foods seem to be of little note (Culot, 2003). This suggests tentatively that if more dietary data were available there would be a significant difference between this and the olive baboon.

There is also only one dietary study for the hamadryas baboon (table 3.1). This is the baboon that is most different in environment from the others, occupying semi-desert (Kummer, 1968). A dietary difference would thus be expected. Though Swedell (2008) reported that hamadryas baboons at Filoha spend less time feeding than other baboons, the study suggested this may be down to the presence of doum palms at the site. These are rich in carbohydrate and protein allowing reduced foraging activity. However this is not a representative food for the subspecies at a whole, as the doum palm is not found across the entirety of the subspecific range. This species spends considerable time foraging in trees, more so it was argued than the olive baboon (Kummer, 1968). The implication then is of a more frugivorous diet, though of dry seed pods rather than succulent fruits. Further studies will be required to prove this.

The Kinda baboon is the least studied of all baboons. Indeed its range falls in the sampling blind spot (fig. 3.2) between East and southern Africa (Jolly, 1993). Its distinctively small size and paedomorphic skull shape have long been recognised (Osman Hill, 1971, Leigh, 2006), along with distinct pelage colourations (Phillips-Conroy et al., 2009). Emerging details reveal that this subspecies exhibits reduced sexual dimorphism and males that exhibit female-typical behaviours and vice versa (Phillips-Conroy et al., 2009). As this subspecies has diverged so much in size-related morphology and social behaviour is it particularly unfortunate that we cannot test for related dietary differentiation. We can only speculate that as it inhabits Miombo woodland (Phillips-Conroy et al., 2009) it is probably most similar to the yellow baboon, which is the adjacent subspecies, and indeed there is purported to be clinal variation from one to the other in morphological features (Freedman, 1963). Whether there is corresponding dietary potential clinal variation is unknown.

3.4.3 Vervet Diet

The present study failed to find statistical evidence for differences between the vervet subspecies. Previous qualitative comparative work has tentatively suggested that diets are different between sites but paucity of studies and differences in methods render comparison difficult (Harrison, 1984). Since that time more data have emerged bolstering the number of dietary studies (Mekonnen, 2008, Agmen et al., 2010, Barrett, 2005, Willems, 2008). In spite of this the sample sizes are still very small (n=13) with only a single set of dietary data for *C. a. aethiops* and *C. a. djamdjamensis*. Consequently the absence of a statistical difference, when the sample is so small, does not prove there is no real difference in subspecific vervet diet.

The dietary principal components analysis reveals that the major axis of dietary variance runs between the djam-djam and the other taxa. This representation agrees with descriptions of this highly folivorous subspecies (Mekonnen, 2008). This subspecies inhabits bamboo forest on the Bale Massif of Ethiopia; a unique habitat for a vervet monkey. Moreover, it eats much more young leaves (80.2% of the diet) than other vervets and spends a 65.7% of its time feeding. With 76% of its diet being derived from bamboo this monkey is much more of a specialist that the other subspecies. Another interesting feature of this environment is the relative lack of seasonal variation in the diet: levels of folivory decrease from 82 to 79% from winter to summer, with a slight and corresponding increase in frugivory. Unfortunately the djam-djam is both understudied and threatened with extinction (IUCN, 2010).

3.4.4 Baboon and Vervet Diets in the Broader Primate Context

The Baboon

This study numerically corroborates the established view that the baboon is more generalist in diet than other African monkeys (Alberts and Altmann, 2006, DeVore and Hall, 1965, Altmann and Altmann, 1970). The Shannon index, which can be interpreted as a measure of how equal the dietary proportions are, is higher for the baboon than the vervet, blue monkey and red colobus. This proves that the baboon does not tend to specialise on one particular food category and is thus broad in its diet. The vervet is purported to be the next in dietary generalism, with the other cercopithecines being more specialist frugivores and the colobines highly specialist folivores (Fleagle, 1988). Consequently, though only a few African monkeys have been sampled, the Shannon indices provide strong evidence that the baboon is the most generalist in terms of food categories in its diet.

Aside from occupying the most generalist position, on the dietary evenness-unevenness axis, relative to other monkeys, the baboon also exhibits the broadest spread along this axis, showing considerable niche width. Thus it can be concluded that not only do populations differ in dietary proportions, they also differ in the tendency to focus on a single food category. This is a subtly different finding. Again this demonstrates that the baboons as a species are highly variable. Indeed it is likely once again that this is plasticity, with the baboon dietary niche not being constrained to be composed of a fixed proportion of foods but rather being free to vary. This is concordant with published accounts of the flexibility of baboon ecology, exemplified by studies of dietary switching during environmental change as at Amboseli (Lee and Hauser, 1998) and small scale geographical changes such as with altitude (Byrne et al., 1993). However, as stated before this variation is potentially made up of a nonplastic, genetically constrained component. Certain populations might have developed certain morphological, physiological, or sociobehavioural adaptations to a subtly more or less specialised diet.

In including the red colobus, a taxon with high dietary specialism, this study presents a baseline against which to compare the two generalist study taxa. The colobines are the more specialised sister subfamily of the cercopithecines, diverging just before the papionins split from the guenons (Chatterjee et al., 2009). These animals exhibit physiological and anatomical adaptations to folivory, such as low pH saliva and sacculated stomachs to facilitate fermentative digestion (Lambert, 1998). As expected given these adaptations, the red colobus has a low Shannon index indicative of dietary specialism, and indeed the dietary pie chart shows that leaves dominate. Additionally, the niche width of the red colobus is narrow, suggesting little deviation from specialism, in contrast to the generalist and variable baboon and vervet. This is even more of a contrast when one considers that the red colobus make up a debated number of species (six according to Grubb et al. (2003), of which five are represented), whereas the others all show intraspecific diversity.

The Vervet

Though the vervet is a generalist (Fedigan and Fedigan, 1988, Harrison, 1982), it is secondary in this regard to baboons (Altmann, 1998), eating fewer plant species (Barrett, 2005) and tending towards specialising on a single plant, such as acacias at Amboseli (Wrangham and Waterman, 1981) or *Pterocarpus* in Senegal (Harrison, 1982). In this study the vervet does indeed occupy a position between the highly generalist baboon and the specialist red colobus, confirming this position as being a generalist second only to the baboon.

However, this study throws up two initially surprising results. First, the full vervet sample has a dietary evenness lower than that of the blue monkey. The blue monkey is an arboreal frugivore, and though it is has been described as being quite variable across its range compared with other guenons (Twinomugisha et al., 2006), the finding that this taxon has a greater than average level of dietary generalism is unexpected. Second, the vervets as a whole exhibit a niche width, i.e. variance in the degree of generalism versus specialism that is higher than the baboon. This is discordant with reports that baboons are the most plastic and ecologically variable monkeys (Alberts and Altmann, 2006, Jolly, 2001), with vervets being more reliant on fewer plant species (Harrison, 1982, Wrangham and Waterman, 1981).

Comparison of the full vervet and djam-djam excluded dietary samples throws light on these unexpected findings. Exclusion of the djam-djam from the vervet dietary data shows a reduction in niche width to a range lower than that of baboons. It also brings the average level of vervet generalism to a higher level than that for the blue monkey, in line with what we would expect. It is clear from these findings that the djam-djam is a dietary outlier with a profound effect on the vervet Shannon index average and niche width. The fact that the niche width is vastly inflated by the addition of this one subspecies suggests that it in fact occupies a distinctly different and nonoverlapping dietary niche from the other subspecies of vervet. Such a conclusion is supported by descriptions of vervet diet and habitat versus those of the djam-djam. Vervets are typically generalists, inhabit savannah woodland and riparian environments, eating a high proportion of fruit and flowers when seasonally available (Fedigan and Fedigan, 1988). The djam-djam is different on all counts. This subspecies is unique amongst the vervets in inhabiting bamboo forest (Mekonnen, 2008). Moreover, it eats a vast amount of young leaves (80.2% of the diet) and 76% of its diet is derived from a single plant species of bamboo. The bamboo forests of the Bale Massif of Ethiopia are characterised by low seasonal variation and low availability of fruit. As expected given its forest environment and folivorous diet it spends most of its time in trees than on the ground (Mekonnen et al., 2010). Indeed in terms of lifestyle it is "more akin to... *Cercopithecus* spp. rather than to other *Chlorocebus* spp." (Mekonnen et al., 2010, page 358). This habitat description resounds with our dietary finding that the djam-djam is the closest to the blue monkey, suggesting this subspecies has jumped niche relative to the rest of the species.

3.4.5 Conclusion

This study found a difference in the proportion of geophyte eating between chacma and olive baboons. It is argued that this reflects environmental variation in seasonality and is effect on vegetation. Caution has to be taken with this conclusion given the limited number and uneven sampling of study sites; in particular the studies of chacma baboons are skewed in favour of temperate environments. In vervets however no differences were detected. However, it seems probable that the djam-djam is discretely different in diet from the other subspecies and that the lack of a difference was the result of low sample size. The djam-djam is characterised by vastly higher levels of folivory and its montane bamboo forest environment is discretely different from the other subspecies. Inclusion of this subspecies gives vervets a vast niche width, which is much smaller when this is removed. This suggests a serious dietary specialism that is discretely different from the other subspecies. Both the vervets and baboons are general and variable in their degree of generality relative to a typical guenon, the blue monkey, and colobines, representing extreme dietary specialism.

CHAPTER 6. DIET AND MORPHOLOGICAL DIVERGENCE

4.1 INTRODUCTION

4.1.0 Overview

Some evidence, albeit not unequivocal, for diversification in dietary ecology of baboons has been established (Chapter 3). Potentially there are stronger morphological differences that relate to or align with this subtle difference. In numerous primates dietary differentiation has been associated with morphological adaptation (Ravosa, 1990, Singleton, 2005, Smith, 1985, Daegling, 1992, Taylor, 2006a). There is considerable morphological variation in the craniofacial form of baboons (Chapter 2) and vervets (Cardini et al., 2007, Elton et al., 2010). The aim of this chapter is to establish if there is a link between intraspecific feeding differences and morphology, asking two basic questions. First, is there a significant correlation between morphology and diet? Second, are the biomechanical features of these morphologies related to the associated food physical properties (toughness, stiffness and size (Lucas, 2004, Strait and Vincent, 1998b, Wright et al., 2008))? Such a relationship would be strong evidence of morphological adaptation. Answering these questions is crucial to establishing whether dietary differences are of sufficient significance to cause morphological specialisation, giving us an indication of the importance of diet as a selective pressure in subspecific divergence. Moreover, comparison of these subspecific patterns between the vervet and baboon will, again highlight overarching similarities or else demonstrate species-specific features. Such information will greatly improve our understanding of how the environment acts, though diet, to drive morphological diversification in primates.

4.1.1 Diet as an Agent of Diversification

Feeding is a fundamental animal behaviour. Consequently traits that facilitate feeding will proliferate. For this reason much of the morphological variation in an adaptive radiation tends to exhibit itself as trophic adaptation (Schluter, 2000). The mammals demonstrate this extensively, incorporating carnivores, herbivores, and piscivore across orders. However, within orders there is extensive variation. Phyllostomid bats represent an extensive adaptive radiation that, from an insectivorous ancestor, have diversified into carnivorous, nectarivorous and pollinivorous, frugivorous, and sanguinivorous forms (Freeman, 2000), with subtle variations in craniofacial and dental forms (Nogueira et al., 2005, Nogueira et al., 2009). The Carnivora contain both hypercarnivores, which eat meat exclusively, as well as insectivores and small prey feeders. The former are adapted to produce high bite forces necessary for killing large prey, while this parameter is relaxed for the small prey and insectivorous carnivores (Christiansen and Wroe, 2007). In contrasts bovids and cervids, which feed on vegetation, exhibit a heterogeneity in diet with some eating tough grasses and others eating browse. Those with tougher diets have developed longer and lower coronoid processes of the mandible. This confers an advantage for the temporalis muscle and consequently allows more efficient mastication of more resistant foods (Pérez-Barbería and Gordon, 1999).

The order Primates is no exception to this mammalian pattern of diet-based adaptation. Folivores must chew repetitively to comminute leaves. This is associated with facial retraction to improve muscle leverage, a deeper and larger ramus increasing masseter attachment area and more robust zygomatic arches (Ravosa, 1990, Singleton, 2005). In contrast, frugivores are characterised by prognathism representing a relaxation of the adaptations associated with folivory. However, within the cercopithecines, which are broadly frugivorous, *Cercocebus* and *Lophocebus*, both of which feed on seeds, demonstrate a more folivore-like increase in masseter muscle attachment (Singleton, 2005). These functional principles extend beyond the cercopithecines and are widely used. For instance facial retraction and deepening has been found in Eskimos (Hylander, 1972, Hylander, 1977) in association with hard food, and has been used to infer dietary specialisations of australopithecines (Du Brul, 1977). A study by Daegling & McGraw (2007) found that the postcanine corpus was deeper for *Lophocebus* than *Cercocebus*. This is expected given the more incisory feeding of the former, and consequent requirement to reduce bending moments in the corporal region of the mandible.

Finer scale dietary discrimination is possible, however. Antón (1996) compared *Macaca nemestrina* and *M. mulatta* to test for craniofacial differences based on diet. An association was confirmed between vertically deeper skulls (facial, vault &

mandible), anteroposteriorly shorter faces and wide mandibular corpora and comparatively tougher diets. The study also noted the more anterior dentition in *M. mulatta* versus *M. nemestrina* and suggested the increase in mechanical advantage was an adaptation to produce a greater bite force to facilitate mastication of harder foods. In another intrageneric study, Taylor (2006b) found bark feeding was associated with deeper corpora and symphyses of the mandible in *Pongo*. Indeed, the dietary status of an extinct species of *Pongo* was proposed on the basis of this link.

Given the considerable evidence of dental (Hayes et al., 1990) and cranial (Chapter 2, Frost et al., 2003, Leigh, 2006) variation in baboons, it seems possible that some of this variation is adaptive and relates to dietary differences (Chapter 3). If any such relationship is present however it will be mediated by food physical properties.

4.1.2 Food Physical Properties

Animals exist in a physical world governed by physical laws. Craniofacial morphology can adapt only to the material properties of given food s, and not chemical or nutritional properties (Lucas, 2004, Yamashita, 1998). The relevant properties are stiffness (related to elasticity i.e. Young's modulus), strength (the force requires to cause a fracture) and toughness (the energy required to propagate a crack). However such data often go unreported, with field researchers typically being interested in food nutritional contents such as total tannins, phenolic or alkaloids (Whiten et al., 1991b, Cowlishaw, 1997) or the spread of resources (Barton et al., 1996). Consequently studies split foods with the same physical properties, while those with totally different properties are conflated. For instance subterranean foods are quite variable in toughness and stiffness (Dominy et al., 2008). Also, as Barton (1989, p. 138) points out the rather broad term fruit includes what we usually think of as fruit, or in his words “fleshy, fructose-containing varieties (mainly berries and drupes)” which are designed to be appealing and comestible for subsequent dispersal and the “drier, less digestible achenes and capsules,... leguminous pods and seeds.” Fruits in most studies included seeds, yet these have different properties and seed crushers have different morphologies from seed spitters or swallowers (Lucas, 2004).

However, these data are available in the literature (Lucas, 2004), but are limited, and have been measured in a number of studies relating to primate diet (Strait and Vincent, 1998a, Lambert et al., 2004, Williams et al., 2005, Norconk et al., 2009). Material properties are ecologically relevant with fruits being selected on this basis (Happel, 1988, Kinzey and Norconk, 1990). While obviously each dietary item has its own physical properties, certain generalisations can be made. For instance leaves are a very tough food (Wright et al., 2008, Lucas, 2004), meaning that lots of energy is required to break them up and make them digestible. Young leaves are less tough than old leaves (Lucas, 2004). Fruits on the other hand are typically not tough, though they may be rather stiff necessitating a high bite force to break them. Hard-food eating by baboon does take place. Baboons at Amboseli eat a good deal of fallen fever tree seeds, which are so hard they can be heard to crunch (Altmann and Altmann, 1970). The same is true for the hard fruits eaten by hamadryas baboons (Nystrom, personal communication).

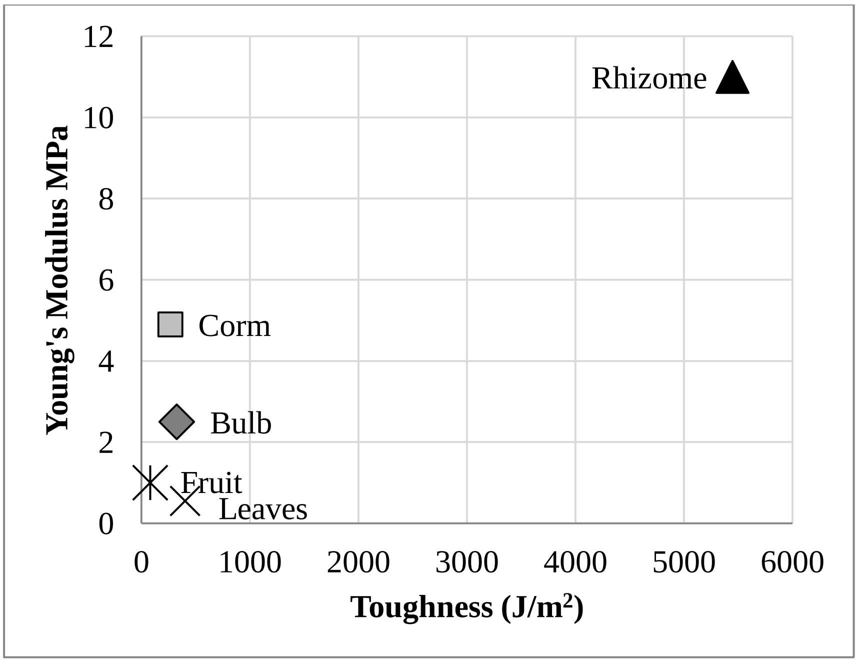


Figure 6.1. Modified from Dominy et al.(2008). A toughness/stiffness scatter plot for five major food types in baboon diet.

Subterranean foods or geophytes, are of considerable importance to most subspecies of baboons, and the chacma baboon in particular (Chapter 3). However, lumping this food category together conflates three different sorts of subterranean foods: corms, bulbs and rhizomes (Dominy et al., 2008). Relative to most fruits and leaves all three of these subterranean foods have a higher Young's modulus than leaves and fruits, while all three have a higher toughness than fruits (fig. 4.1). However, while corms and bulbs are similar in toughness to leaves (fig. 4.1), rhizomes are tougher and stiffer than all other foods. Thus while there is considerable variation in the physical properties between the categories of diet there is also confounding variation within categories. Both are likely to influence skull morphology via biomechanical adaptation. This study only has access to between-category variation (Chapter 3), but this is likely to be greater than within-category variation, and will be used to establish the presence or absence of dietary adaptation in skull morphology.

4.1.3 Biomechanical Adaptation to Food Physical Properties

Mastication is the most constraining function of the numerous roles of the skull (Sakka, 1985). It involves force production at the muscles, transmission of this force to the food object and dissipation of the stresses in the mandible (Constantino, 2007). The efficiency and efficacy of these actions are governed by a number of well described parameters. Perhaps the most important of these biomechanical parameters is bite force. This parameter may be measured directly (Dechow and Carlson, 1990) or estimated using the temporal fossa as a proxy for muscle cross sectional area (Christiansen and Wroe, 2007, Sakamoto et al., 2010) and modelling the mandible as a simple lever third order lever (Hylander, 1979, Ravosa, 1990, Dechow and Carlson, 1990, Du Brul, 1977, Demes and Creel, 1988). Consequently bite force can be improved in two ways: by increasing the size, and hence force output, of the masticatory muscles or by increasing the leverage of these muscles. Leverage is improved by maximising the in lever length relative to the out lever length, a ratio known as mechanical advantage (Du Brul, 1977). For example, if the in lever is twice the length of the out lever (as, for instance in something like a nutcracker) the mechanical advantage will be 2. In such as case the muscle has to deliver a lower force than if the in lever were shorter or if the out lever were longer. Mechanical advantage is therefore a measure of geometrical efficiency of the transmission of force from the muscle to force at the bite point. In anatomical terms the in lever is the distance between the muscle insertion point on the mandible and the temperomandibular joint, which acts as the pivot. The out lever is the distance from the temperomandibular joint to the bite point, which may be at any point on the dental arcade depending on the nature of the bite.

Mechanical advantage is a ratio and so its value is invariant of size. However, bite force is absolute. *In vivo* therefore this value will limit what foods an animals can eat, as the size of food object and resistance to being bitten are thresholds values (Lucas, 2004). As size increases the relationships between lengths, areas and volumes change owing to scaling laws (Emerson and Bramble, 1993), with significant biomechanical consequences. An isometric increase in size would result in no change in mechanical advantage, as this is a ratio between two lengths, but a significant increase in muscle cross sectional area and therefore force generation. Animals have complex patterns of growth and in nature size changes are almost always anisometric (Bouvier, 1986). As such allometric scaling may change the positioning of muscle attachments and thus mechanical advantage to some degree. A typical allometric pattern is of relatively smaller neurocranium relative to the face and mandible. This is because the brains and eyes are relatively smaller in large animals: they are able to fulfil their role a relatively lesser increase in size. However, this makes the skull surface relatively smaller and limits muscle attachment. This problem is often circumvented with sagittal and nuchal crests, providing additional surface area for muscle attachment. However, while mechanical advantage may drop off somewhat with increases in size, this is likely to be outpaced by increases in muscle cross sectional area, as this increases to an exponent of two. In the anisometric case muscle cross sectional area is the dominant parameter in determining bite force. While theory can make general predications about the relationship of functional parameters such as bite force and size, complex and lineage-specific allometry means this relationship has to be empirically derived. Work on macaques, closely related to but smaller than the baboon, revealed that bite force was proportional to jaw length (Dechow and Carlson, 1990). In New World monkeys fruit size and toughness were correlated to body size (Janson and Boinski, 1992), one interpretation being that large size and thus larger muscles is an adaption to producing the muscle forces necessary for consuming tough foods.

4.1.4 Aims

This first aim of this chapter is to determine, using partial least squares, if there is a diet-shape covariation in the baboon and vervet. In the case of the baboon, subspecific dietary differences have been found, albeit slight (Chapter 3). This study aims to establish if these potential ecological differences have an association with craniofacial morphology. In vervets, possibly as a result of small sample size, no statistically valid differences in subspecific diets were found. Nevertheless, a morphology diet covariation may exist in spite of this. This study will use partial least squares (Rohlf and Corti, 2000) to correlate multivariate shape and categorical dietary data. An assumption in this analysis is that the morphological specimens, which were collected at various times over the last century and a half, were eating similar foods to those described in dietary studies, i.e. that temporal variation is less than between subspecies variation.

Morphological differences necessarily have biomechanical implications. A second aim of this chapter is to test the hypothesis that the axis of morphological variation relates to the physical properties of the associated foods, with the assumption that morphology is biomechanically adapted to best process the food. Subterranean foods and leaves are tough (Dominy et al., 2008) while fruits are not (Lucas, 2004). There are known morphological responses to differences in toughness , with tough food eaters displaying short faces for improved muscle leverage, larger masticatory muscle areas, and more robust zygomatic arches than non-tough food eaters such as frugivores (Ravosa, 1990, Singleton, 2005, Hylander, 1972). Given the difference in subterranean food eating in baboons(Chapter 3), and the higher average toughness of this food item(Dominy et al., 2008), one would predict a greater mechanical advantage and thus shorter rostrum for consumers of this food.

It is assumed that the dataset contains enough morphological specimens with associated dietary data that, if present, a correlation between dietary categories and morphology can be found. If such a relationship is found it implies adaptation, but is not unequivocal. However, by establishing a biomechanical link between food physical properties and morphology, according to the predictions above, the case for adaptation can be advanced. Additionally subspecific differences in parameters reflecting masticatory muscle efficiency can further establish that shape is related to food physical properties and that morphology is adaptive. This assumes that crude proxies for masseter and temporalis mechanical advantage, which are often used in morphological analyses (Jablonski, 1993, Du Brul, 1977, Dechow and Carlson, 1990), can reliably characterised from landmark data. Finding a link between morphology and diet or not will give us insight into the importance of food physical properties and emergent dietary specialisation in structuring subspecific variation.

4.2METHOD

4.2.1 Diet

This study uses dietary data collected from a number of sites at which baboons and vervets are studied (Chapter 3, tables 1 & 2). These data are not ideal because the food categories are not based on their physical properties, the feature of food to which morphology is likely to become adapted. However, the generalities (fig. 1) of toughness and stiffness for the dietary categories are sufficient for testing hypotheses and represent a good starting point for relating baboon intraspecific morphology to diet.

4.2.2 Relating Diet and Morphology

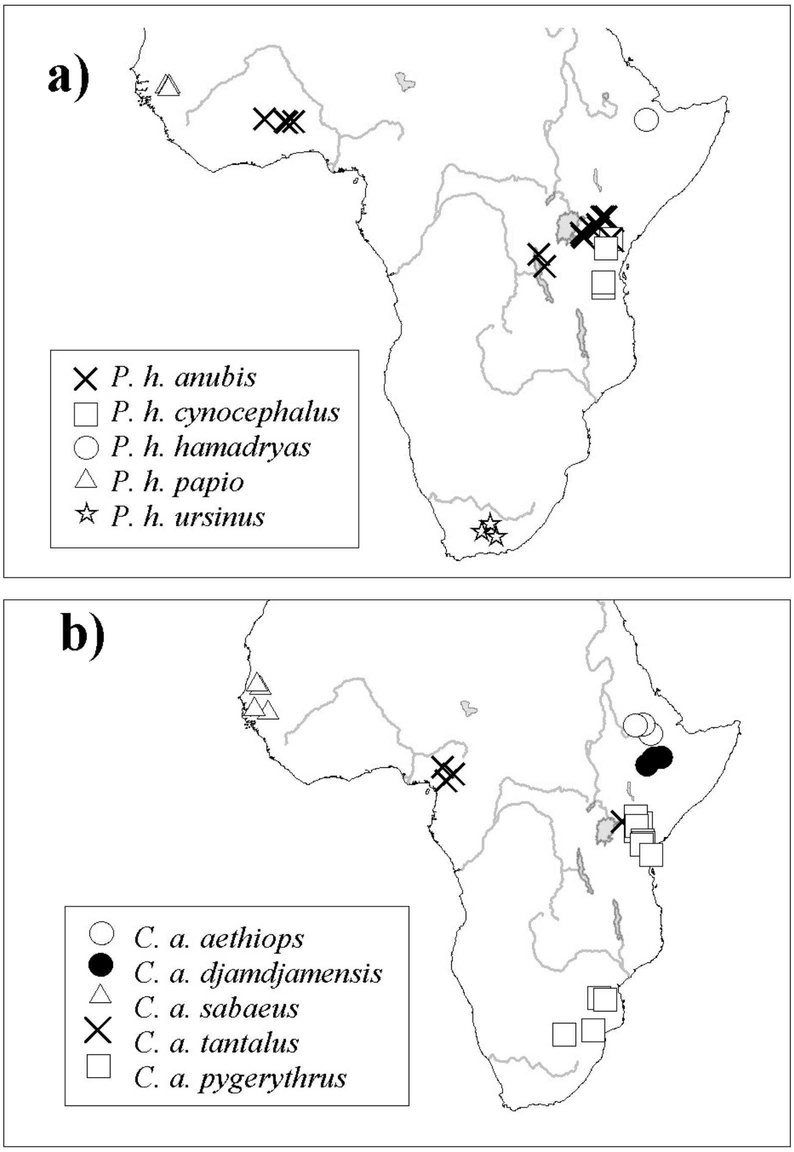


Figure 6.2. Showing the location of ***a)*** *baboon and* ***b)*** *vervet morphological specimens for which dietary data from extant, geographically adjacent populations were were available.*

Dietary data were extracted from the literature (Chapter 3, tables 3.1 & 3.2). These study sites were plotted on a map with the sites from which the morphological sample was derived. The morphological data used were the masculinised landmark data (see Chapter 2). Vervet and baboon morphological specimens were linked with the dietary information from a site if they were taken from within100km of that site and were within the same vegetation zone. It is assumed here that diets can be generalised to localities within this distance and similar ecotype. White’s (1983) vegetation map of Africa was used to demarcate vegetative zones and has been used to demarcate zones in primate studies (Kunz and Linsenmair, 2008a). It is assumed that within zones diets are potentially generalisable but, knowing *a priori* that there are differences in vegetation, between zones, given differences in vegetation type, they are not.

Forty five of the 368 baboon specimens and 41 of 278 vervet specimens were associated with a dietary site (tables 4.1 & 4.2). The remaining morphological sample was collected from sites too remote from the dietary studies and could not be used in the analysis. This reflects the poorly dispersed nature of the dietary sites which are concentrated in certain areas such as East and southern Africa. Also, diet data for three of the total 19 dietary sites could not be extrapolated to morphological specimens as there were none in the defined proximity and vegetation zone. This reflects the biases in the morphological sample which is based on museum collections and is heavily dependent on where collectors happened to visit.

Table 6.1. Showing the baboon morphological specimens associated with dietary studies for the shape-diet analyses. Dietary data for each site is presented in Chapter 3, table 3.1. White's designation of vegetative zone is also given.

Site	Subspecies	White's Designation	Long	Lat	Specimen
Mt Assirik	*P. h. papio*	Moist interfertile savannah	13.3	-12.9	USNM381435
			13.3	-12.9	USNM381434
			13.3	-12.9	USNM381430
			13.3	-12.9	USNM381437
			13.3	-12.9	USNM381433
			13.3	-12.9	L82.214
Comoe	*P. h. anubis*	Moist interfertile savannah	9.3	0.8	B74866
			9.4	1.5	Te73.009M049
			9.7	-1.8	L71.2352
			9.4	0.6	L71.2352
Erer-Gota	*P. h. hamadryas*		9.6	41.9	B74844
			9.6	41.9	B16705
			9.6	41.9	B17256
			9.6	41.9	Zu6933
			9.6	41.9	Zu6936
Gombe	*P. h. anubis*	Moist interfertile savannah	-5.2	30.3	B75015
			-4.0	29.6	Te12575
Masai Mara	*P. h. anubis*	Arid Fertile Savannah	-2.1	34.6	USNM216605

			-1.8	34.5	MCZ21160
			-1.8	34.5	MCZ21161
			-2.3	34.8	FMNH73028
			-1.3	35.6	MCZ27557
Cholo	*P. h. anubis*	Arid Fertile Savannah	-1.0	36.3	USNM162899
			-1.2	36.4	FMNH135067
			-1.2	36.4	FMNH135055
			-1.2	36.4	FMNH135069
Gilgil	*P. h. anubis*	Unpalatable grassland	-0.2	37.3	NY80207
			-0.4	37.0	MCZ17343
			-0.2	36.8	L62.25
			-0.2	37.0	L36.12.28.1
			-0.2	37.0	L36.12.28.2
Amboseli	*P. h. cynocephalus*	Arid Fertile Savannah	-2.6	38.1	USNM384239
			-2.4	37.9	B74877
			-2.4	37.9	B74930
			-2.4	37.9	B74943
			-3.4	37.3	B74994
Mikumi	*P. h. cynocephalus*	Mosaic of forest	-6.8	37.0	MCZ23082
			-7.3	37.0	B11541
			-6.8	37.0	L27.2.9.1
			-6.8	37.0	L24.1.1.6
			-6.8	37.0	L24.1.1.4
Giant's Castle	*P. h. ursinus*	Shrubland and grassy semi-desert	-31.8	22.8	FMNH101803
			-32.3	24.5	B74898
			-32.3	24.5	L6.5.12.2
			-31.0	23.8	L3.6.4.1

Table 6.2. Showing the vervet morphological specimens associated with dietary studies for the shape-diet analyses. Dietary data for each site is presented in Chapter 3, table 3.2. White's designation of vegetative zone is also given.

Site	**Subspecies**	**White's Classification**	Long	Lat	**Specimen**
N'Dioum	*C. a. sabaeus*	Arid fertile savannah	-14.4	16.3	B41184
					B40414
					B41186
					B40421
					B40416
Mt Assirik	*C. a. sabaeus*	Moist interfertile savannah	-12.8	12.9	USNM381440
					USNM381438
					USNM381441
					USNM381439
					USNM378662
Kamaloue	*C. a. tantalus*	Hydromorphic grassland	14.9	12.1	USNM452605
Ngel Nyaki	*C. a. tantalus*	Mosaic of forest	11.0	7.0	L69.1152
					L23.1.22.4
					NY120376
					NY120377
					NY120379
Bole Valley	*C. a. aethiops*	Dry forest and thicket	38.0	9.4	USNM399281
					FMNH27177
					FMNH27178
					FMNH27176
					L64.2177
Oldoyo	*C. a. djamdjamensis*	Unpalatable grassland	40.2	6.9	L9.6.1.4
					FMNH27174
					FMNH27170
					FMNH27062
					FMNH27066
Samburu Isiolo	*C. a. pygerythrus*	Arid fertile savannah	37.5	0.5	MCZ16152
					USNM452610
					USNM452609
					L0.11.24.2
					L2.7.6.1

Amboseli	*C. a. pygerythrus*	Arid fertile savannah	37.0	-2.5	MCZ31947 MCZ31975 B33.A49.08 USNM181827 1Te2098
Diani Beach Forest	*C. a. pygerythrus*	Mosaic of forest	39.6	-4.3	L72.23
Lajuma	*C. a. pygerythrus*	Mapone savannah	29.5	-22.0	USNM470263 USNM352267
Blydeburg	*C. a. pygerythrus*	Moist interfertile savannah	28.2	-24.4	FMNH38135 L6.8.2.29

4.2.3 Partial Least Squares

To quantify the overall correlation between covariates such as diet and shape, 2 block partial least squares was used. This method gives a value of overall correlation, the RV coefficient, but also extracts axes of maximum covariation between two blocks of variables (Rohlf and Corti, 2000). Multivariate morphological variation can be visualised at the extremes of these axes. Here the morphological block of data was the shape coordinates, while the dietary block was the table of food proportions (Chapter 3, tables 3.1 and 3.2). Morphologika (O'Higgins and Jones, 2006) was used to visualise the wireframes of the 3D landmark data corresponding to the extremes of the partial least squares axes. For diet, the importance of dietary data can be interpreted by the loadings, where high loadings indicate an important factor in the covariation. The overall correlation coefficient or RV coefficients were calculated in MorphoJ (Klingenberg, 2011) as were PLS scores.

4.2.4 Mechanical Advantage

Lever arm mechanics was used to assess biomechanical function. This method models the mandible as a third order lever (Hylander 1975). This method represents an extrapolation from bony morphology to soft tissue, but is often used in functional morphology studies (Jablonski, 1993, Du Brul, 1977, Dechow and Carlson, 1990). Additionally these simple lever arm studies have the advantage of not requiring complex software (e.g. Davis et al., 2010, Moazen, 2008).

Here the mechanical advantage was calculated from measurements and angles between muscle insertion and origin points derived from the landmark data. Measurements were made in Morpheus et al.(Slice, 1999) and trigonometric calculations were carried out in Microsoft Excel (2007). The landmark data were not taken with this purpose in mind, and so not all the most useful measurements can be taken. However, enough shape is captured to derive certain masticatory parameters. The mechanical advantage was calculated for a vector between the inferior margin of the attachment site of the masseter on the ramus, corresponding to the insertion, and the anteroinferior point of the zygomaxillary suture. This corresponds, in the lateral view, to a point adjacent to the anterior attachment to the masseter, and gives a reasonable approximation of the masseter line of action (fig. 4.3).

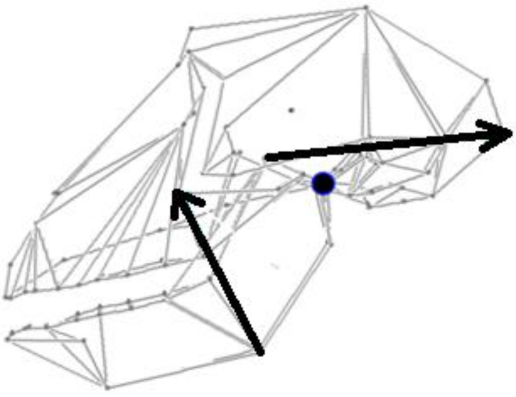


Figure 6.3. Wireframe connecting anatomical landmarks for a baboon. The arrows indicate force vectors and the circle indicates the temporomandibular joint.

The temporalis muscle is a complex fanlike organ. Preliminary observations show that most cranial variation is in the occipital region of the skull. Consequently this study focussed on a muscle vector corresponding to the posterior temporalis, whcih is defined here as running from the tip of the coronoid process to the inion. The pivot was defined at the distalmost point of the postglenoid process. The bite point was assumed to be the first molar in all cases. These vectors correspond to those observed from dissection (Wall et al., 2008), and the roughening on the skull indicative of muscle attachment (personal observation).

Biomechanical analyses used the full dataset of 368 specimens, male and female. Values of mechanical advantage were regressed on size and the MANCOVA approach was used to determine differences in this relationship between subspecies.

4.3 RESULTS

4.3.1 Baboon Diet-Shape PLS

Table 6.3. Singular values and pairwise correlations of PLS scores between the dietary and shape blocks. For the whole PLS RV = 0.3303 , p < 0.0001. For morphological specimens, n = 45, and for associated dietary data n =12. Significant p values are shown in bold.

	Singular value	% Total covariance	Correlation	P-value
PLS1	0.43138	83.531	0.72533	**<.0001**
PLS2	0.17236	13.336	0.72168	0.0844
PLS3	0.06313	1.789	0.62518	0.3256
PLS4	0.04982	1.114	0.62162	0.1198
PLS5	0.0226	0.229	0.7868	0.2405
PLS6	0.00065	0	0.6557	0.0114

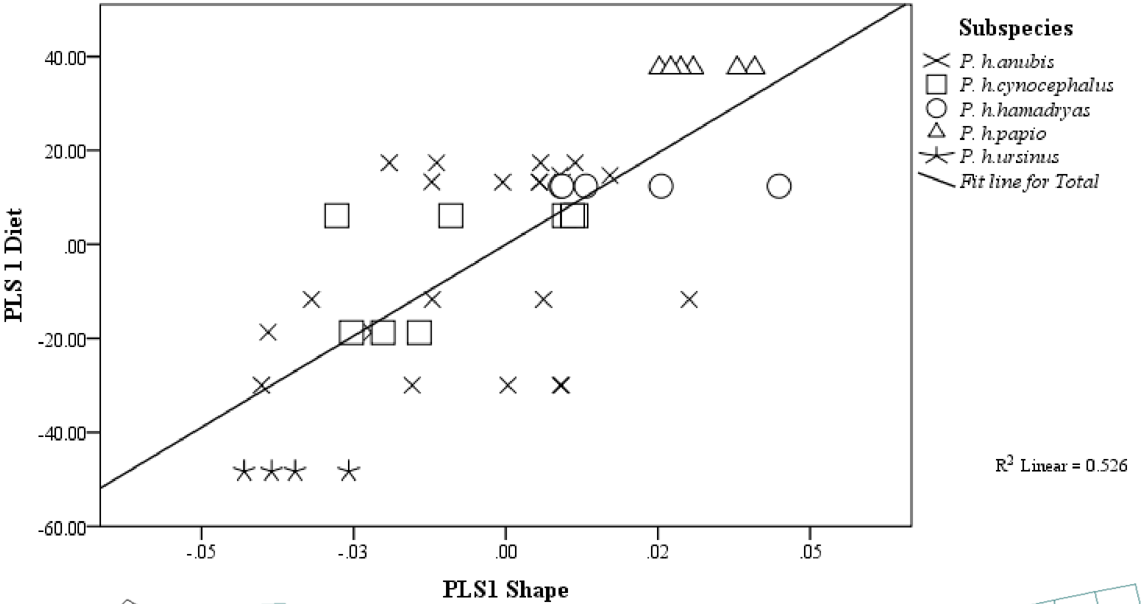
There is a significant correlation between baboon shape and diet (RV = 0.3303, p < 0.0001, (table 4.3). The first and only significant partial least squares axis reveals morphological extremes of an elongated, ventrally flexed morphology versus an unelongated slightly dorsally flexed morphology (fig. 4.4). The former corresponds to a diet high in subterranean foods while the latter high in fruit (fig. 4.4).

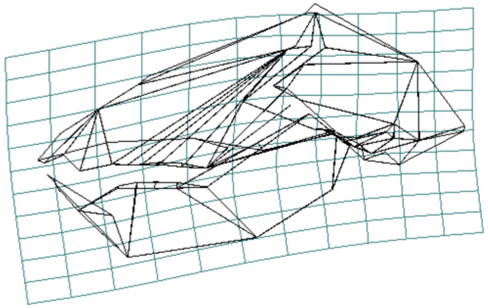
To examine the possibility that the chacma baboon was not driving the whole trend the same analysis was carried out without this subspecies.

Table 6.4. Singular values and pairwise correlations of PLS scores between the dietary and shape blocks, with P. h. ursinus *excluded. For the whole PLS RV = 0.2656, p = 0.008. For morphological specimens, n = 41, and for associated dietary data n =11. Significant p values are shown in bold.*

	Singular value	**% Total covariance**	**Correlation**	**P-value**
PLS1	0.33597326	77.48	0.71289	**0.0016**
PLS2	0.16440227	18.552	0.72083	0.1014
PLS3	0.05497679	2.075	0.62505	0.672
PLS4	0.04720539	1.53	0.66949	**0.0244**
PLS5	0.0230183	0.364	0.70617	0.1106
PLS6	0.00037771	0	0.59439	**0.0339**

Food	PLS1
Fruit	0.79
Subterranean	-0.6
Leaves	-0.01
Flower	-0.08
Animal	-0.01
Other	-0.1





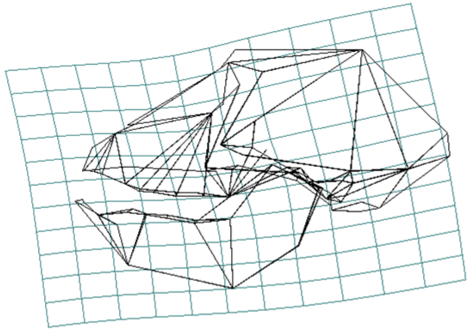


Figure 6.4 A scatter plot of scores for the first PLS between diet and shape for all baboon subspecies. Loadings for interpretation of the dietary axis are given in the table beside the axis and wireframes show the morphological extremes of the axis of covariation (exaggerated by a factor of 3).

	PLS1
Fruit	0.85
Subterranean	-0.44
Leaves	-0.21
Flower	0
Animal	0
Other	-0.2

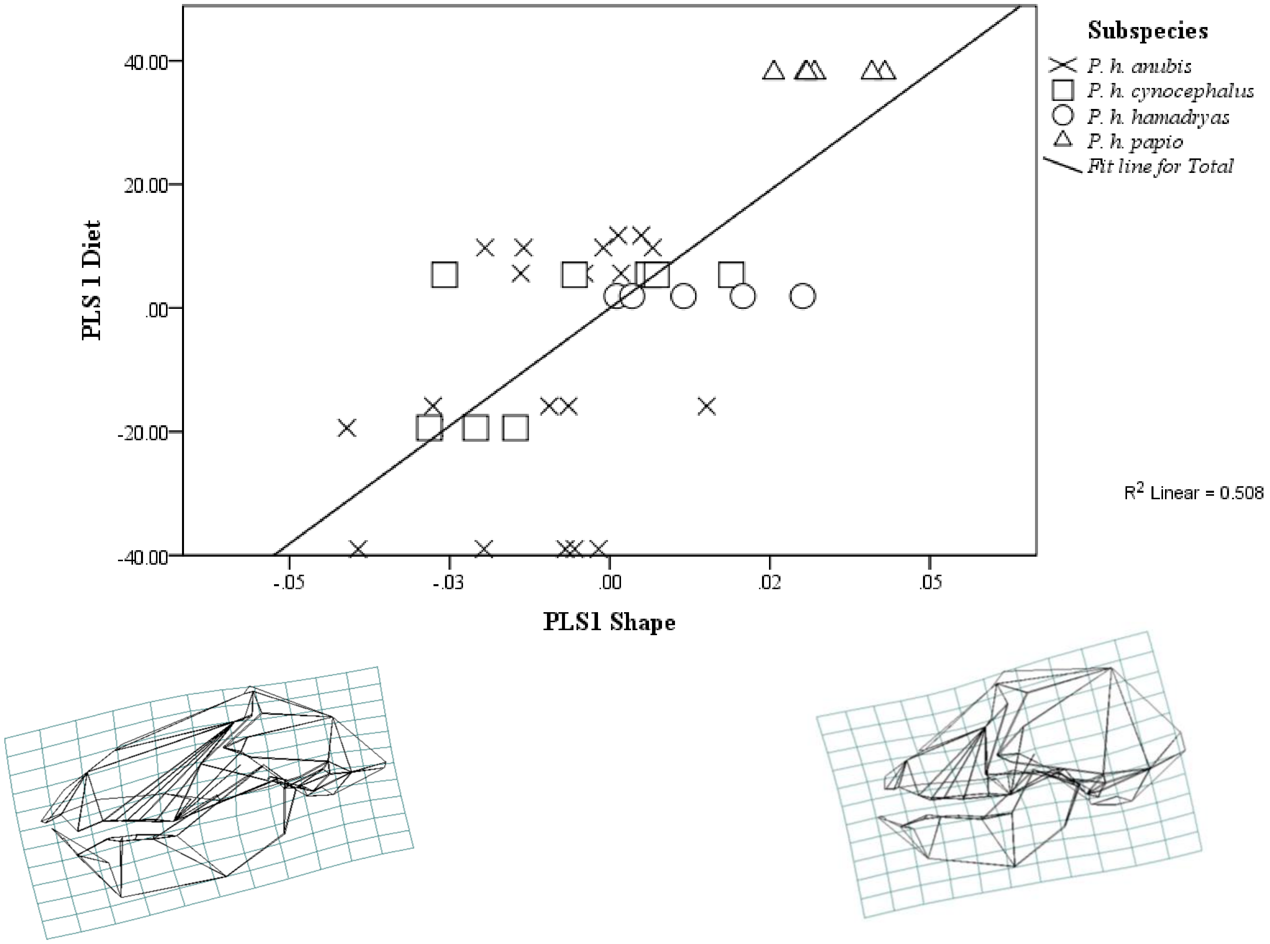


Figure 6.5. A scatter plot of scores for the first PLS between diet and shape without P. h. ursinus. *Loadings for interpretation of the dietary axis are given in the table beside the axis and wireframes show the morphological extremes of the axis of covariation (exaggerated by a factor of 3).*

Removal of the chacma baboon does not eliminate the significance of the relationship between shape and diet (table 4.4). Loadings of the Diet PLS 1 reveal that the elongated, now no longer ventrally flexed, morphology corresponds to a high subterranean diet, as was the pattern before, while the unelongated morphology corresponds to a fruvigorous diet (fig. 4.5). This reveals the ventral flexion is chacma-specific. Removal of the chacma baboon reduced the RV coefficient from 0.337 to 0.271 demonstrating the chacma baboon is an important component of this relationship, but that the trend exists without this taxon.

4.3.2 Size-Controlled Baboon Shape and Diet PLS

Size has a strong effect on shape owing to allometric scaling. Size was regressed out for each subspecies in order to estimate the important of size-related shape.

Table 6.5. Singular values and pairwise correlations of PLS scores between the dietary and size-controlled shape blocks. For the whole PLS RV = 0.2162, p = 0.0020. For morphological specimens, n = 45, and for associated dietary data n =12. Significant p values are shown in bold.

	Singular value	**% Total covariance**	**Correlation**	**P-value**
PLS1	0.28172	76.822	0.70749	**0.0039**
PLS2	0.13714	18.205	0.59102	0.1112
PLS3	0.05666	3.108	0.51538	0.1371
PLS4	0.03896	1.469	0.38817	0.1343
PLS5	0.02023	0.396	0.62423	**0.0605**
PLS6	0.00041	0	0.54258	0.1593

	PLS1
Fruit	0.72
Subterranean	-0.67
Leaves	0.13
Flower	-0.13
Animal	0.01
Other	-0.07

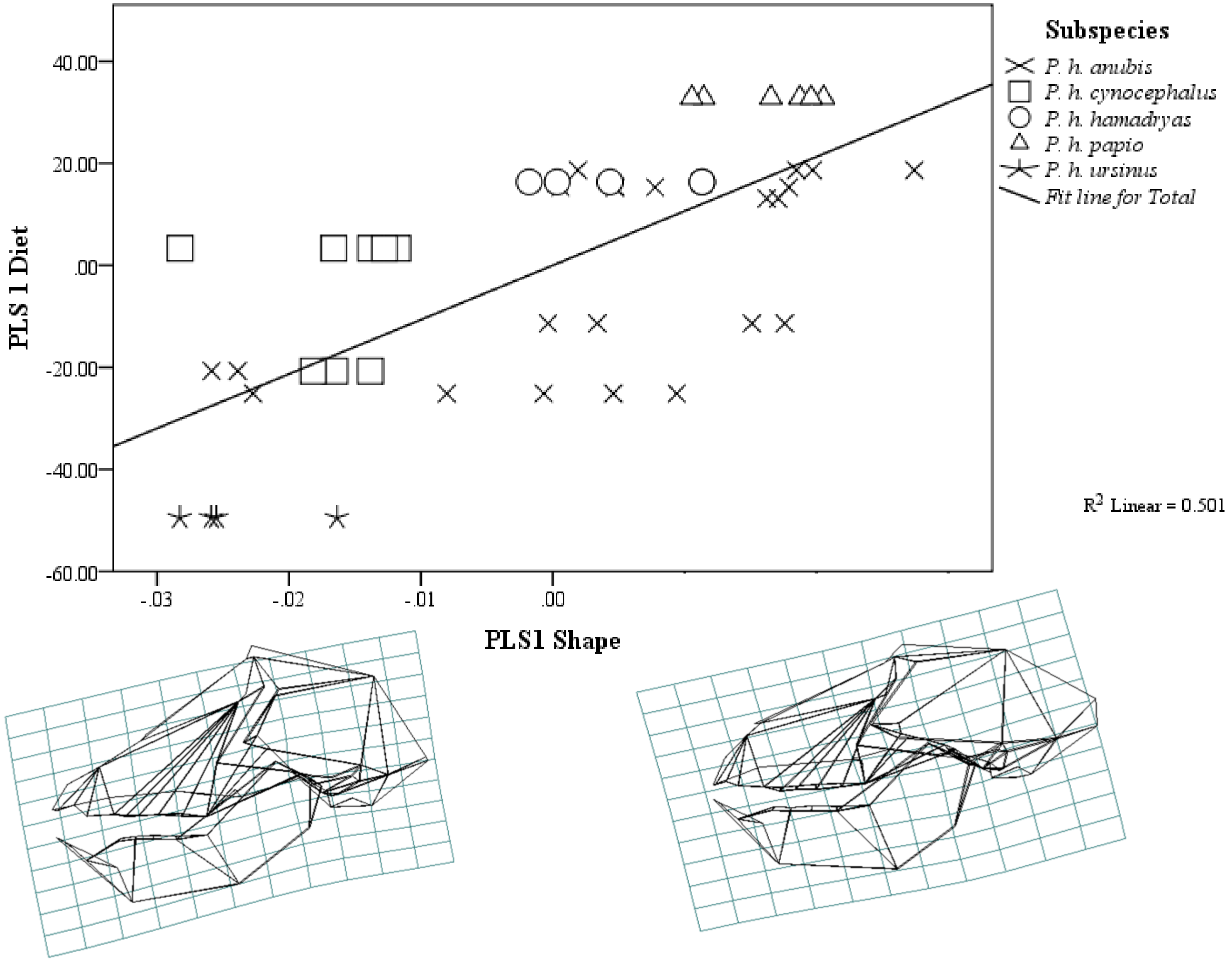


Figure 6.6. A scatter plot of scores for the first PLS between diet and size-controlled shape without. Loadings for interpretation of the dietary axis are given in the table beside the axis and wireframes show the morphological extremes of the axis of covariation (exaggerated by a factor of 3).

Table 6.6. Singular values and pairwise correlations of PLS scores between the dietary and size-controlled shape blocks, with P. h. ursinus *excluded. For the whole PLS RV = 0.1948, p = 0.0154. For morphological specimens, n = 41, and for associated dietary data n =11. Significant p values are shown in bold.*

	Singular value	**% Total covariance**	**Correlation**	**P-value**
PLS1	0.23285	70.184	0.72735	**0.0321**
PLS2	0.13848	24.822	0.60946	0.0701
PLS3	0.04288	2.38	0.39873	0.6724
PLS4	0.04079	2.153	0.54563	**0.0068**
PLS5	0.01888	0.461	0.60279	0.0670
PLS6	0.00029	0	0.49949	**0.0459**

Size-corrected shape has reduced covariance with diet (83.5 to 76.8%, tables 4.3 & 4.5). However the correlation is still significant (table 4.5) . The scatter is broadly the same (fig. 4.7) but with *P. h. anubis* and *P. h. cynocephalus* more dispersed. The morphological extremes show a klinorhynch form at the subterranean food eating extreme and an airorhynch form at the fruit eating extreme. The chacma removed sample shows the same reduction (77.5 to 70.1%, tables 4.4 & 4.6), but remains significant (table 4.6). Removal of the chacma removes the ventral flexion of the rostrum, and the subterranean food eating form appears more robust, with the frugivorous form appearing gracile (fig. 4.7).

	PLS1
Fruit	0.83
Subterranean	-0.51
Leaves	-0.13
Flower	-0.01
Animal	0.01
Other	-0.17

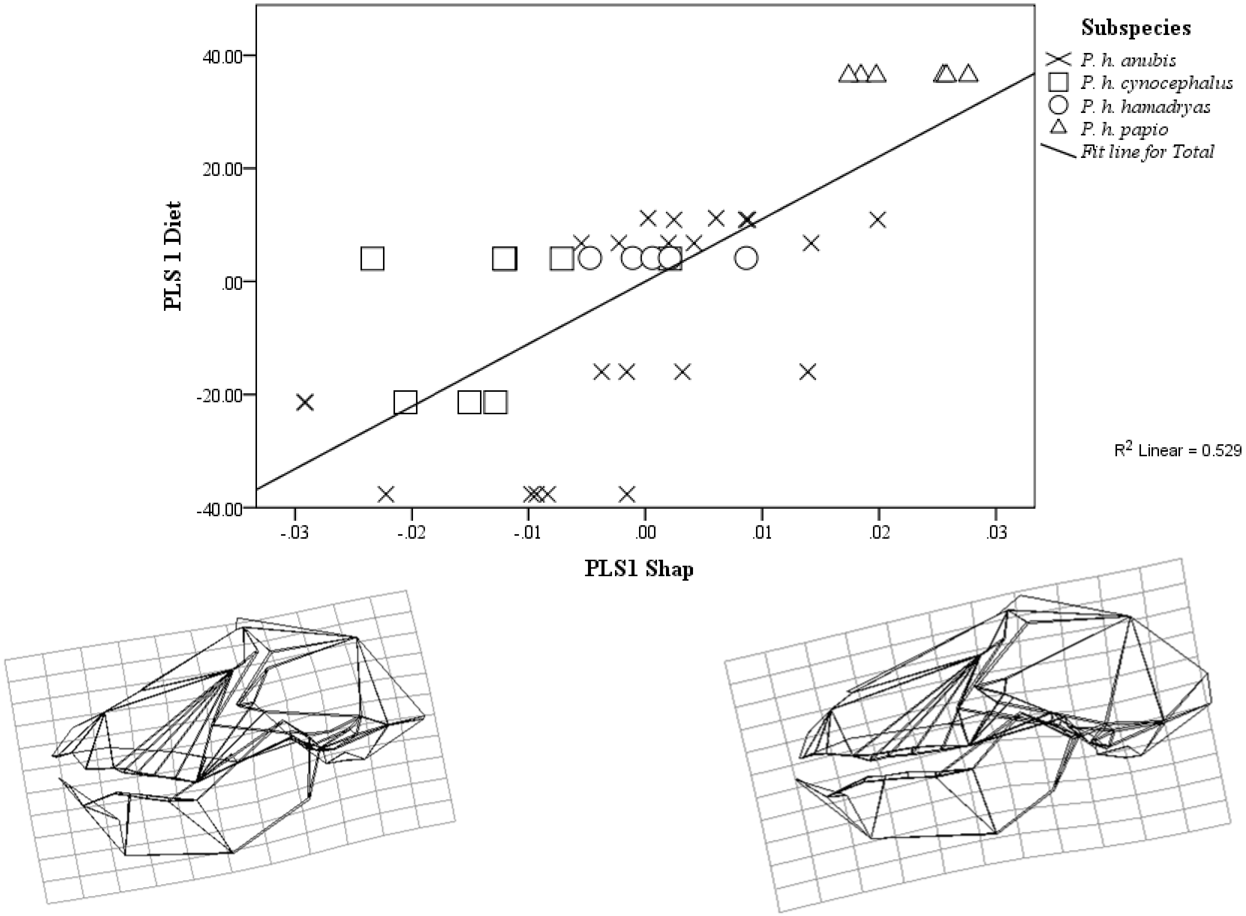


Figure 6.7. A scatter plot of scores for the first PLS between diet and size-controlled shape without P. h. ursinus. *Loadings for interpretation of the dietary axis are given in the table beside the axis and wireframes show the morphological extremes of the axis of covariation (exaggerated by a factor of 3)*

4.3.3 Baboon Biomechanics

The ratios representing the mechanical advantage of muscle vectors were regressed onto size for baboons.

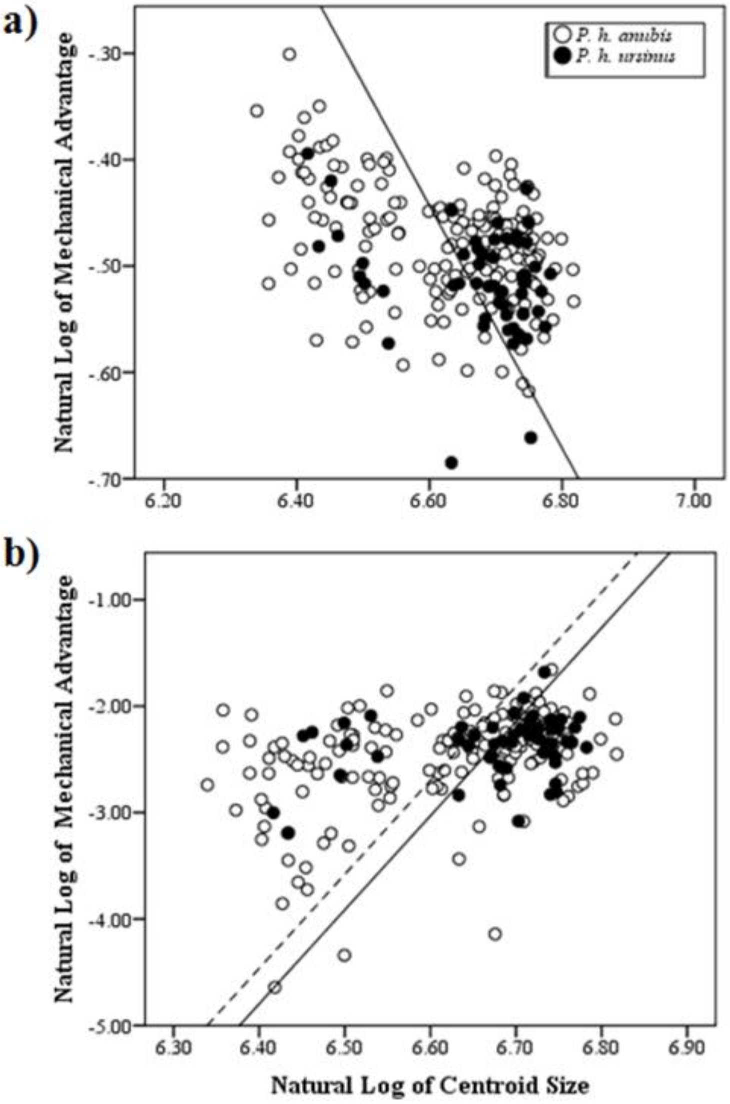


Figure 6.8. The relationship between size and mechanical advantage for ***a)*** *the anterior masseter muscle and* ***b)*** *posterior temporalis for* P. h. anubis *and* P. h. ursinus. *For the anterior masseter there is no significant difference in the regression of centroid size on mechanical advantage. For the posterior temporalis there is a significant difference between the mechanical advantage size regressions. The regression is represented for* P. h. anubis *by a dashed line, and for* P. h. ursinus *by a solid line.*

The anterior masseter muscle vector is significantly predicted by centroid size in the olive (Fig. 4.8a, $F_{1,178}$ = 33.684, p<0.0001) and the chacma baboon ($F_{1,53}$ = 4.810 p =

0.033). The two are not different in slope for this relationship (interaction term: $F_{1,232}$=1.092, p=0.297) or intercept (subspecies term: $F_{1,232}$=1.128, p = 0.289, fig. 4.8).

The posterior temporalis muscle vector is significantly predicted by size in the olive ($F_{1,178}$ = 38.9, p<0.0001) and the chacma ($F_{1,53}$ = 4.823 p = 0.033). The two are not different in slope (interaction term: $F_{1,232}$=0.086, p = 0.769) but are significantly different in intercept (subspecies term: $F_{1,232}$=5.084, p=0.025, fig. 4.8b).

4.3.4 Vervet Diet-Shape PLS

Table 6.7. Singular values and pairwise correlations of PLS scores between the vervet dietary and shape blocks. For the whole PLS RV = 0.1395, p = 0.1425. For morphological specimens, n = 41, and for associated dietary data n =12. Significant p values are shown in bold.

	Singular value	**% Total covariance**	**Correlation**	**P-value**
PLS1	0.00328641	71.094	0.69305	0.1863
PLS2	0.00165205	17.965	0.53225	0.2183
PLS3	0.00088134	5.113	0.75085	0.3976
PLS4	0.00083527	4.592	0.79426	**0.0081**
PLS5	0.00043295	1.234	0.71628	0.1205
PLS6	0.00001285	0.001	0.67613	0.2557

The first PLS axis (fig. 4.9) between diet and shape shows morphological extremes corresponding to high levels of fruit versus high levels of leaves in the diet, although this trend is not significant. The djam-djam is conspicuous at the negative dietary extreme, while the other subspecies are dispersed about the trend line at the positive dietary extreme.

	PLS1
Fruit	0.69
Leaves	-0.72
Flowers	-0.01
Animal	0.04
Sap	-0.01
Other	0.09

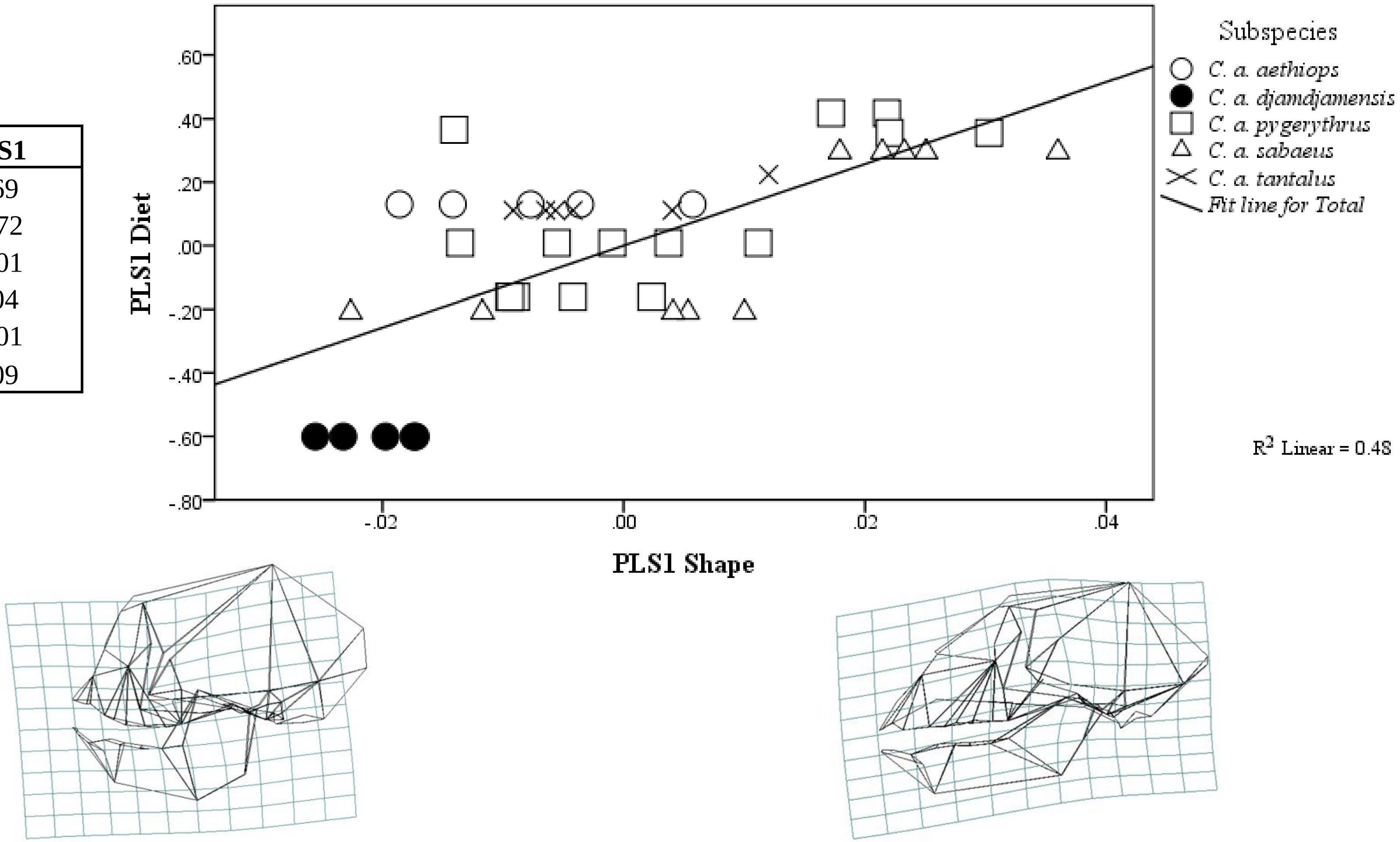


Figure 6.9. A scatter plot of scores for the first PLS between diet and shape for all vervet subspecies. Loadings are displayed in a table beside the dietary axis and wireframes show the morphological extremes of the axis of covariation (exaggerated by a factor of 3).

	PLS4
Fruit	-0.05
Leaves	-0.06
Flowers	-0.24
Animal	-0.53
Sap	0.78
Other	0.22

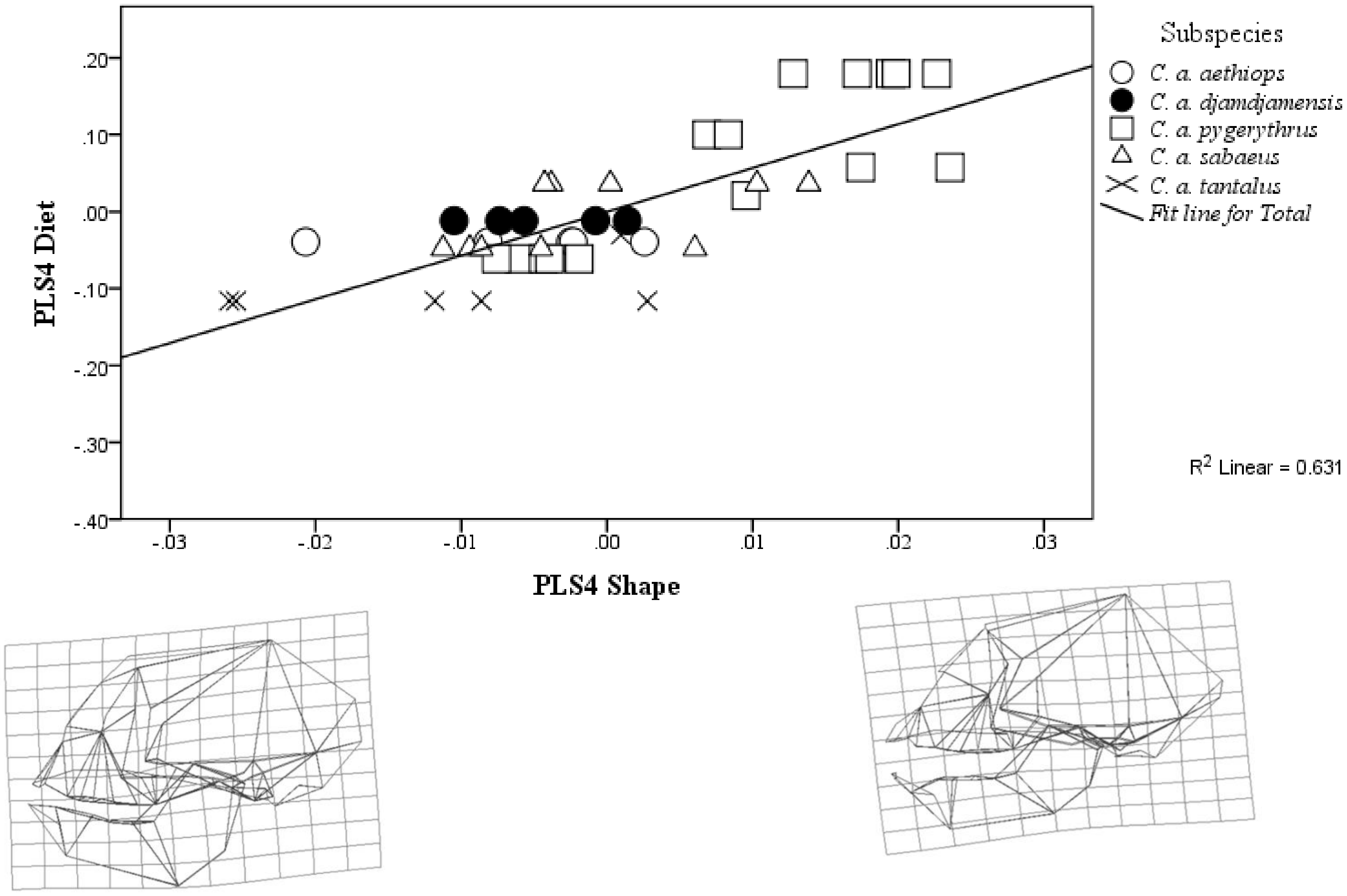


Figure 6.10. A scatter plot of scores for the fourth PLS between diet and shape for all vervet subspecies. Loadings are displayed in a table beside the dietary axis and wireframes show the morphological extremes of the axis of covariation (exaggerated by a factor of 3).

The fourth dietary morphological PLS (fig. 4.10) is significant (p = 0.0081), although it only accounts for a small proportion of the variance (4.6%). The axis is between insect eating and sap eating, with sap eating appearing to take place for most but not all *C. a. pygerythrus* populations versus the other subspecies. The djam-djam is intermediate between these two dietary extremes. The insect eating morphology corresponds to larger face to neurocranium but is also more prognathic, showing a larger more anteriorly translated mandible.

The known dietary outlier, the djam-djam, was removed to determine if this was driving the trend.

Table 6.8. Singular values and pairwise correlations of PLS scores between vervet diet and shape blocks with the djam-djam removed. For the whole PLS RV = 0.1604, P=0.1845.

	Singular value	**% total covariance**	**Correlation**	**P-value**
PLS1	0.0026122	61.03	0.61171	0.2447
PLS2	0.0016842	25.368	0.63958	0.2122
PLS3	0.0009682	8.385	0.81617	0.1605
PLS4	0.0006551	3.838	0.64195	0.0553
PLS5	0.0003926	1.378	0.78157	**0.0454**
PLS6	1.23E-05	0.001	0.58958	0.1468

With the djam-djam removed the overall PLS is still weak (RV = 0.1817) and nonsignificant correlation (p = 0.1086, table 4.8). Removal of the djam-djam reveals the same first PLS between the high levels of leaf eating versus fruit eating with an almost identical pattern of shape change (fig. 4.11), although the amount of variance explained by this axis has diminished (table 4.8). Only the fifth PLS was significant (table 4.8) accounting for only 1.4% of the total covariance. This produced an axis between leaf-eating and animal-eating.

	PLS1
Fruit	0.82
Leaves	-0.46
Flowers	-0.29
Animal	0.04
Sap	-0.16
Other	0.12

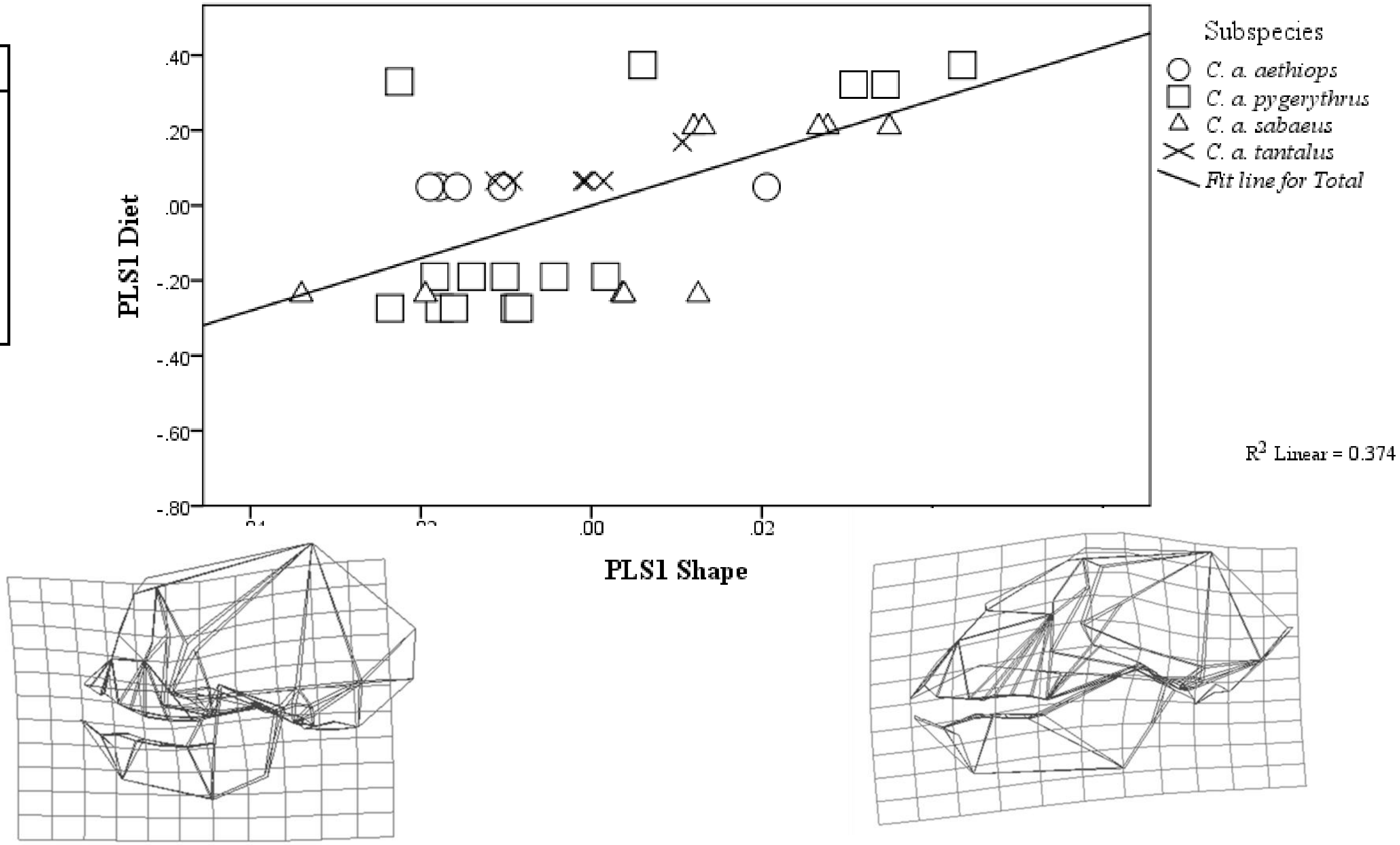


Figure 6.11 A scatter plot scores for the first PLS between vervet diet and shape for all the subspecies excluding C. a. djamdjamensis. *Loadings are displayed in a table beside the dietary axis and wireframes show the morphological extremes of the axis of covariation (exaggerated by a factor of 3).*

	PLS5 Diet Loadings
Fruit	0.36
Leaves	0.5
Flowers	0.05
Animal	-0.39
Sap	-0.24
Other	-0.64

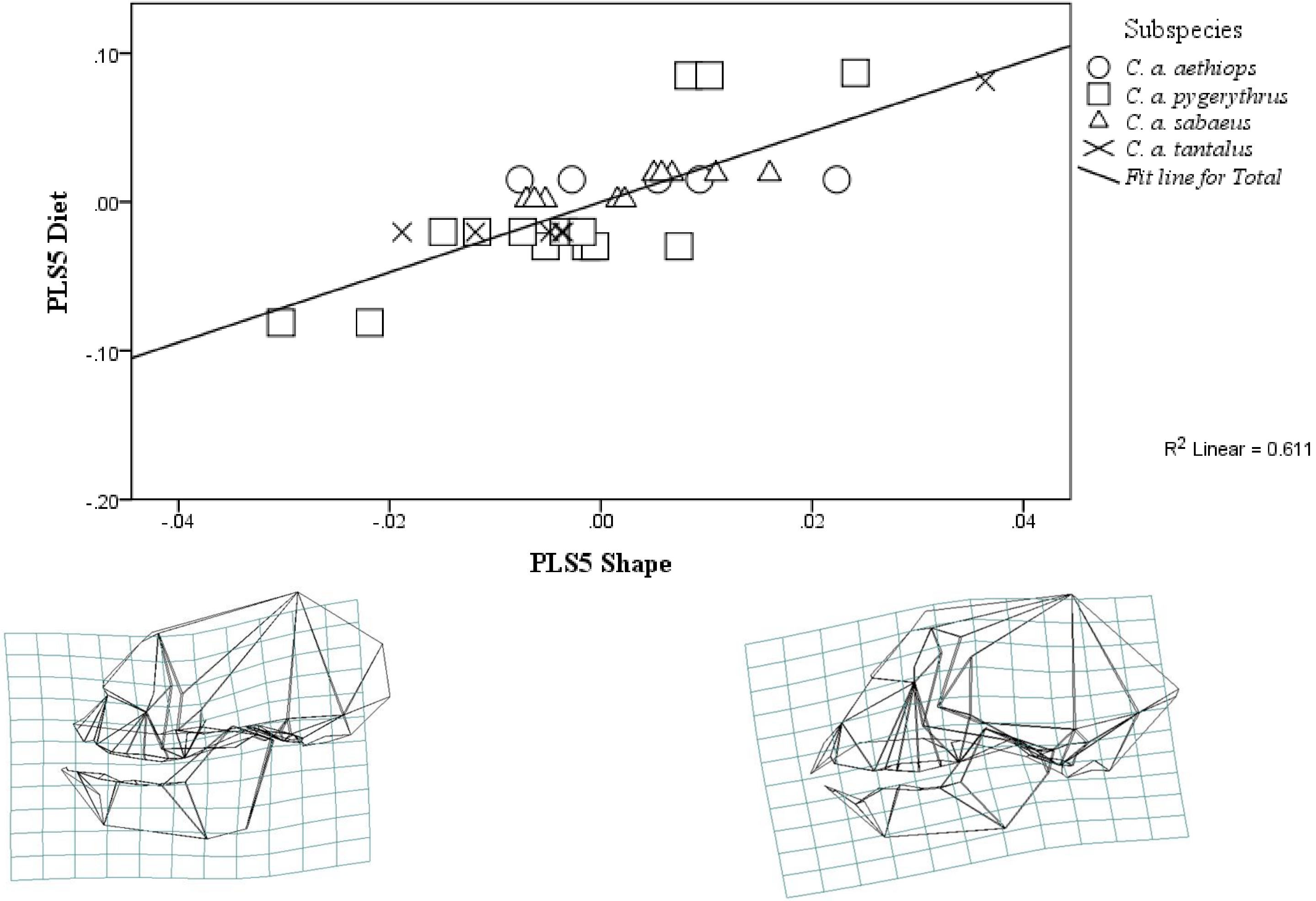


Figure 6.12. A scatter plot of scores for the fifth PLS between diet and shape for all the subspecies excluding C. a. djamdjamensis. *Loadings are displayed in beside the dietary axis and wireframes show the morphological extremes of the axis of covariation (exaggerated by a factor of 3).*

4.3.5 Size-Controlled Vervet Shape and Diet PLS

To control for the all-pervading effects of size on shape size was regressed out and the residuals were added to the mean morphologies for each subspecies.

Table 6.9. Singular values and pairwise correlations of PLS scores between blocks. For the whole PLS RV = 0.1270, P=0.1261.

	Singular value	**% Total covariance**	**Correlation**	**P-value**
PLS1	0.00299	77.939	0.69317	0.1316
PLS2	0.00113	11.229	0.53017	0.6148
PLS3	0.00083	5.958	0.54425	0.1372
PLS4	0.00067	3.928	0.48587	**0.0125**
PLS5	0.00033	0.946	0.66335	0.158
PLS6	1.09E-05	0.001	0.44901	0.1207

Size-correction reduces the RV value from 0.1395 to 0. 1270 with neither being significant (tables 4.7 & 4.9). Visualisation demonstrates differences in morphological extremes (figs. 4.13 & 4.14) but not in the in the general trend, other than an increase in scatter. The folivorous extreme has a more robust cranium and mandible after size correction, while the more frugivorous extreme exhibits a shallow mandible and gracile skull (fig. 4.13). The fourth PLS shows animal-eating forms have a more prognathic skull relative to frugivorous forms (fig. 4.14).

	PLS1
Fruit	0.67
Leaves	-0.74
Flowers	0.02
Animal	0.05
Sap	0
Other	0.06

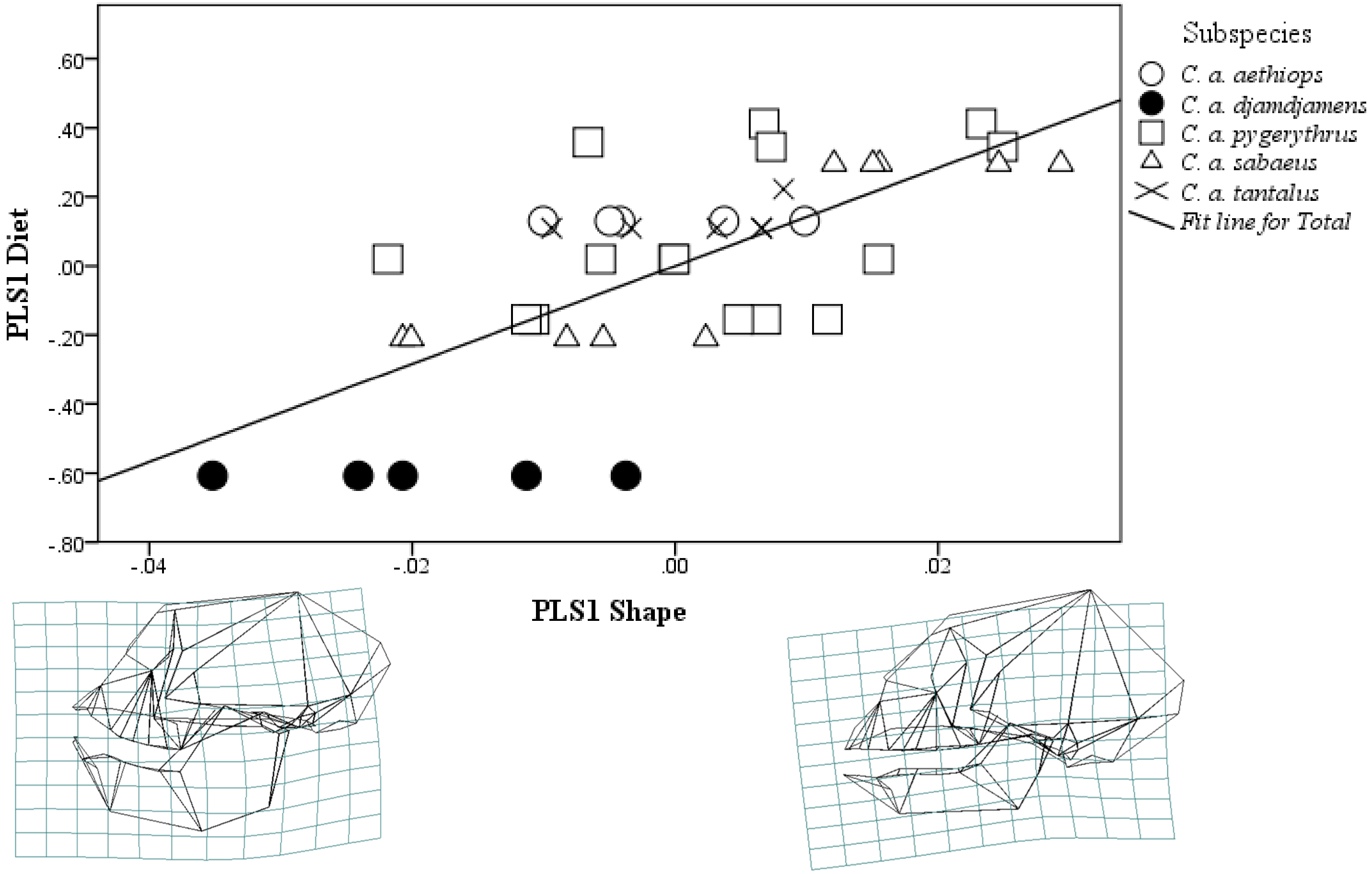


Figure 6.13. A scatter plot of scores for the first PLS between vervet diet and size-controlled shape. Loadings are displayed in a table beside the dietary axis and wireframes show the morphological extremes of the axis of covariation (exaggerated by a factor of 3).

	PLS4
Fruit	-0.39
Leaves	-0.35
Flowers	-0.09
Animal	0.13
Sap	0.83
Other	-0.02

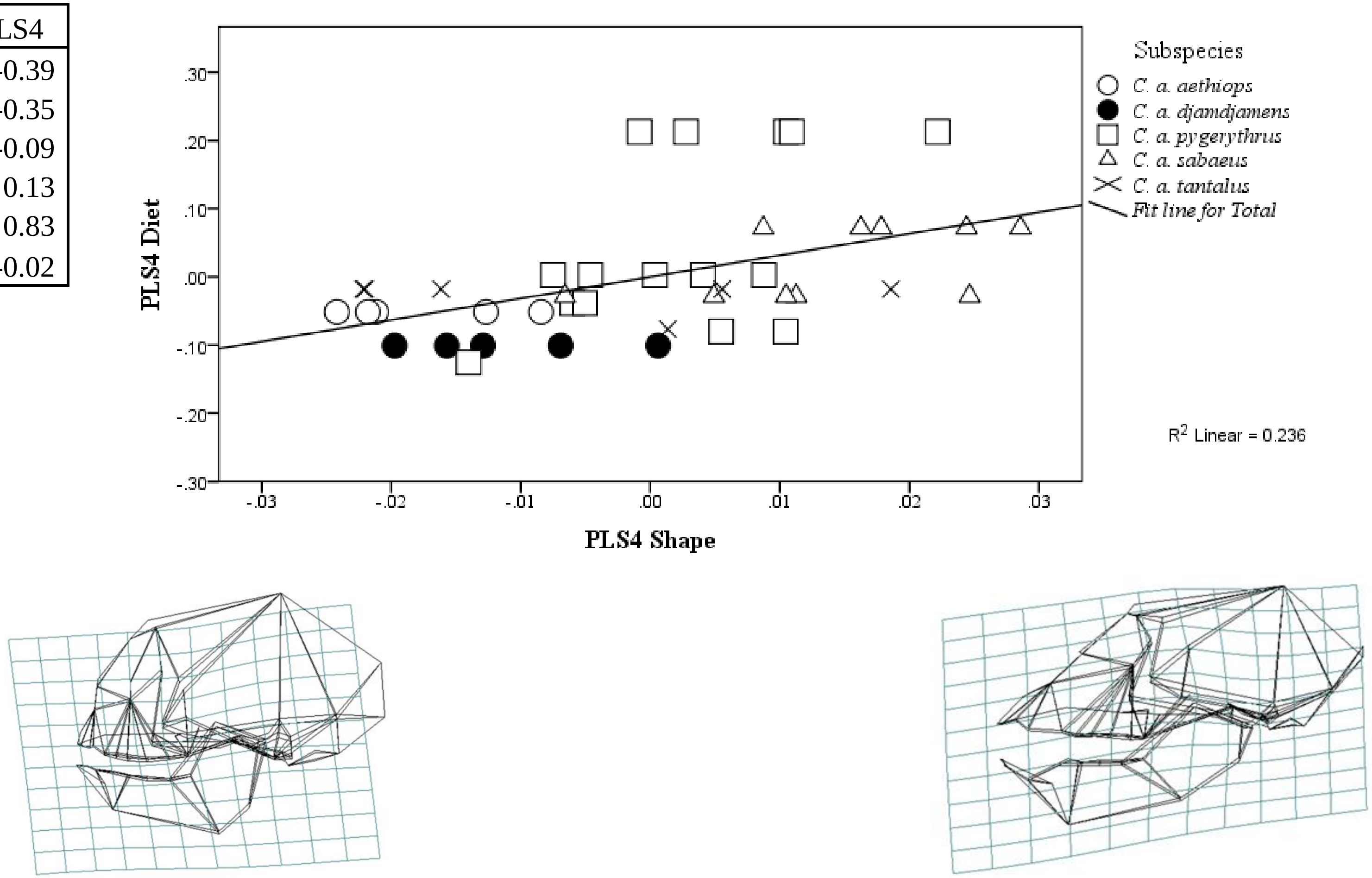


Figure 6.14. A scatter plot of scores for the fourth PLS between vervet diet and size-controlled shape. Loadings are displayed in a table beside the dietary axis and wireframes show the morphological extremes of the axis of covariation (exaggerated by a factor of 3).

4.4 DISCUSSION

4.4.1 Baboon Diet-Morphology Covariation

This study has found significant covariations between baboon dietary and morphological variation. This axis corresponds to long-faced specimens, with a diet high in subterranean foods, versus short faced animals, associated with a diet containing a higher proportion of fruit. This axis is robust to the removal of the chacma baboon, proving that this long-faced and highly subterranean food-eating subspecies was not driving the trend. Of course this finding is based on a small sample, with data from current dietary studies extrapolation to specimens from different locations and times. However, it seems unlikely a strong trend would be detected if there were not genuine broad scale differences in diet that truly related to morphology: strong regional morphologies and tendencies to dietary specialisations do seem to exist and are related. This to some extent this resounds with Chapter 3, which found that subterranean foods were the food category where a difference lay, albeit only between the olive and chacma baboons. Indeed, given this difference it might be expected that the two dietarily different subspecies might be at opposite ends of a dietary-shape axis. The olive baboon, is highly dietarily variable, eating subterranean foods in the savannah at Amboseli, but also a higher proportion of fruit in the forests of the moist savannah (Rowell, 1966) and in West Africa (Kunz and Linsenmair, 2008b). Indeed this subspecies occupies a wide but middle-centred spread across the diet-shape axis. It is interesting therefore that removal of the chacma baboon still shows a link between long-faced skulls and subterranean food eating. This suggests that the olive baboon tends towards the same dietary-shape covariation as found in the chacma baboon, rather than being discretely different. That a significant difference was found between these subspecies (Chapter 2) when they are adjacent rather than opposing in baboon dietary variation, suggests that but for the lack of studies there would be more significant differences between the other subspecies. As has been mentioned, the Guinea baboon is known to be highly frugivorous (Culot, 2003), no doubt as a result of its wetter, more productive and fruit rich environment (Anderson and McGrew, 1984).

As the chacma is large, and the olive baboon has comparably large populations, the long-faced-subterranean food association might be argued to be the result of size alone. However, size-corrected shape demonstrated an only slightly reduced correlation coefficient, and clear morphological extremes were present. When the chacma is present this relates to a ventrally flexed rostrum, agreeing with the size-controlled findings of Chapter 2. However, exclusion of this taxon showed a robust morphology with a deep mandibular corpus and rostrum corresponding to subterranean food eating, versus a more gracile form, corresponding to fruit eating and the Guinea baboon.

Given the apparently strong correlation between long-faced morphologies and subterranean foods it is particularly unfortunate that no dietary variation is available for the Kinda baboon. This diminutive subspecies is found adjacent to yellow and chacma baboon, sharing a contiguous environment (Freedman, 1963, Jolly, 1993, Jolly et al., 2011), and is thus likely to be dietarily similar. This would therefore seem to go against the trend detected in the other subspecies. Given how different this is in size, which rendered it an outlier in earlier spatial analysis (Chapter 2), it is possible that there is some deep and enduring ecological or socioecological difference for its small size, perhaps unrelated to diet. In Chapter 2 parallels were drawn between this subspecies and the hamadryas baboon, on the basis of a reduction in sexual dimorphism, with perhaps morphology responding to the social system, rather than to the environment or diet directly. Another explanation might be that this taxon is small because of entirely stochastic effects, such as genetic drift and genetic bottlenecking. Such effects might have pushed this subspecies so far away from the other baboon subspecies on the adaptive landscape that it now occupies a different adaptive peak altogether, and is subject to differing selective forces. If that is the case, its omission does not harm the trend in the same way. Further information from the field will be required to test these hypotheses.

Once again, the methodology employed in this study is likely to add noise to a diet-morphology trend. Relating the morphology to the dietary generalisation of a site is problematical in that the baboons may be from a different population or from a time when baboons were behaving quite differently. For instance, dietary shifts have been noted over time at Amboseli (Alberts et al. 2005). Similarly, ecological data at our disposal list only the food type and we are forced to rely on crude associations of these food items with physical properties. However, from the perspective of broad evolutionary adaptations, one would expect this signal is detectible over this variation which would only add noise rather than a directional bias in any of trends observed.

In terms of physical properties, the dietary axis runs from the corms, rhizomes and tubers that represent the toughest and stiffest foods, to the fruits that represent the least tough and stiff. Biomechanical predictions would be for a high mechanical advantage for the muscles of mastication in subspecies eating more subterranean foods. The two muscle vectors both had a significant though opposing relationship with size (fig. 4.8), with the masseter's mechanical advantage dropping off with size (the out lever increases with size more than the in lever), and the temporalis vector's increasing with size. This reflects the fact that larger animals have a bite point further from the temperomandibular joint as the dental arcade moves forward relative to the origin and insertion of the temporalis. However, for the mechanical advantage of the masseter vector there is no significant difference between the two subspecies. While, there is a significant difference in intercept though not slope for the temporalis vector this is trivial and the scatter is extensive. There is uncertainty in these measurements owing to the crude nature of characterising a muscle with complex fibre geometry. Whether the scatter reflects natural variation, or variation around the real value is impossible to say, though within subspecies variation is extensive relative to between subspecies variation, suggesting there could be considerable natural variation in these proxies. Additionally while we have a notion of the muscle's line of action, the fibres are pinnate in the masseter (Osman Hill, 1971), which increases the physiological cross sectional area, and is a dimension on which it is impossible to get a handle on . Even the large sample size may not remove systematic errors in these parameters, and so the conclusion of no difference must be taken with caution, as a potential type II error. Without an actual wet skull with the muscles attached, where detailed lever arm mechanics can be measured and compared with the dry skull, the accuracy of this method is difficult to establish empirically, however strong the theoretical basis. However, if the finding of no significant difference is taken as being true, then this might reflect the high integration of the skull (Marroig and Cheverud, 2005) and the short time depth of subspecific divergence (Zinner et al., 2009b), constraining skull parameters from diverging. Indeed, baboons are dietarily generalist (Alberts and Altmann, 2006) and might thus not face a high selection pressure on tending towards morphological specialisation. Here only one aspect of biomechanical adaptation has been considered and the skull, aside from optimising muscle leverage, is also optimised to reduce stress and strain (Kupczik et al., 2009, Kupczik et al., 2007). The finding of a more robust morphology, after size-correction, being associated with tough, subterranean foods might argue for such an effect. More detailed analyses which take into account surface geometry such as finite element analysis might have sufficient power to detect such an adaptation (Panagiotopoulou, 2009, Rayfield, 2007), but at the moment biomechanical adaptation to diet remains equivocal.

4.4.2 Vervet Diet-Morphology Covariation

None of the vervet morphology-dietary partial least squares analyses was significant. However, this nonsignificance is likely the result of a small sample size, and thus might reflect the covariation if n were larger. In vervets the first partial least squares axis between shape and diet, accounting for most of the total diet-shape covariation, was between the djam-djam, with high levels of folivory, versus the other subspecies, with dominant frugivory. This is unsurprising given the djam-djam is discretely different in its extremely high levels of folivory, circa 80% (Chapter 3, Mekonnen et al., 2010), and appears to be in a different dietary niche from rest of the vervet subspecies (Chapter 3). Second, the djam-djam is distinct in its morphology, clustering separately in PC plots and cluster analyses, with and without allometric correction (Elton et al., 2010). If more djam-djam dietary studies and specimens were available is seems likely that this would be significant. If so this is a different axis of diet-morphology variation from that found in baboons, suggesting the vervets have expanded into a different niche altogether.

Removal of the djam-djam dramatically reduces the covariation between shape and diet, showing that this is a major cause of the trend. However, the morphological extremes are similar in both analyses suggesting the djam-djam might extend a diet-morphology trend common to the other vervet subspecies. In both djam-djam included and excluded analyses an axis corresponding to sap-feeding versus faunivory was found. The sap feeding specimens were all *C. a. pygerythrus*, while the more faunivorous specimens comprised the other subspecies and other populations of *C. a. pygerythrus*. That this split falls within *P. a. pygerythrus* rather than at a subspecies division is unexpected. However, *P. a. pygerythrus* has the largest geographic range, found in East and southern Africa. Again, this is not significant, but potentially this is a type II error owing to a small n. Interpreting the partial least squares with the dietary data on which the PLS was based (table 3.2), it is evident that this trend is driven by the Amboseli population which feed on 25 % sap. This is much greater than the less than 5 % values found at other populations. This value would appear not to be an outlier biologically as it is an average of Lee's (1981) data for three sites at Amboseli. Additionally Wrangham and Waterman (1981) got a comparably high 22% sap feeding in their study. This is not too dissimilar to Klein's (1978) values of between 6 and 18%. It is possible that the high incidence of sap feeding is related to the reliance of the vervets on acacia at Amboseli (Wrangham and Waterman, 1981).

The visualisation of this trend showed a more paedomorphic morphology in the sap-feeding *C. a. pygerythrus*, with a large neurocranium relative to the face. This is a classic allometric pattern and indeed the shape scores for PLS 4 are explicable in terms of size in a regression analysis (tables 5 & 7). Clinal variation in size is known to be the prevailing and robust trend across Africa with large animals in the west and small animals in the east (Chapter 2, Cardini et al., 2007, Elton et al., 2010). The finding that sap-feeding is more prevalent in smaller East African savannah animals, specifically at Amboseli, while insect feeding is prevalent in West Africa, hints at a nutritional difference across this size cline. Sap, though rich in energy, is poor in protein, while animal matter is a rich source of protein. As such Amboseli vervets might have less protein resources to invest in growth, accounting for their smaller size. This conclusion however cannot be substantiated for certain with such a low sample size and statistical nonsignificance.

4.4.2Conclusion

Baboons show significant covariation between dietary and morphological variation, robust to the removal of the outlying chacma baboon. A long-faced morphology is associated with subterranean foods and a shorter one with diets richer in fruit. Size-correction does not significantly lessen this trend. However, the biomechanical parameters chosen here, namely mechanical advantages for vectors representing an anterior masseter vector and posterior temporalis vector failed to show any significant covariation with diet. As such this study has failed to prove adaptive causality behind this correlation, which may be spurious. That said limitations in the biomechanical proxies and the likely subtlety of any differences between subspecies means that biomechanical adaptation cannot be ruled out.

Vervets in contrast showed no significant morphological variation with diet. However, some of the covariation detected agrees with the field data. Again the analyses suffered from a small sample size. In particular additional djam-djam specimens and dietary data may change the relationship to a positive one. With either no significant subspecific differences, or if we accept a type II error, differences between the djam-djam and other subspecies, the vervet is different in its pattern of diet-morphology subspecific variation.

CHAPTER 7. THE ROLE OF EVOLUTIONARY HISTORY IN SUBSPECIFIC DIVERGENCE

5.1 INTRODUCTION

5.1.0 Overview

Previous chapters have looked at the correlation between subspecific morphological variation and spatial and environmental (chapters 2 & 3) and dietary (chapters 4 & 5) variation in both baboons and vervets. In each case the attempt has been made to uncover evidence of an adaptive response to these variables. However, adaptive genetic change is not free from constraint (Ridley, 2004). Consequently while divergence may be adaptive it is also likely to retain a phylogenetic structure i.e. affinities between taxa more closely related than those more distantly related. Indeed, not all genetic change is adaptive. Genetic drift is more likely to reflect phylogeny as the occurrence of these differences is random and thus proportional to the time since divergence.

While morphology can vary as a result of phenotypic plasticity, some subspecific differences are evidently under direct genetic control, as proved by hybrid intermediacy. The morphology of hybrid hamadryas and olive baboons is intermediate (Phillips-Conroy and Jolly, 1981) as is mating behaviour (Bergman et al., 2008). Similarly yellow-olive hybrids mature at a rate proportional to how much olive or yellow baboon ancestry they have (Charpentier et al., 2008). Also, differences in IGF-I (growth hormones) between the small guinea and large olive baboon (Bernstein et al., 2007) as well as the timing of peak testosterone level (Beehner et al., 2009) between the chacma and yellow baboon seem unlikely to be the result of plasticity. While genetic differences between vervet subspecies exist (Dutrillaux et al., 1978, Formenti, 1975, Shimada et al., 2002, Kuyl et al., 1995), whether these determine the corresponding phenotypic differences is unknown. However, given that hybrids show signs of heterosis (Elton et al., 2010) and subspecific phenotypes are genetically determined in baboons (Phillips-Conroy and Jolly, 1981) and saddleback tamarins (Kohn et al., 2001) this is almost certainly the case in vervets too.

The incidence of hybridisation in the wild demonstrates the incomplete reproductive isolation of subspecies. However, subspecific interbreeding does not equate to homogeneity, as any reduction in gene flux is likely to promote differentiation (Mayr, 1963). Natural selection can more easily favour adaptations to local conditions in isolated populations if genetic recombination is low. Also nonmixing populations accrue random differences, with no selective benefit, through a process of genetic drift (Mayr, 1963). Given the extent of the baboon and vervet ranges panmixia is impossible: there is not an equal risk of any one individual mating with any other of the opposite sex. Consequently regional structuring of the genome arises, despite interbreeding. Indeed gene flux probably has been reduced to zero at certain points in the Pleistocene (Zinner et al., 2008), exacerbating population differences and probably resulting in much of the subspecific differentiation.

Past genetic isolation and present spatial extent have resulted in genetically fixed differences between subspecies. Consequently phylogenetic relatedness in spite of incomplete cladogenesis is likely to account for a good deal of morphological variation. This chapter looks at how other species have been affected by the same environmental forces over evolutionary history to make predictions about the magnitude of phylogeny in baboons and vervets. These predictions are tested by phylogenetic partial least squares to quantify and graph the association between shape and phylogeny. The magnitude of these differences between the two subspecies is compared, to establish if phylogeny is equally important in subspecific divergence in the two taxa.

5.1.2 Prevalence of the Phylogenetic Signal

Closely related taxa tend to be more similar than distantly related taxa for any given trait, such that the trait is said to exhibit a phylogenetic signal (Klingenberg and Gidaszewski, 2010). Such signals are present in behavioural, life history or morphological features throughout the animal kingdom and at all levels of the taxonomic hierarchy (Blomberg et al., 2003). For instance animal vocalisations exhibit a phylogenetic signal in taxa as diverse as frogs (subfamily Dendrobatinae (Erdtmann and Amézquita, 2009) and family Strabomantidae (Goicoechea et al., 2010)), herons (family Ardeidae (McCracken and Sheldon, 1997)), red colobus monkeys (*Piliocolobus* spp. (Struhsaker, 2010)) and gibbons (family Hylobatidae (Geissmann, 2002)). This signal is detectible at the family level in spite of the extensive evolutionary lability of behavioural traits. Morphology typically demonstrates stronger phylogenetic signals (Blomberg et al., 2003). The skull in particular, owing to its complexity of function and genetic underpinning, exhibits morphological divergence that approximate temporal divergence (Caumul and Polly, 2005). This is well demonstrated in a broad analysis of lizard skull morphology (17 families in the order Squamata), which found that though skull shape was determined by diet and ecology, the primary influence was phylogeny (Stayton, 2005). Lizards appear not to be unique in this regard. Phylogeny is a major factor influencing the skull morphology of several orders of carnivorous mammals. In the extant Carnivora and Creodonta and the extinct Thylacoleonidae, Dasyuromorphia, Didelphidae and Borhyaenoidea (Goswami et al., 2011) functional factors such as bite force are secondary to the phylogenetic signal. However, functional adaptation can cause morphologies to converge and obfuscate any phylogenetic affinities. This is the case in the Testudinoidea (turtles), where skull form is shaped by environment and diet more than specific phylogenetic relatedness (Claude et al., 2004). A similarly weak signal was observed in the great cats (*Neofelis* and *Panthera*) (Christiansen, 2008), and convergence in procyonids means morphology is quite different from genetic phylogeny (Koepfli et al., 2007).

The prevalence of phylogenetic structuring of morphology in the primate order seems to vary with clade. Within the strepsirhine suborder, lemur skull morphological variation was largely independent of phylogeny (Viguier, 2004). However, among the New World haplorhines, morphological and phylogenetic covariation was high in the skulls (Marroig and Cheverud, 2001). No comparable Old World monkey study exists. However, smaller scales studies reveal discrepancies between morphology and phylogeny. For instance shape analyses have consistently placed mandrills and baboons together in spite of their closer phylogenetic affinities to *Cercocebus* and *Lophocebus* respectively (Disotell et al., 1992, Collard and Wood, 2001). This pattern resounds with that of the taxonomically different but geographically similar Africa apes. Classical morphological analysis suggested a *Pan-Gorilla* clade to the exclusion of *Homo*, in contrast to genetic information showing a phylogenetic arrangement of a *Pan-Homo* clade to the exclusion of *Gorilla* (Page and Goodman, 2001). Morphological convergence of phylogenetically less related forms has been at the heart of the difficulty with taxonomically placing the robust australopiths. These species *Paranthropus boisei*, *P. robustus*, and *P. aethiopicus* all exhibit a hypermasticatory trend in morphology, in particular large premolars, and robust mandible. On the basis of numerous traits some authors have considered them a monophyletic group. However, all these characters are really underpinned by a single functional trait (Wood, 2007, Collard and Wood, 2001), namely mastication. It is entirely possible that these features have evolved independently in each taxon. This may well be quite common, as it is in bovids (Turner and Wood, 1993) and indeed *Homo rudolfensis* is convergent in premolar morphology with the robust australopiths (Wood, 1991).

While higher order taxa have been assessed for the strength of the phylogenetic signal few studies have examined this in the subspecific case in vertebrates. This probably reflects a lag in genetic analyses which naturally first seek to establish higher order taxonomic relationships. However, a few studies have shown that a phylogenetic signal is still detectible even in very subtle subspecific differentiations. For instance a good congruence was found between frontal bone and cranial base morphology and phylogeny of the snake *Vipera aspis* (Gentilli et al., 2009). However, bluethroat (bird) morphology and genetics were only crudely related, with even less correspondence between plumage and colour (Johnsen, 2006). However, as with many avian studies morphology in this case was characterised by three lengths: wing, tarsus and bill, and so the majority of the geometric information was lost in these crude morphological indices.

More common are findings of correspondence between taxon, based on morphological criteria, and mtDNA. Subspecific designations were concordant with mtDNA differentiation in bats of the species *Corynorhincus townsendii* (Piaggio and Perkins, 2005) and in caiman (Venegas-Anaya et al., 2008). However, in the latter case the divergence dates between subspecies was six million years old. This is a vastly longer time period than that for which many extant primates have existed (Delson et al., 2000), demonstrating the temporal nonequivalence of taxonomic status. Two primate cases of subspecific morphological variation argue for the importance of phylogeny. In saddleback tamarins allopatric subspecies were morphologically divergent according to the hypothesis of evolutionary history rather than geographic proximity (Cheverud and Moore, 1990). In papionin primates *Macaca thibetana* subspecific designations, based on morphotype, agreed with mitochondrial differences (Sun et al., 2010).

5.1.3 Deriving Phylogeny from Molecular Markers

Given that detecting the phylogenetic signal in morphology is founded on the premise that an accurate phylogeny is inferable, evaluation of this assumption is required before discussion of vervet and baboon phylogeny. In many of the preceding cases an underlying assumption has been that molecular markers (nuclear DNA, RFLPs, mtDNA) are more phylogenetically informative than morphology. Indeed, genetic variation is held to so accurately reflect phylogenetic variation that by comparing morphological variation with DNA phylograms one can assess the phenotypic signal. However genetic variation is not the same as phylogenetic variation. With this in mind the question then becomes to what extent this phylogenetic signal exists, and how does it compare with morphological phylogenetic reconstruction?

Numerous cases of morphological convergence resulting in incorrect phylogenetic hypotheses have been listed. The skull is highly functional and convergence in ecology results in convergence in form. Morphology is often highly integrated, such that finding independent characters, in the skull especially, is difficult. Indeed Collard and Wood (2001) demonstrated that whatever cranial characters they analysed in the papionins the true phylogenetic relationship, reliably derived from genetics, did not emerge. As in the controversy with robust australopiths a single trait, adaptation to eating tough foods, can result in numerous characters that are all underpinned by this (Wood, 2007, McHenry, 1984). Genetic reconstructions of phylogeny lack the flaw of nonindependence of characters, as in the case of DNA each nucleotide represents an independent character (Scotland et al., 2003). The second advantage of DNA is that convergence is less likely to be a confounding factor in phylogenetic reconstruction. Parts of the genetic code are noncoding and functionless and therefore all differences are likely to be the result of drift and not selection.

As a result of these two major strengths genetics has revolutionised our understanding of the affinities between the major branches of the tree of life. For instance we now recognise a group called the Ecdysozoa comprising the phyla Arthropoda, Onychophora and Tardigrada and the five introvert bearing worms (Nematoda, Nematomorpha, Priapulida, Kinorhyncha and Loricifera) to the exclusion of Annelida. Previously annelids were thought to be closely related to arthropods on the basis of the shared character of segmentation (Telford and Budd, 2003, Aguinaldo et al., 1997); we now know this is a convergent trait. At the finest grain of the taxonomic hierarchy, genetic studies have identified cryptic species, which are reproductively isolated populations, but morphologically similar to another. These are common in nature (Bickford et al., 2007) being found in neotropical butterflies (Hebert et al., 2004), shrew tenrecs (Olson et al., 2004) and the African elephant (Roca et al., 2001). The identification of cryptic diversity is important as it directs attention to subtle differences in vocalisation, life history and crucially prompt a re-evaluation of putative morphological similarity (Bickford et al., 2007). Moreover, it draws our attention to hidden mechanisms in the process of speciation as well as informing conservation (Bickford et al., 2007).

In spite of what genetics has achieved, it is not free of pitfalls, and numerous genetic phenomena reduce its capacity to produce accurate phylogenies. The fact that there are only four character states (A, C, T and G) means that the genetic sequence can easily diverge and then converge, for instance in the case of a C becoming a G, an A and then a C again, creating a homoplasy (Maley and Marshall, 1998). This is of particular concern over very long periods of time (Philippe et al., 2011, Maley and Marshall, 1998). Similarly, when the codes between two taxa have diverged beyond recognition finding homologous regions is challenging. Another problem with genetic variation is incomplete lineage sorting. Polymorphic nucleotides may endure for some time in two recently diverged populations with different nucleotides coming to fixation much later than the date of divergence, resulting in the appearance of a shallower split. Indeed if a third more anciently divergent line contains the same polymorphism and only comes to fixation later for the same character as the one of the other two a false impression of phylogenesis will be given (Philippe et al., 2011). Also, in general when divergences happen at roughly the same time the precise order of divergence can be difficult to resolve (Philippe et al., 2011).

Of major concern is the type of DNA used. Nuclear DNA undergoes Mendelian recombination, while mtDNA is maternally inherited. This can result in serious disparities between the two genetic line of information when a population has received its mtDNA from one population and its nuclear DNA in the other (Zinner et al., 2008). This is the case in male introgression, where nuclear genes invade a population, but clearly cannot bring in mtDNA. This pattern of male introgression leaves a characteristic mismatch between nuclear and mtDNA. Such mismatches are widely observed across the animal kingdom, being found in crickets (Shaw, 2002), toads (Fontenot et al., 2011), turtles (Wiens et al., 2010) cetaceans (Kingston et al., 2009), lemurs (Pastorini et al., 2009) macaques (Tosi et al., 2002) and, as will be discussed later, baboons (Zinner et al., 2009b, Wildman et al. 2004).

Indeed the newly discovered papionin *Rungwecebus kipunji* has the mtDNA of adjacent subspecies of yellow baboons but the nuclear DNA of a distinct taxon, placing it as a sister clade to *Papio* (Zinner et al., 2009a). This clearly implies hybridisation and backcrossing in the past, although there is no evidence for this in the present. The prevalence of this form of speciation is unknown, but if common it is a serious problem for creating accurate phylogenetic trees.

Aside from these biological constraints of using genetics, there are many methodological problems of phylogenetic construction. Identifying orthologous sequences is a computational problem (Huang et al., 2010), and once these have been identified using whatever algorithm there are various ways of building trees (Bayesian, neighbour joining, parsimony) all with slightly different statistical assumptions (Holder, 2005) and produce slightly different results. Moreover, accuracy does not seem to be achieved by simply sequencing more genes: the error increases with the sequences used (Huang et al., 2010, Philippe et al., 2011). Additionally most methods group fast evolving lineages to the exclusion of slow evolving lines, even though the genetic affinity may be low (Philippe et al., 2011). While it is argued that many of these problems can be solved by choice of genes, i.e. getting noncoding ones, and ones with the right amount of accumulated variation

(Philippe et al., 2011), this introduces a subjectivity similar to that employed by morphological cladistics in defining characters.

In many cases these problems and sources of variation are minor. However, in other cases these effects can accumulate to have serious consequences in the case of the brine shrimp (Maley and Marshall, 1998), where inclusion of this taxon distorted the whole phylogram changing the relationship between molluscs, arthropods and deuterstomes to an incorrect relationship. In a vertebrate study, several molecular studies found that the guinea pig appeared not to be monophyletic with other rodents (Graur et al., 1991, D'Erchia et al., 1996, Li et al., 1992); a position that has now been reversed (Sullivan and Swofford, 1997) with the finding that these studies employed a false model. More recent studies over the space of a few years can come to opposite conclusions. Earlier genetic studies have found evidence of no or very little interbreeding between Neanderthals and human (Currat and Excoffier, 2004, Hodgson and Disotell, 2008) and yet Green et al. (2010) found that there were definite interbreeding with non-African humans showing affinities with Neanderthals that were lacking in African populations.

Given the difficulties with genetics abandoning morphology entirely for genetic reconstruction is foolish. Morphology contains extensive phylogenetic information (Wiens, 2004) and indeed for fossil data it is the only phylogenetic information we have in the absence of molecular markers (Wiens, 2004). Moreover, genetically derived divergence dates are calibrated by fossils, and genes cannot reconstruct the morphology of animals of the past. As we have seen there is to some extent a subjective decision in which genes to use, which method to use and how many sequences to include; the very criticisms that have been levelled at morphological phylogenetic reconstruction. It is certainly true that while most phylogenies based on morphology have been incorrect in papionins, certain characters are more phylogenetically informative than others, and will yield the true phylogenetic affinities (Fleagle and McGraw, 1999). Thus genetics can point to informative morphological characters. Additionally, modern imaging techniques provide characters that were not formerly available (Wiens, 2004).

There is no method of phylogenetic reconstruction free of error. In the subspecific case, with which this thesis is concerned, morphological differences are slight and unambiguous characters few. However, unambiguous genetics differences do exist at this level (Zinner et al., 2009b, Brown et al., 2007, Dunnum and Salazar-Bravo, 2010), and though biological difficulties such as incomplete lineage sorting and introgression exist, genes probably reflect the best obtainable phylogeny.

5.1.4 Baboon Phylogeny

No quantification of the phylogenetic influence on shape has been made for the baboon. Frost *et al.* (2003) mapped the geographical pattern of skull shape change in baboons finding a north-south gradient of change, accounting for about 60% of the total variation, a pattern corroborated by this study (Chapter 2). They suggested this was related to phylogeny on the grounds that the species originated in southern Africa with the chacma as the more basal subspecies. A study of mitochondrial DNA found the chacma was the most basally divergent group relative to the others, with the Guinea baboon secondarily and much more recently divergent, with a tight cluster of the other subspecies (Newman et al., 2004). Zinner et al. (2009b) uncovered more extensive variation than Newman et al. (2004). They found that mitochondrial haplogroups did not align with subspecific designation. Mitochondrial haplogroup split certain subspecies and grouped parts of others. For instance a single haplogroup lumped hamadryas baboons with north-eastern populations of olive baboons, while eastern olives clustered with northern yellow baboon. Olive baboons were further found to be separated quite deeply into a western clade including the Guinea baboon and an Eastern with the yellow. Moreover a northern population of yellow baboons showed greater affinities with northern taxa, while southern populations grouped with the chacma and Kinda baboon.

This unexpected nonclustering of subspecific groups and discrepancy between morphotype and genetics is initially puzzling. However, this can be understood in light of the previously stated fact that mitochondrial DNA is maternally inherited and is not a part of the nuclear genome; it codes neither for morphological nor behavioural traits. The baboon social structure is one of female philopatry and male dispersal and so while males are able to spread nuclear DNA and thus morphological and behavioural traits they cannot spread mtDNA. Wildman et al. (2004) proposed a mechanism of male introgression to account for the mtDNA subspecies discordance. They suggest a protracted period of male invasion of adjacent mtDNA haplogroups, effectively “swamping” the new population and interbreeding until all the original characteristics of that population are bred out. While the appearance and behaviour of the invading morphotype comes to prevalence crucially the original mtDNA remains as a relic of the original population.

Observations at current hybrid zones lend credence to this mechanism of genetic introgression. (Jolly et al., 2011). In the Luangwa region of Zambia native Kinda baboons (the smallest of the subspecies) are observed to hybridise with invading chacma baboons (the gray-footed population), the largest subspecies. Kinda-chacma hybrids exist and are fertile. As one would expect under a system of male introgression Kinda mtDNA is prevalent among these hybrid populations. The greater incidence of hybridism on the chacma side of the hybrid zone provides evidence of its northward movement, leaving hybrid forms in its wake. Continued to its completion this genetic swamping of Kinda baboons by introgressing chacmas would result in the diminution and eventual loss of the morphological characters of this subspecies leaving only the mtDNA behind. This process, whatever the underpinning, is evidently what has happened with the northern or gray-footed chacmas already, and according to the scheme of Zinner et al. (2009) has been a feature of baboon subspecific interactions in several locations.

While male introgression exists and is likely to create mitochondrial phylogenies at odds with those derived from nuclear DNA, the latter do not exist. However the deep mitochondrial divide between the northern and southern taxa is likely to be in keeping with the nuclear and thus morphological phylogeny. Importantly it is not the chacma baboon that is basally divergent as Newman found (Newman et al., 2004) . This finding was the result of sampling yellow baboons in East Africa only; a population that is likely to have recently introgressed into an ancestrally northern population. Of course nuclear DNA will be needed to corroborate this.

5.1.5 Vervet Phylogeny

Vervet phylogeny has not been investigated as thoroughly as that of baboons. The most recent analysis found differences between subspecies which were only slightly larger than within subspecies differences suggesting high levels of dispersal and genetic homogeneity (Shimada et al., 2002). However results must be interpreted with caution. First, like the study by Newman et al. (2004) the genetic sampling of specimens was a poor representation of the full range, with *C. a. tantalus* and *C. a. pygerythrus* being each represented by a single site (Kala Maloue National Park, Cameroon, and a captive population in Kenya respectively). As demonstrated by Zinner et al. (2009b), extensive genetic sampling is required for geographically widespread animals as limited sampling provides a misleading picture.

With the poor sampling of the other taxa, the wide sampling of *C. a. aethiops* adds significant bias to the analysis. This subspecies was sampled across most of the Awash River system; a distance in excess of 600 km and 2 000m in altitude (Shimada, 2000). Moreover, this environment has a history of pronounced environmental change. Lake Ahbe, from which the Awash flows, has risen and fallen four times over the Holocene, even drying out at one point between 17,000 and 10,000 years ago (Shimada, 2000). It is likely that populations would have gone extinct and been fragmented over this period. Isolation and bottlenecking should exaggerate genetic differences to give a higher than average genetic diversity. Also, this study did not recognise *C. a. djamdjamensis*.

The study by Shimada et al. (2002) study finds *C. a. pygerythrus* to have diverged first, with *C. a. tantalus* nested within the extensive variation of *C. a. aethiops*. The basal position of *C. a. pygerythrus* does agree with the proposed southern African origin of vervets (Kingdon, 1971). However *C. aethiops* do not appear in the fossil record of southern Africa until the middle to late Pleistocene at Border Cave and Black Earth Cave (Elton, 2007). Given the good representation of ecologically similar papionins in this region (Elton, 2007) it is more likely that vervet were not present rather than not preserved, suggesting they arose elsewhere and entered southern Africa with advent of more open environments (Elton, 2007). Indeed fossils of vervets do exist in East Africa at 0.6 Ma (Frost and Alemseged, 2007) where they appear alongside *Papio.*

Provisional mitochondrial DNA analysis implies a West African origin (Hauser, personal communication), with *C. a. sabaeus* as the most divergent taxon. The same finding was reported by van Kuyl et al. (1995). However, the breadth of this study, including papionins and colobines reduces the accuracy of resolution of their phylogram. Indeed *C. a. pygerythrus* appears three times clustering within *C. a. aethiops* and *C. a. tantalus* suggesting either introgression or poor genetic resolution.

The only additional study on genetic variation was carried out on *C. a. pygerythrus* in South Africa. While one allele could differentiate between three populations (Eastern Cape, Kwazulu Natal and Former Transvaal) in South Africa this represents slight differentiation between population with genetic distances of 0.001 to 0.003 being comparable to intrapopulation variation (Grobler and Matlala, 2002). This argues for a panmictic population and a complimentary morphological analysis suggested monotype. This seems to corroborate the notion of a low genetic diversity in vervets. However, the study looks at only one subspecies at three sites within a few hundred kilometres. There is no obvious habitat break between sites, and so dispersal ought not to be limited. The study cannot yield any information on variation between the subspecies in the species as a whole.

The precise relationship between three *C. a. pygerythrus*, *C. a. sabaeus*, and *C. a. tantalus* is not clear, with even less to be said about *C. a. cynosuros* and *C. a. sabaeus* (Shimada et al., 2002). The nesting of *C. a. tantalus* within *C. a. aethiops* is unexpected. Again the presence of introgression makes this a difficult question to resolve: the mtDNA may not be representative of the true phylogenetic position. Taken at face value this relationship suggests *C. a. tantalus* emerged from *C. a. aethiops* stock. Fossil evidence shows that *C. aethiops* was present in Ethiopia at 0.6 Mya (Frost and Alemseged, 2007). A long history of endemism usually equates to genetic diversity, and certainly this value fits with Shimada's haplogroup diversification of 1.2-0.4 Mya, although this is a broad time range.

5.1.6 Past Environmental Drivers of Phylogenesis

Genetic variation in both baboons and vervets suggests a history of separation and contact (Zinner et al., 2009b, Shimada et al., 2002). It seems likely that this is the result of climatic fluctuation causing range contraction and expansion according to environmental variation; a suggestion made before DNA evidence to account for morphological disparity of baboons (Jolly, 1993, Jolly, 2001). Indeed contact between the olive and hamadryas baboons is probably recent with the two subspecies formerly being separated by desert during the middle Pleistocene (Wildman et al., 2004). Climatic fluctuation during the Pleistocene was extensive with oscillating wet and dry periods (de Menocal, 2011). Increasing aridification appears to take place after 2.8 Ma peaking between 1.8 and 1.6 Ma as shown by increases in African wind-borne dust and the expansion of savannah as shown by soil carbon nodules (de Menocal, 2011). This appears to have had a marked effect on sub-Saharan African fauna. Bovid turnover was high at 2.8, and 1.8 Ma with increases in hypsodonty; a dental adaptation to grazing (de Menocal, 2011, Vrba, 1993). Frost (2007) failed to find a turnover pulse at this time period in cercopithecids as a whole, although this includes forest-dwelling taxa as well as savannah-dwelling ones, and so this may be less relevant to our study taxa.

P. hamadryas first appears in the fossil record at 2.6 Ma (Szalay and Delson, 1979). Given that this is some time after the bovid turnover pulse it is hard to say whether baboons arose in response to this environmental shift to exploit an arid savannah habitat like the bovids in the same environment or whether there was a lag, or whether shorter scale environmental fluctuations indetectible from global patterns were responsible. Long term studies on baboons have shown extensive climatic change over a few decades (Alberts and Altmann, 2006), which may be an important influences on divergence too. The later divergence between northern (olive, Guinea, hamadryas) and southern (chacma, yellow, Kinda) is estimated at circa 2.1 Ma (Zinner et al., 2009a), which was within the range of Newman et al.(Newman et al., 2004). This corresponds to a period of low aridity at which time the rainforests may have extended into East Africa, creating impassable forests splitting the baboons in Africa. Numerous sub-Saharan savannah animals show a north-south split such as Eland (Lorenzen et al., 2010) giraffe (Brown et al., 2007) and hartebeests (Flagstad et al., 2001) and numerous others (Hewitt, 2004). Indeed the hartebeest mtDNA shows a north south split reminiscent of that found by Zinner et al. (Flagstad et al., 2001). However, at 0.5 Ma it is later than in baboons. This shows that though environmental variation in terms of expansion and contraction of the forests and East

African great lakes is important to subspecific divergence each species is perhaps affected by environment in a different way, such that not all isolation events take place at the same time.

5.1.7 Aims and Hypotheses: Morphological Implications of Phylogeny

Many taxa sharing a long term association with a common habitat and environment exhibit similar patterns of subspecific divergence (Hewitt, 2004). This argues for past environmental processes being an important part of the phylogenetic structure of a species and consequently its morphology. While so far present environmental conditions have been considered (Chapter 2) here we consider environmental variation and its influence on phylogeny and modern morphological variation. One goal of this chapter is to quantify this phylogenetic signal in the two taxa and to compare the magnitude of these correlations. Baboons are more flexible with a wider dietary niche, and greater ability to withstand environmental change than vervets (Alberts and Altmann, 2006). Baboons also range further than vervets and spend more time away from trees in the savannah. (Struhsaker, 1967a), while vervets can be separated by environments of “exposed rock and sand” and “savanna and cultivated fields” (Shimada 2002). Indeed the riverine association means that vervets are more likely to disperse along narrow belts of this habitat than across savannah. Given that divergence arises via reductions in gene flux (Mayr, 2000) the lesser capacity of vervets for dispersal might be predicted to result in greater genetic and hence morphological divergence between subspecies. Indeed the high allometric component of baboon skull shape might argue for a less phylogenetically determined morphology, on the grounds that shape-size associations are harder to change (chapter 2). This chapter aims to establish if these predictions are true, by testing the null hypothesis that both taxa have approximately the same phylogenetic signal. Here we use the correlation between shape and phylogeny as a proxy for this signal, using partial least squares to acquire a correlation value (Rohlf and Corti, 2000). For vervets no phylogeny is available so taxon is used, and the representativeness of this is tested using baboons for which a phylogeny is available. Thus a crucial assumption is that the phylogeny is accurate. Given the phylogeny it mtDNA certain adjustments must be made. The implications of this are evaluated.

Testing the hypothesis of similar phylogeny-morphology correlations will provide useful information about how much isolation and genetic drift has taken place between subspecies in the two taxa. This will therefore bring us closer to understanding to the magnitudes of the forces that have sculpted subspecific variation in these two similar African primates.

5.2 METHODS

5.2.1 Partial Least Squares

The multivariate correlation between shape and phylogeny was carried out using partial least squares (Rohlf and Corti, 2000): a method of maximising the covariation between two blocks of data (using MorphoJ, Klingenberg, 2011; see Chapter 4). The shape block comprised the landmark data with 465 landmarks (see Chapter 2), for specimens falling within geographically defined haplogroups (Zinner et al., 2009b) and for which dietary data were available so that results can fit into a path analysis with dietary data (Chapter 6, baboons n = 45, vervets n = 41). A consequence of this was no data for *P. h. kindae* or *C. a. cynosuros*. The phylogenetic block was constructed from principal coordinates, using Past (2000) from a phylogenetic distance matrix using the values of Zinner et al. (2009), a method commonly employed in phylogenetic PLS. In order to remove the effects of allometry from analyses allometry controlled shape was used, where size was regressed out according to the allometric trajectory for each subspecies (see Chapter 2).

5.2.2 Phylogenetic Models

Baboons

In the absence of genetic data directly associated with morphological data, specimens are assigned to one of the mitochondrial haplogroups of Zinner et al. (2008) on the basis of geographic locality. MtDNA haplogroups are endemic to one region and so this assumption is not unrealistic.

Zinner et al. (2009) concluded that their mtDNA phylogeny was unlikely to match nuclear DNA phylogeny because of introgression events. Under this scenario populations interbreed with and acquire the mtDNA of a new population, while overriding the nuclear DNA and morphological distinctiveness of the new population. When assessing the phylogenetic signal of morphology nuclear DNA is the best proxy. This study uses the mtDNA phylogeny of Zinner et al. (2009). However, in order to remove the effect of introgression which obfuscates the true phylogenetic signal we also used an adjusted version of the mtDNA phylogeny of Zinner et al. (2009). This adjusted phylogeny attempts to control for the introgression that led northern yellow and eastern olive baboons to share a haplogroup, in spite of the fact that these two subspecies belong on opposite sides of an ancient north south split (Zinner et al., 2009b). This is achieved by reallocating the northern population of yellow baboons the haplotype of the southern population. This ought to more realistically approximate nuclear DNA and hence actual heredity. Partial least squares of unadjusted and yellow baboon adjusted phylogenies and shape were carried out using MorphoJ (Klingenberg, 2011).

Vervets

There is no complete vervet phylogeny incorporating all subspecies. However, given that subspecific affiliations, represent phylogeny, albeit imperfectly, taxon is used as a crude proxy. This is not completely representative as certain subspecies are likely to cluster to the exclusion of others, rather than to all have diverged equally from the same ancestral point. Indeed, Shimada et al. (2003) show this to be the case for three of the five subspecies. However, the utility of this approach is assessed by carrying it out for baboons and comparing it with the shape-phylogeny correlation.

5.3 RESULTS

5.3.1 The Phylogenetic Component of Baboon Morphological Variation.

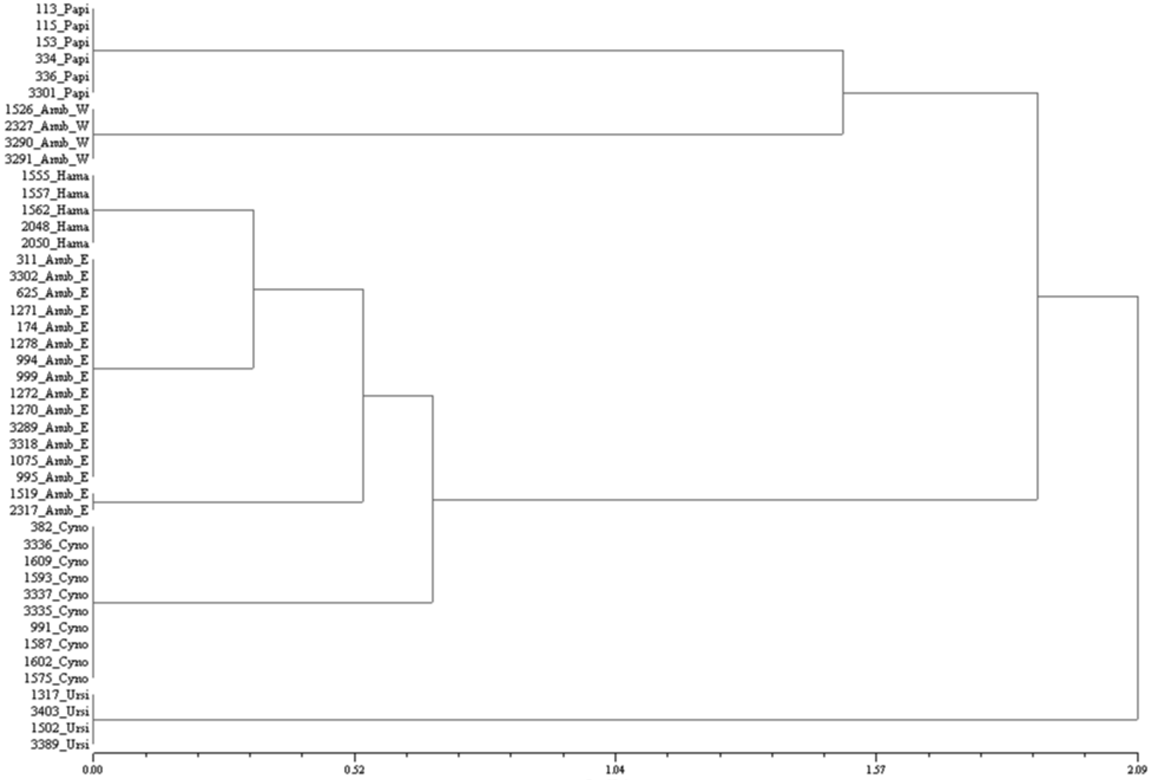


Figure 7.1. A phylogenetic cluster analysis of all 45 specimens used in the path analysis on the basis of haplogroup affiliation. Phylogenetic distances between haplogroups were taken from Zinner et al .(2009b). Papi = P. h. papio, *Anub_W = Western* P. h. anubis, *Hama =* P. h. hamadryas, *Anub_E = Eastern* P. h. anubis, *Cyno =* P. h. cynocephalus, *Ursi =* P. h. ursinus.

A cluster analysis of the specimens on the basis of mtDNA haplogroups reveals splits that broadly correspond to subspecific affiliations (Fig. 5.1). However, *P. h. anubis* split into eastern and western clades, with the latter clustering with the Guinea baboon.

Table 7.1. Singular values and pairwise correlations of PLS scores between phylogenetic principal coordinates and shape blocks. For the whole PLS RV = 0.2024, p < 0.0057, n = 41. Significant p values are shown in bold.

	Singular value	**% Total Covariance**	**Correlation**	**P-value**
PLS1	0.0490597	69.393	0.81776	**0.0354**
PLS2	0.0271755	21.292	0.74668	**<0.0001**
PLS3	0.0141334	5.759	0.76687	**0.0011**
PLS4	0.0101493	2.97	0.75355	**0.0044**
PLS5	0.0041962	0.508	0.80969	**0.0022**
PLS6	0.0016428	0.078	0.74682	0.4698

The PLS between shape and phylogeny is significant (table 2, p = 0.0057) overall and for all but the last PLS axis. However, the first two account for 91% of the covariation and only these are visualised.

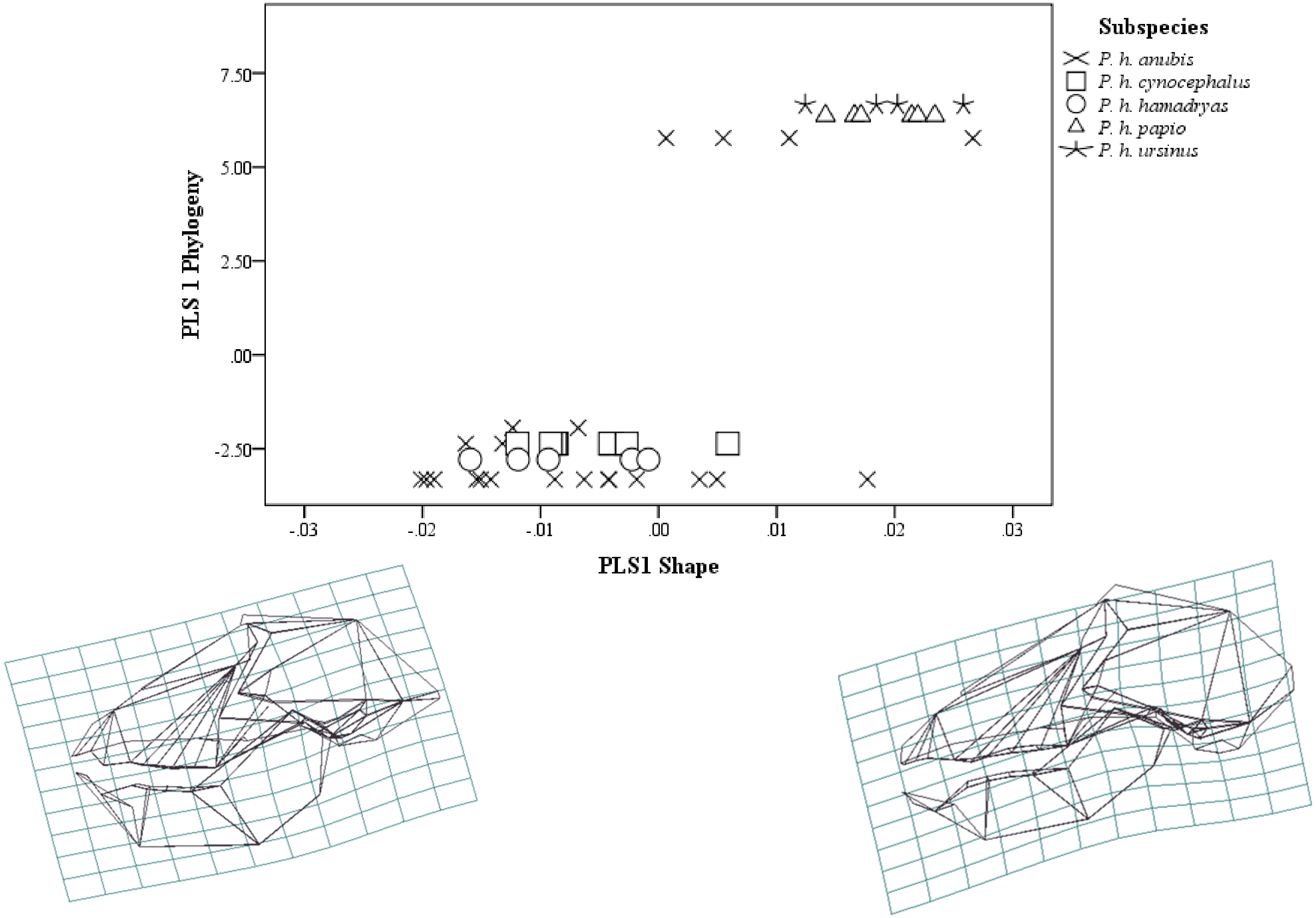


Figure 7.2. A scatter plot of scores for the first PLS between phylogeny and baboon shape. Wireframes show the morphological extremes of the axis of covariation (exaggerated by a factor of 3).

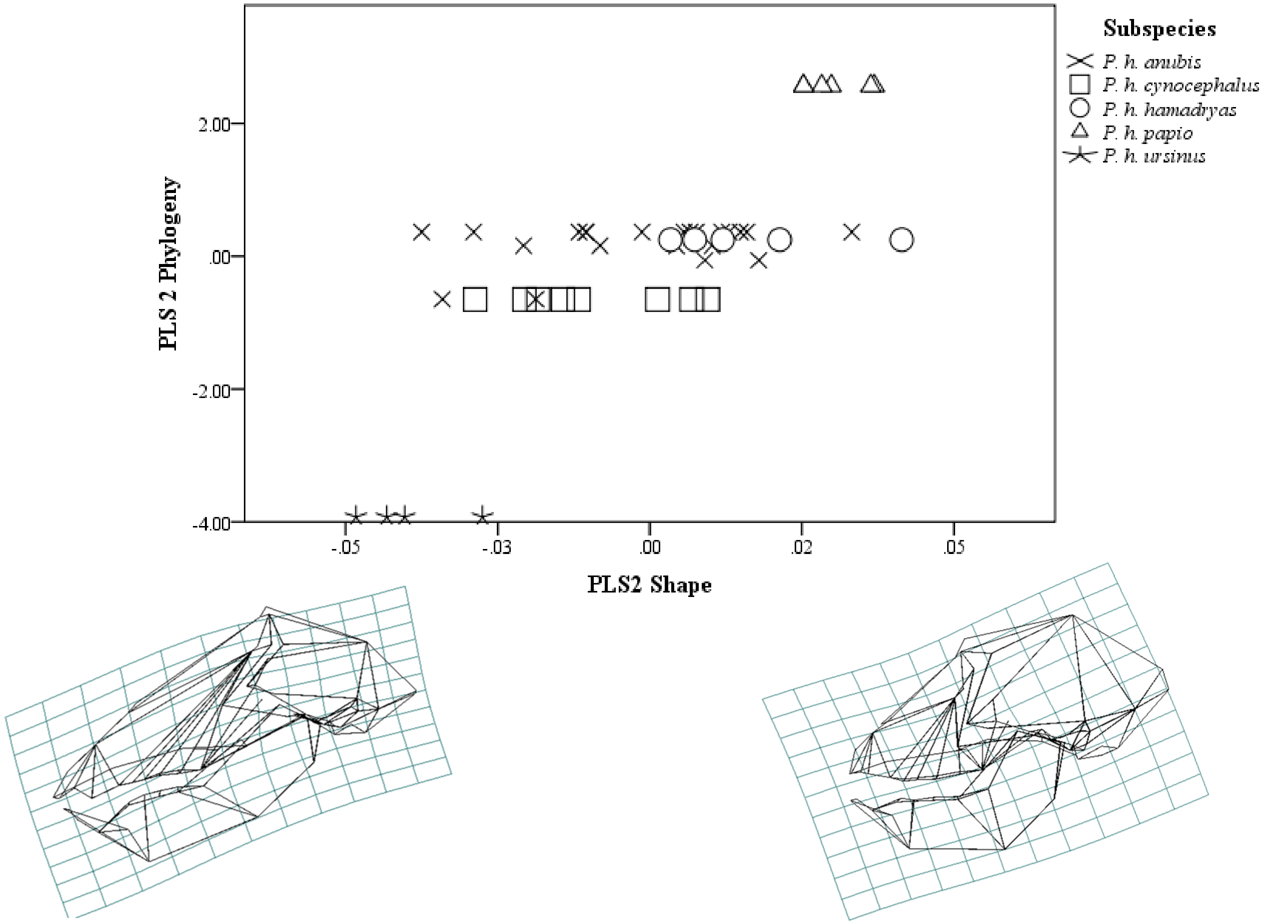


Figure 7.3. A scatter plot of PLS scores for the second PLS axis between phylogeny and baboon shape. Wireframes show the morphological extremes of the axis of covariation (exaggerated by a factor of 3)

The first PLS axis (69.3% of the total covariation) corresponds to the major split between the chacma-guinea-western olive clade and the yellow-eastern olive-hamadryas clade (fig. 5.2). This phylogenetic axis corresponds to a deep versus a shallow mandible and inferiorly versus superiorly deflected rostrum. The second PLS axis (21.3% covariation) separates the chacma from the guinea baboon while the remainder are intermediately scattered (fig. 5.3). This describes morphology largely relating to allometry, detectible from the neurocranium to facial size ratio.

5.3.2 The Phylogenetic Component of Baboon Size-Controlled Variation

Much of the shape variation is likely to be size-related (Chapter 2). To account for this the same analysis was carried out using allometry-controlled morphological shape (Chapter 2).

Table 7.2. Singular values and pairwise correlations of PLS scores between phylogenetic principal coordinates and allometry-controlled shape blocks. For the whole PLS RV = 0.2024, p < 0.0026. For morphological specimens, n = 41. Significant p values are shown in bold.

	Singular value	**% Total Covariance**	**Correlation**	**P-value**
PLS1	0.04335	76.466	0.75013	**0.0131**
PLS2	0.02057	17.217	0.78728	**<.0001**
PLS3	0.00892	3.242	0.61906	**0.184**
PLS4	0.0078	2.479	0.62284	**0.0131**
PLS5	0.00355	0.513	0.80127	**0.0015**
PLS6	0.00143	0.084	0.49159	0.1383

Allometric correction does not increase the correlation (RV = 0.2024) overall, though the first PLS axis accounts for more of the variation (table 5.2) than with full shape (table 5.1).

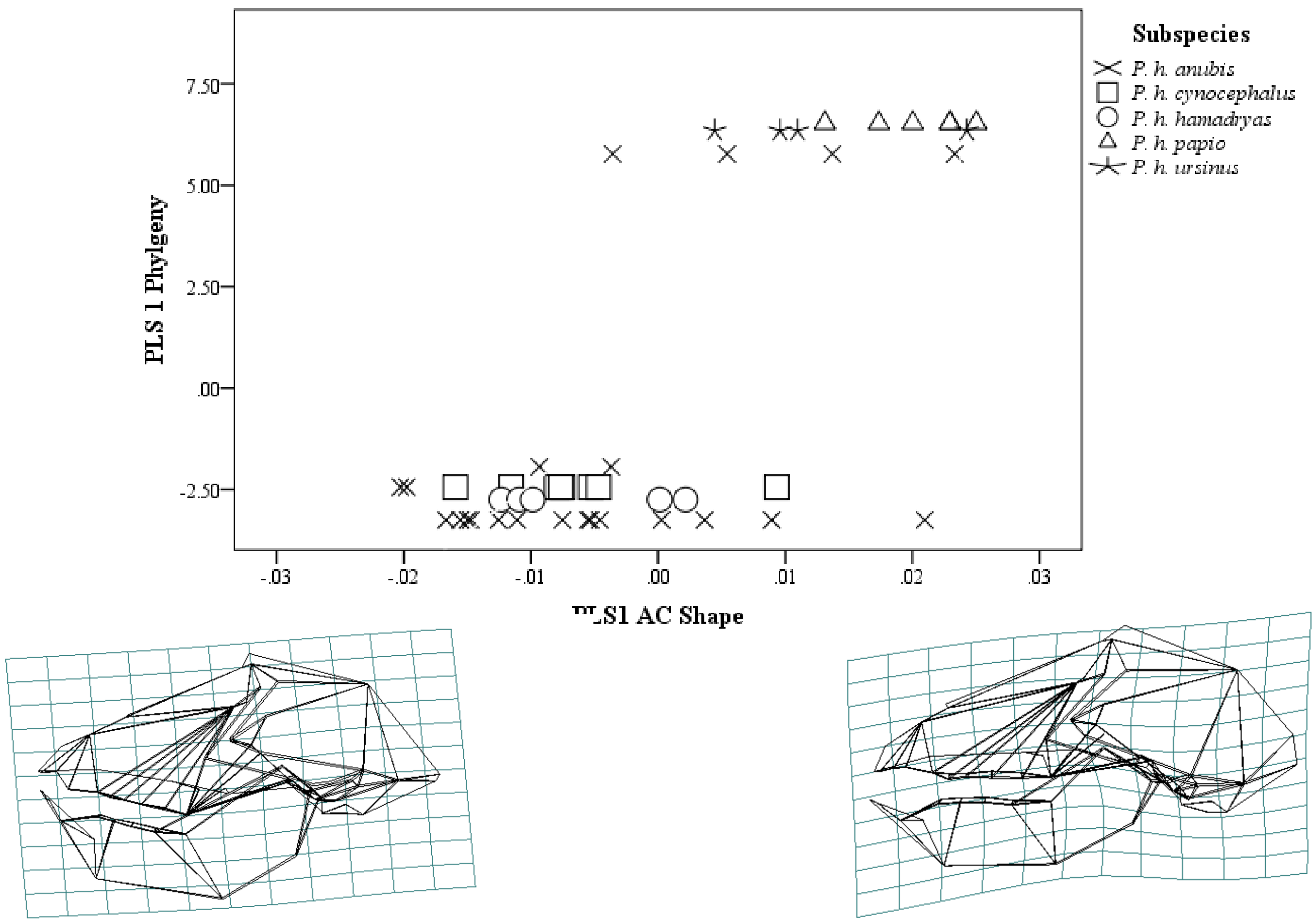


Figure 7.4. A scatter plot of PLS scores for the first PLS axis between phylogeny and size-controlled (SC) baboon shape. Wireframes show the morphological extremes of the axis of covariation (exaggerated by a factor of 3).

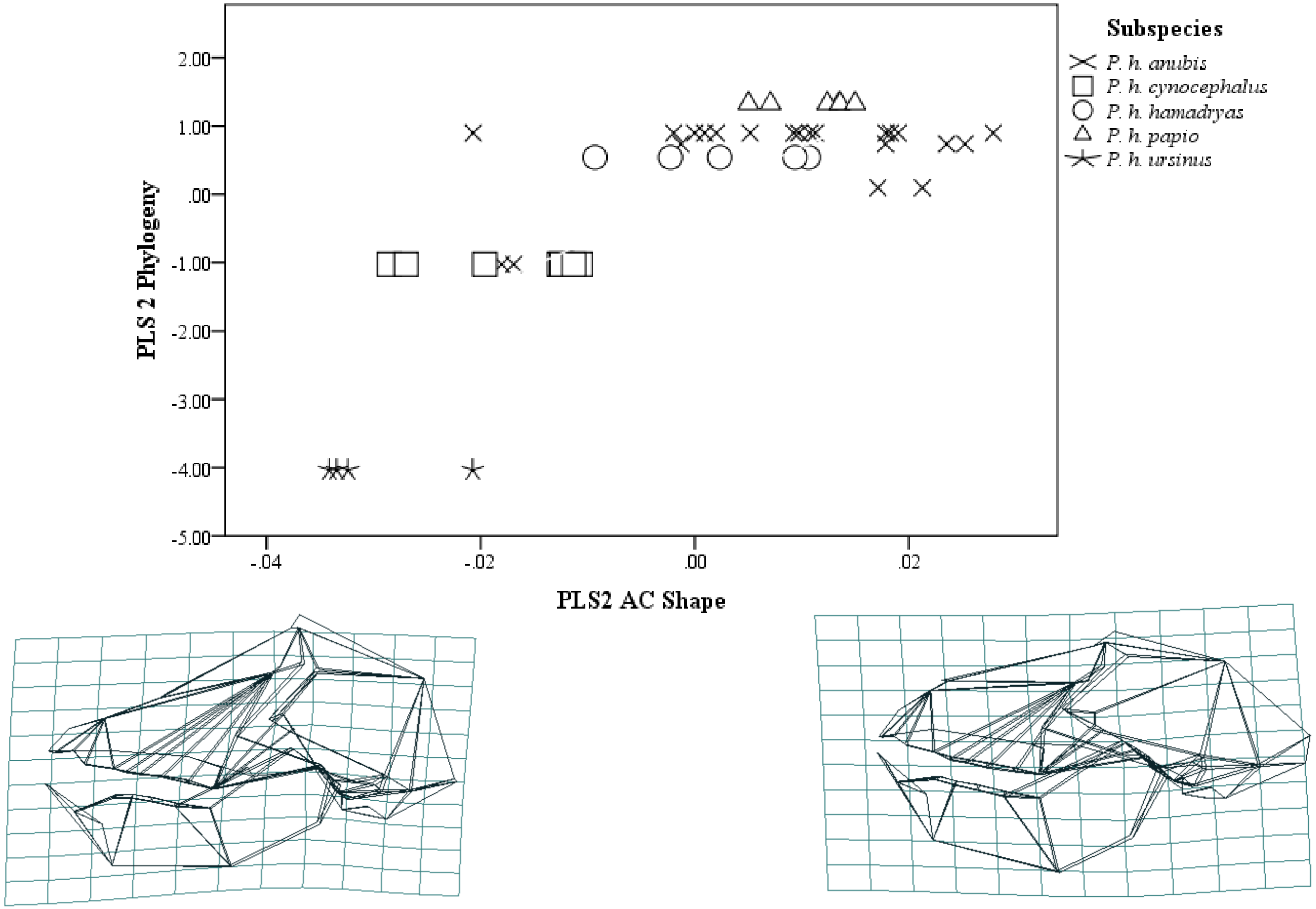


Figure 7.5. A scatter plot of PLS scores for the second PLS axis between phylogeny and size-controlled (SC) baboon shape. Wireframes show the morphological extremes of the axis of covariation (exaggerated by a factor of 3).

The first allometrically controlled PLS shows the same pattern of scatter (fig. 5.4) as the nonallometrically controlled PLS (fig. 5.2). The morphological extremes show the same pattern of downturned and shallow muzzle, and straight jaw for the chacma and yellow baboon versus the more curved mandible and slightly upturned morphology of the other subspecies. However, with size removed the two have broadly the same ratio of neurocranium to facial dimensions. The second allometry-controlled PLS, like the first, is hardly different in scatter but different in morphological extremes relating to face: neurocranium dimensions (fig. 5.5).

5.3.3 *P. h. cynocephalus*-Adjusted Phylogeny

This study uses the molecular phylogeny of Zinner et al. (2009) to quantify the correlation between phylogeny and morphology. However, recent introgression is likely to render the mtDNA used in that study less representative of true phylogeny, as under this system distinct populations can acquire the nuclear genetic information of another population and thus exhibit their morphological features. This is of particular concern with the northern yellow baboon which is phenotypically different from eastern olive baboon yet, shares a haplogroup as a result of past introgression. A phylogeny more representative of reality would unite these northern yellow baboons with southern yellows and chacma baboons on the “correct” side of the ancestral north-south split.

This study uses the phylogeny of Zinner et al. (2009) as well as an adjusted phylogeny where the yellow baboon is reallocated to a southern mitochondrial haplogroup as described. The correlations are compared to see if phylogenetic adjustment improves the correlation with shape.

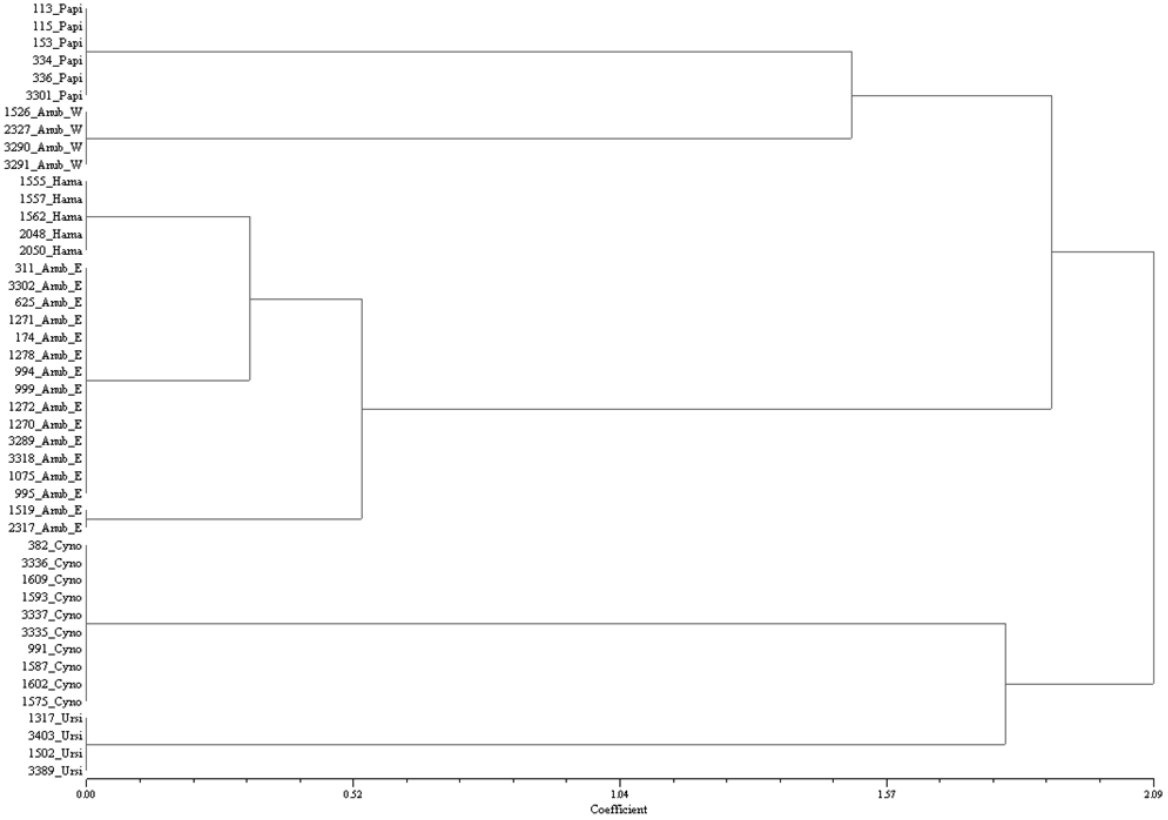


Figure 7.6. A phylogenetic cluster analysis of all 45 specimens used in the path analysis on the basis of haplogroup affiliation, with northern P. h. cynocephalus *given the distance values for the southern haplogroup. Phylogenetic distances between haplogroups were taken from Zinner et al. (2009b). Papi* = P. h. papio, *Anub_W* = *Western* P. h. anubis, *Hama* = P. h. hamadryas, *Anub_E* = *Eastern* P. h. anubis, *Cyno* = P. h. cynocephalus, *Ursi* = P. h. ursinus.

The reattribution of the yellow baboons to the southern population creates a split between northern and southern taxa (fig. 5.6).

Table 7.3. Singular values and pairwise correlations of PLS scores between P. h. cynocephalus adjusted phylogenetic principal coordinates and shape blocks. For the whole PLS RV = 0.2151, p = 0.0034. For morphological specimens, n = 41. Significant p values are shown in bold.

	Singular value	**% Total Covariation**	**Correlation**	**P-value**
PLS1	0.054617	66.921	0.76305	**0.0256**
PLS2	0.031833	22.734	0.73671	**0.0006**
PLS3	0.017668	7.003	0.62652	**0.0006**
PLS4	0.010832	2.632	0.75571	**0.0069**
PLS5	0.004749	0.506	0.76429	**0.0046**
PLS6	0.003018	0.204	0.65118	0.0522

The PLS between shape and *P. h. cynocephalus adjusted* phylogeny (as shown in fig. 5.6) is significant (table 3, p = 0.0034) overall and for all but the last PLS axis. The overall RV correlation is 0.2151 which is only slightly higher than the 0.2024 value for the nonadjusted phylogeny. The first two axes account for 89% of the covariation and only these are visualised.

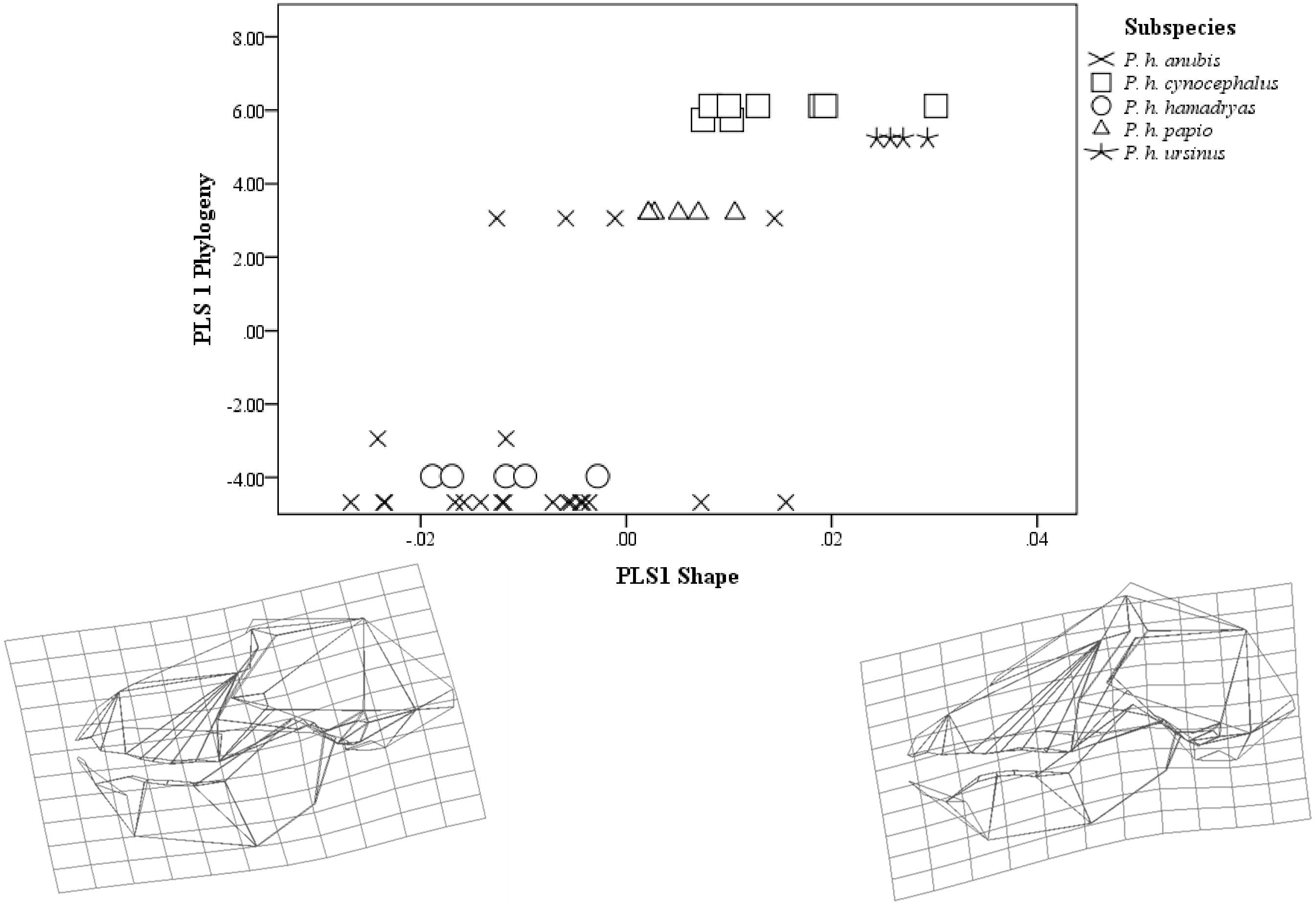


Figure 7.7. A scatter plot of PLS scores for the first PLS axis between P. h. cynocephalus *adjusted phylogeny and baboon shape. Wireframes show the morphological extremes of the axis of covariation (exaggerated by a factor of 3).*

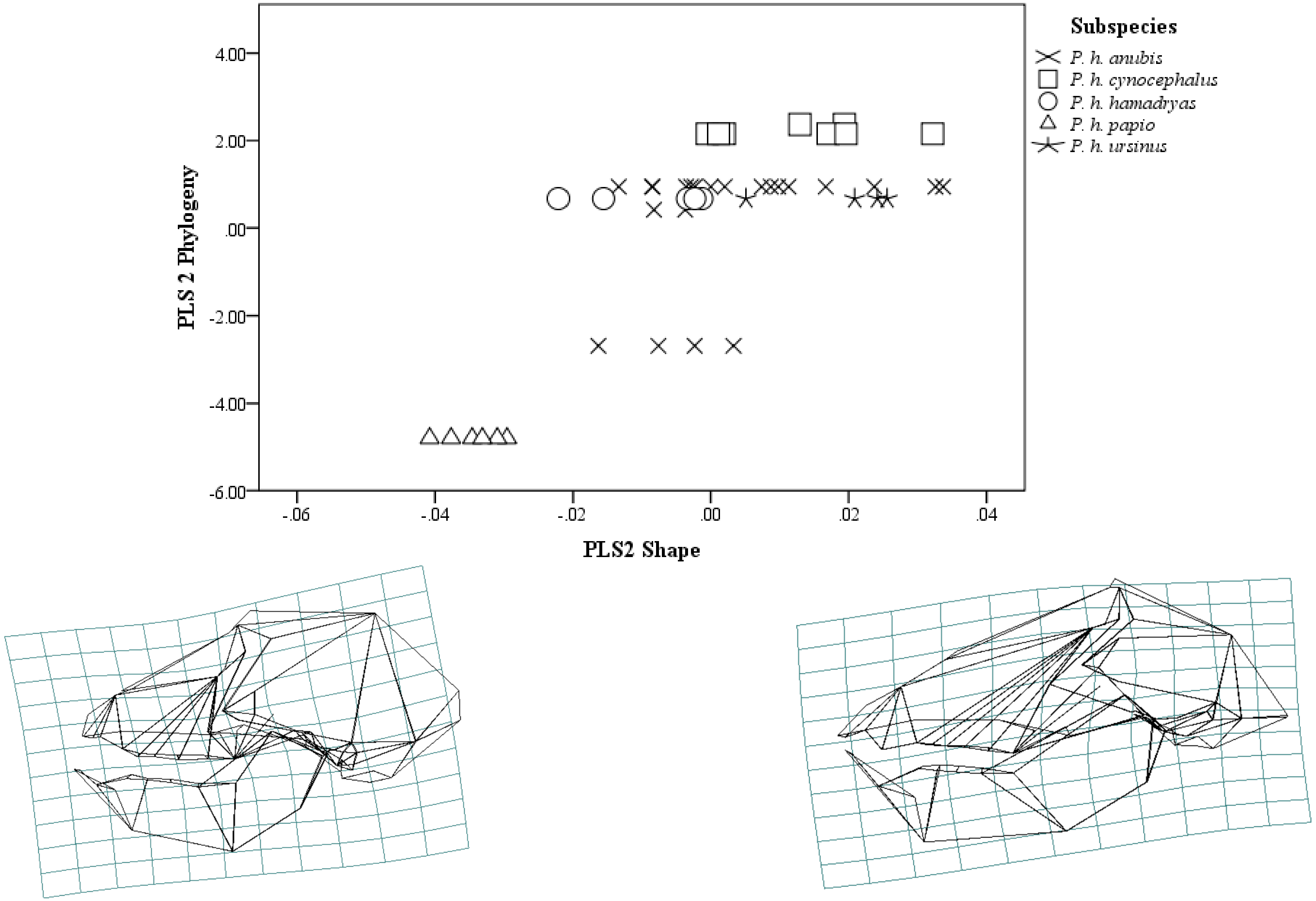


Figure 7.8. A scatter plot of PLS scores for the second PLS axis between P. h. cynocephalus *adjusted phylogeny and baboon shape. Wireframes show the morphological extremes of the axis of covariation (exaggerated by a factor of 3).*

Adjusting the phylogenetic position of *P. h. cynocephalus* results in a clustering of that taxon with *P. h. ursinus*, corresponding to a morphology with a high glabella, downturned rostrum and more gracile jaw, while the hamadryas and most of the *P. h. anubis* exhibit a deep mandible, short skull and deeper non-flexed rostrum (fig. 5.7). *P. h. papio* is intermediately positioned on this axis. While *P. h. anubis* is clustered at the left extreme it is well distributed across the board. This pattern is similar to the nonadjusted phylogeny except for the position of the *P. h. cynocephalus,* however the correlation is slightly higher.

The second axis differentiates *P. h. papio* with features associated with small size such as a relatively larger neurocranium and smaller rostrum but also a flexed up rostrum and curved mandible (fig. 5.8). The other have a straighter mandible and a higher glabella, as well as size associated features.

5.3.4 Size-Controlled *P. h. cynocephalus* Adjusted Phylogeny

As with the nonadjusted phylogeny the adjusted phylogeny is subject to the influence of size related shape (Chapter 2). In the following analyses this is controlled.

Table 7.4. Singular values and pairwise correlations of PLS scores between P. h. cynocephalus adjusted phylogenetic principal coordinates and size-controlled shape blocks. For the whole PLS RV = 0.2309, p = 0.0006. For morphological specimens, n = 41. Significant p values are shown in bold.

	Singular value	**% Total Covariance**	**Correlation**	**P-value**
PLS1	0.04924	71.478	0.71164	**0.0053**
PLS2	0.0279	22.96	0.77891	**0.0001**
PLS3	0.01041	3.196	0.58117	0.1598
PLS4	0.00767	1.732	0.67569	0.0579
PLS5	0.00385	0.437	0.69988	**0.0056**
PLS6	0.00259	0.197	0.47791	**0.0078**

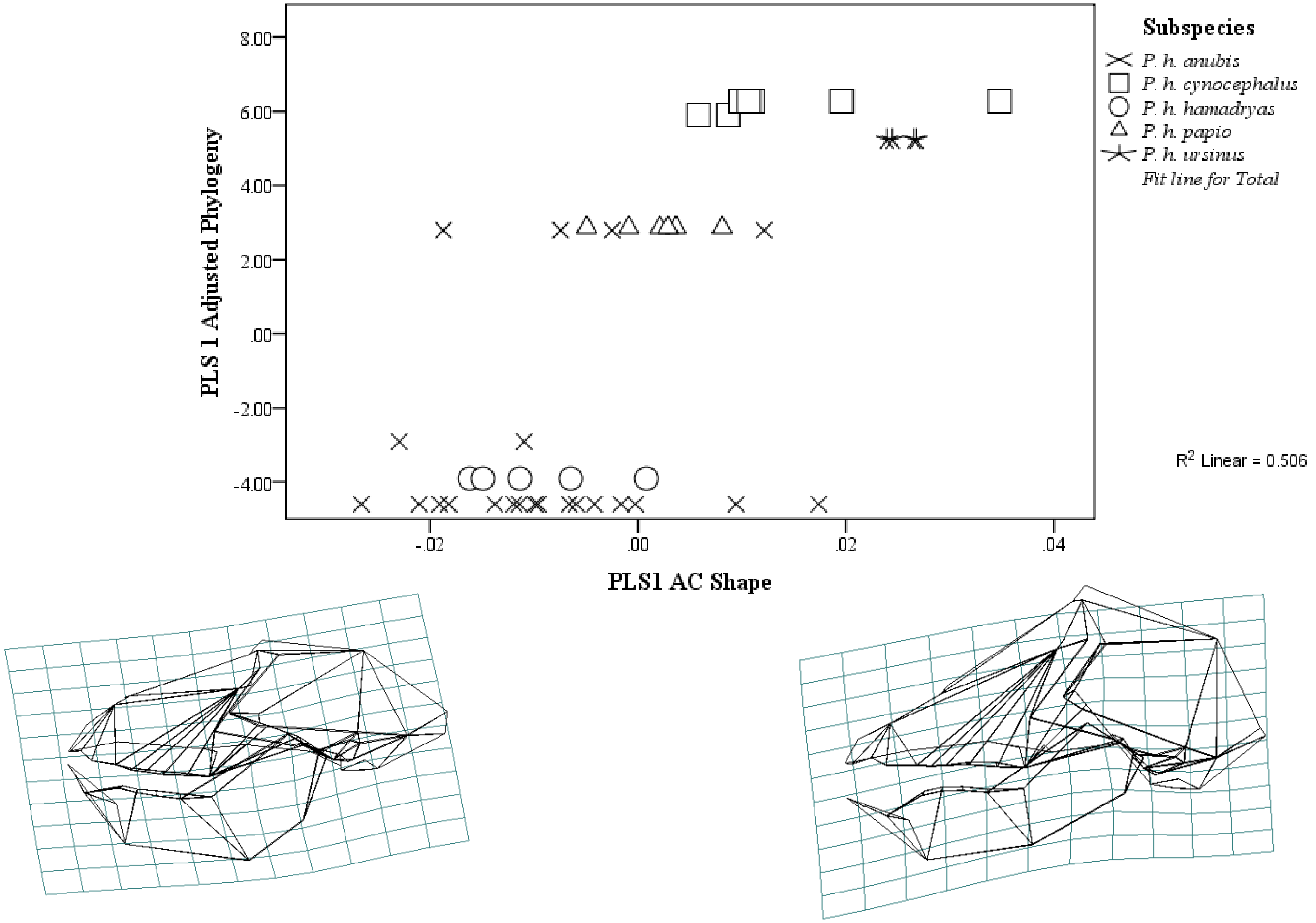


Figure 7.9. A scatter plot of PLS scores for the first PLS axis between P. h. cynocephalus *adjusted phylogeny and size-controlled baboon shape. Wireframes show the morphological extremes of the axis of covariation (exaggerated by a factor of 3).*

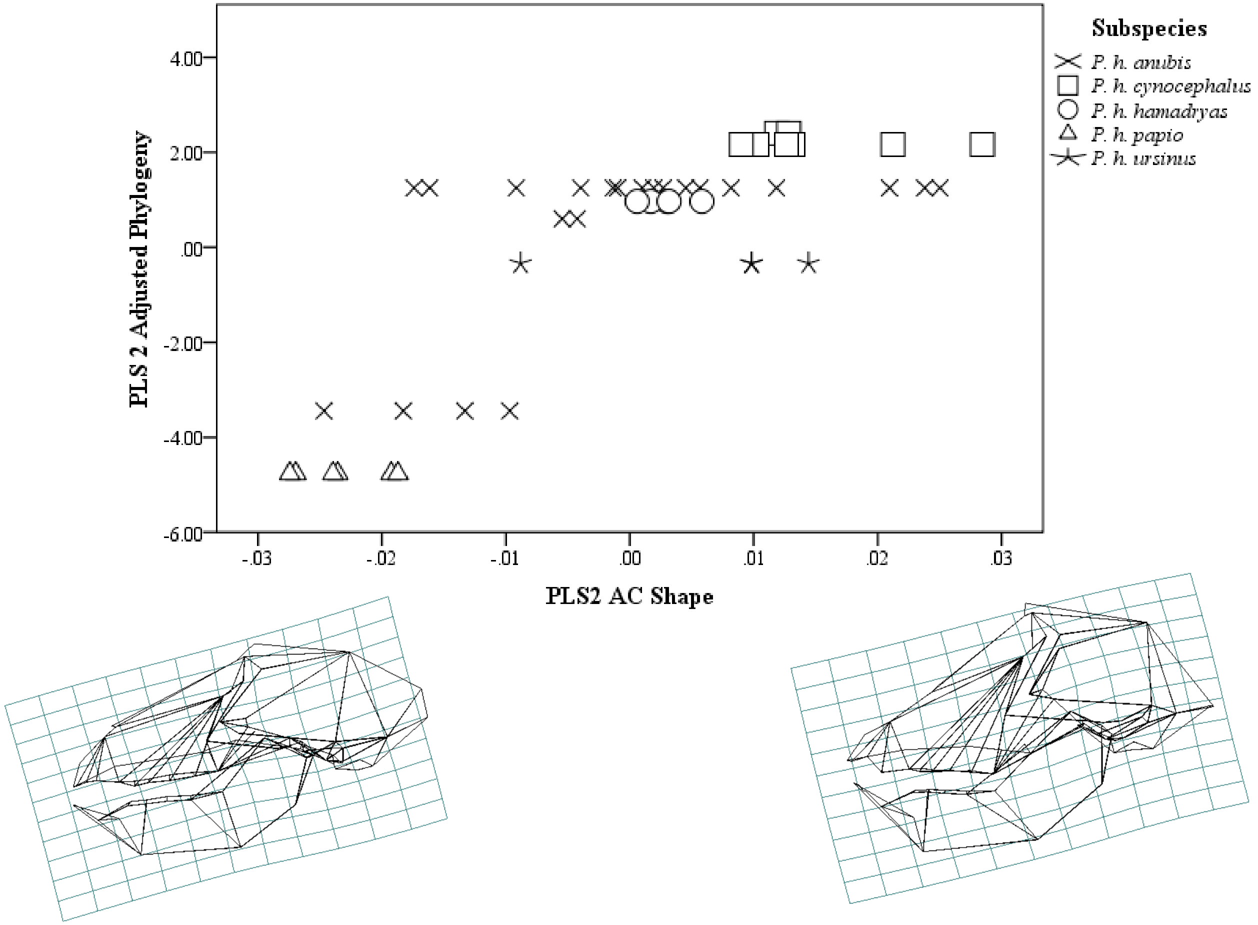


Figure 7.10. A scatter plot of PLS scores for the second PLS axis between P. h. cynocephalus *adjusted phylogeny and size-controlled baboon shape. Wireframes show the morphological extremes of the axis of covariation (exaggerated by a factor of 3).*

Removal of size-related shape variation from the *P. h. cynocephalus* phylogeny results in the highest correlation of all at RV = 0.2309, although this is only marginally higher than the others. Again, allometric control does not alter the scatter of data significantly nor the morphological extremes save by reducing the effect of those factors related to allometry such as face to neurocranial dimensions.

5.3.5 Taxon as a Baboon Phylogenetic Proxy

In the absence of phylogenetic data for vervets taxon will be used as a crude phylogenetic proxy. In order to see how useful a proxy this is, taxon is also used as a morphological covariate for baboons.

Table 7.5. Singular values and pairwise correlations of PLS scores between baboon taxon and shape. For the whole PLS RV = 0.3637, p < 0.0011. For morphological specimens, n = 45. Significant p values are shown in bold.

	Singular value	% Total Covariance	Correlation	P-value
PLS1	0.008259	51.719	0.77551	**0.0012**
PLS2	0.006016	27.442	0.74052	**<0.0001**
PLS3	0.003966	11.928	0.77706	**0.0003**
PLS4	0.003428	8.912	0.77476	**<0.0001**

Taxon correlates more highly with shape than phylogeny (table 5.5). All PLS axes are significant with the first accounting for more than half of the variation. The major axis of shape-taxon covariation is between the olive baboon and the other taxa (fig. 5.11). However, the olive baboon has such a broad spread that it overlaps extensively with the other taxa. The second axis partitions the northern and southern taxa, again with *P. h. anubis* showing extensive spread between these (fig. 5.12).

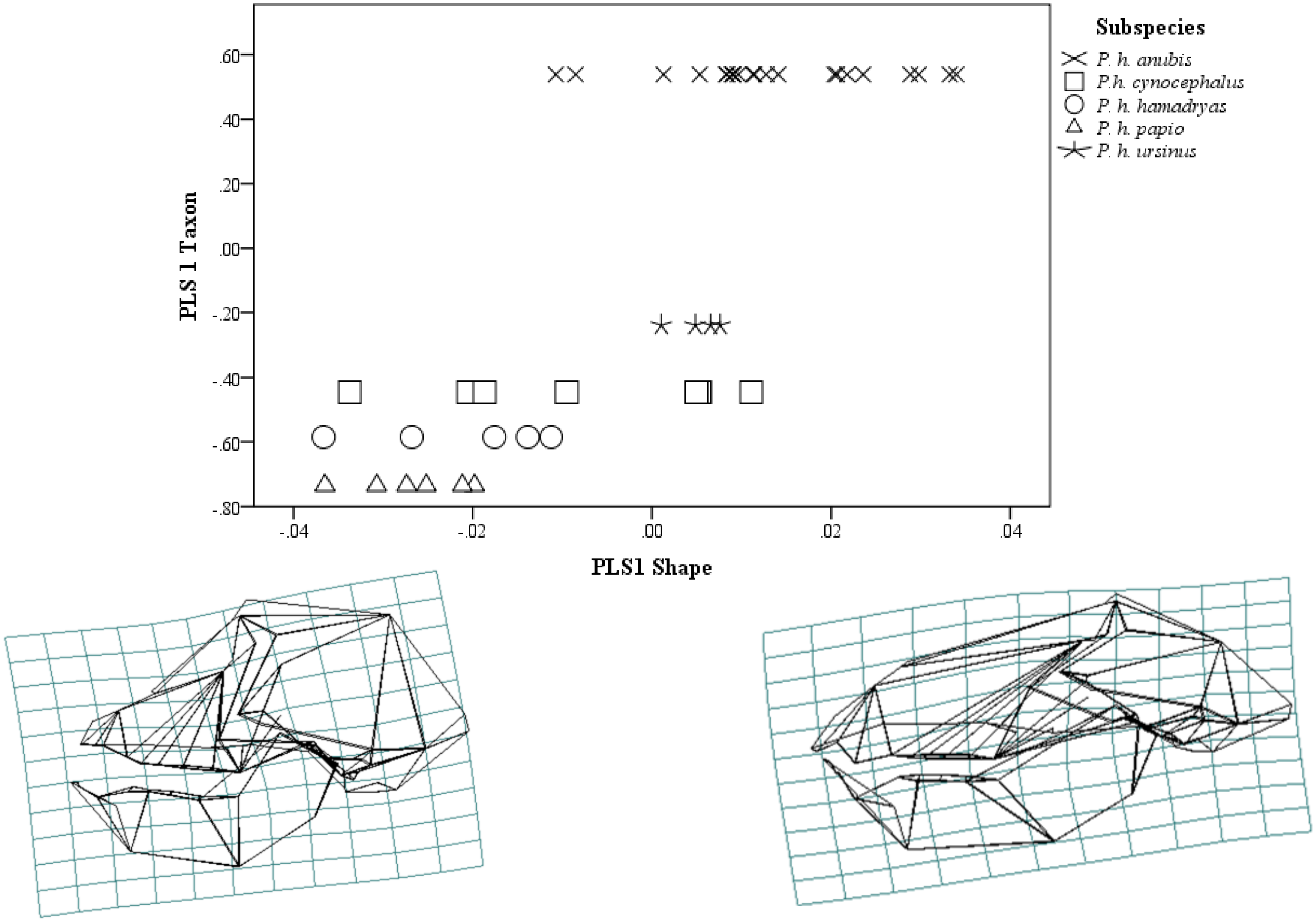


Figure 7.11. A scatter plot of scores for the first PLS between taxon and baboon shape. Wireframes show the morphological extremes of the axis of covariation (exaggerated by a factor of 3)

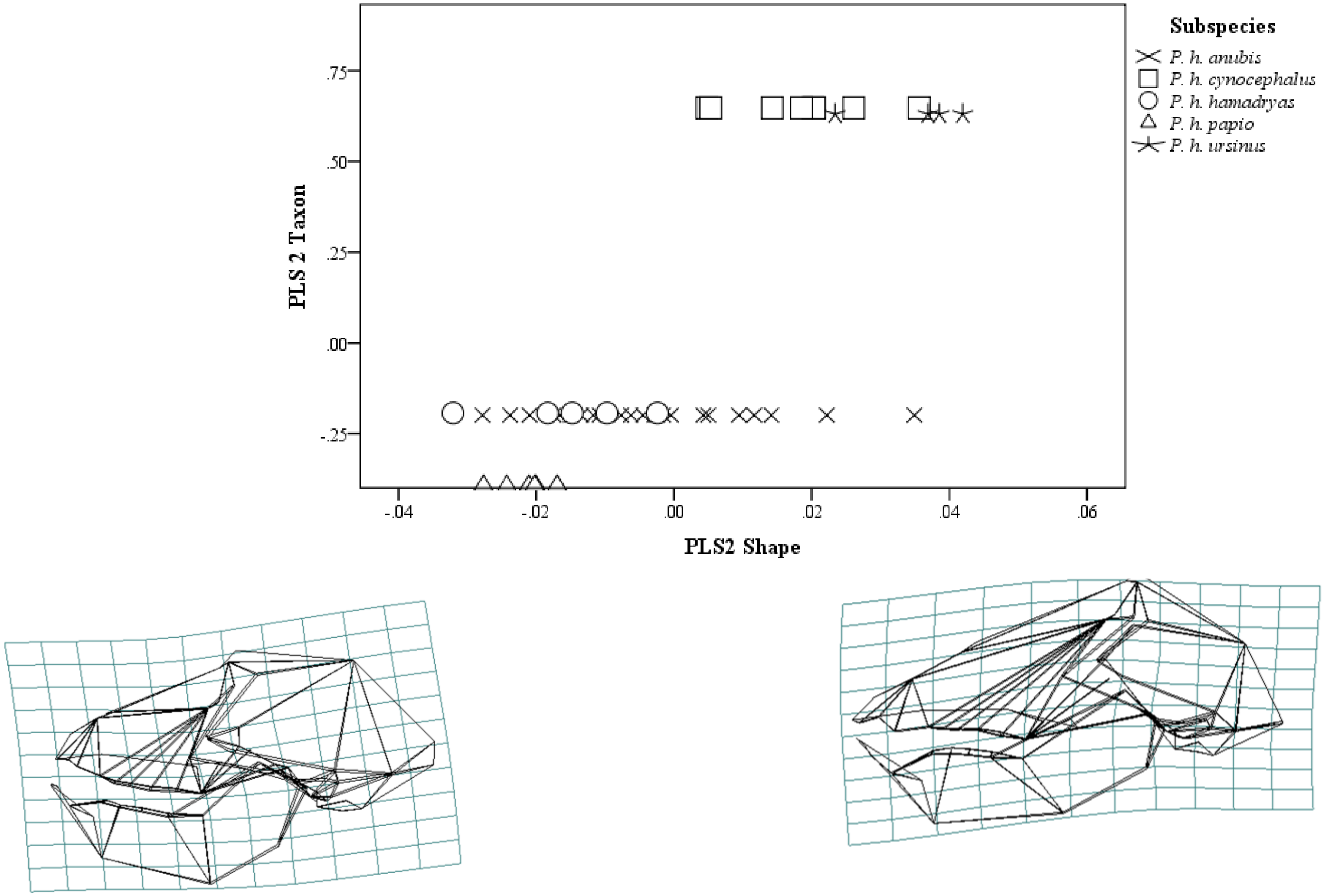


Figure 7.12. A scatter plot of scores for the second PLS between taxon and baboon shape. Wireframes show the morphological extremes of the axis of covariation (exaggerated by a factor of 3).

5.3.6 Taxon as a Vervet Phylogenetic Proxy

In the absence of molecular phylogenetic data for vervets taxon will be used as a crude phylogenetic proxy. A PLS of shape and taxon dummy was carried out.

Table 7.6. Singular values and pairwise correlations of PLS scores between the taxon and shape blocks. For the whole PLS RV = 0.2940, p < 0.0011. For morphological specimens, n = 41. Significant p values are shown in bold.

	Singular value	**% Total Covariance**	**Correlation**	**P-value**
PLS1	0.009493	63.09	0.69322	**0.0055**
PLS2	0.005426	20.61	0.82978	**0.0063**
PLS3	0.003597	9.06	0.80082	0.1701
PLS4	0.003216	7.24	0.65979	**0.0296**

The PLS between shape and taxon is significant (table 6.6, p = 0.0011) overall and for three of the four PLS axes. The first and second PLS together account for most (83.7%) of the variance.

Most of the variance in the first PLS is taken up by the divide betweeen *C. a. sabaeus* and the other subspecies (fig. 5.13). However, there is incomplete separation between the morphologies of *C. a. sabaeus* and the others, although the former tends to have a longer rostrum and smaller braincase relative to the others which tend towards flatter faces, gracile jaws and large neurocrania.

The second axis differentiates *C. a. pygerythrus* from the others with *C. a. sabaus* occupying a middling position (fig. 5.14). The morphological axis is similar in that *C. a. pygerythrus* has a protruding jaw, like *C. a. sabaus*. However it has a less anteriorly protruding mandble. Also, in this instance *C. a. pygerythrus* has the gracile mandible, while those of the other taxa, *C. a. aethiops* in particular, are much deeper.

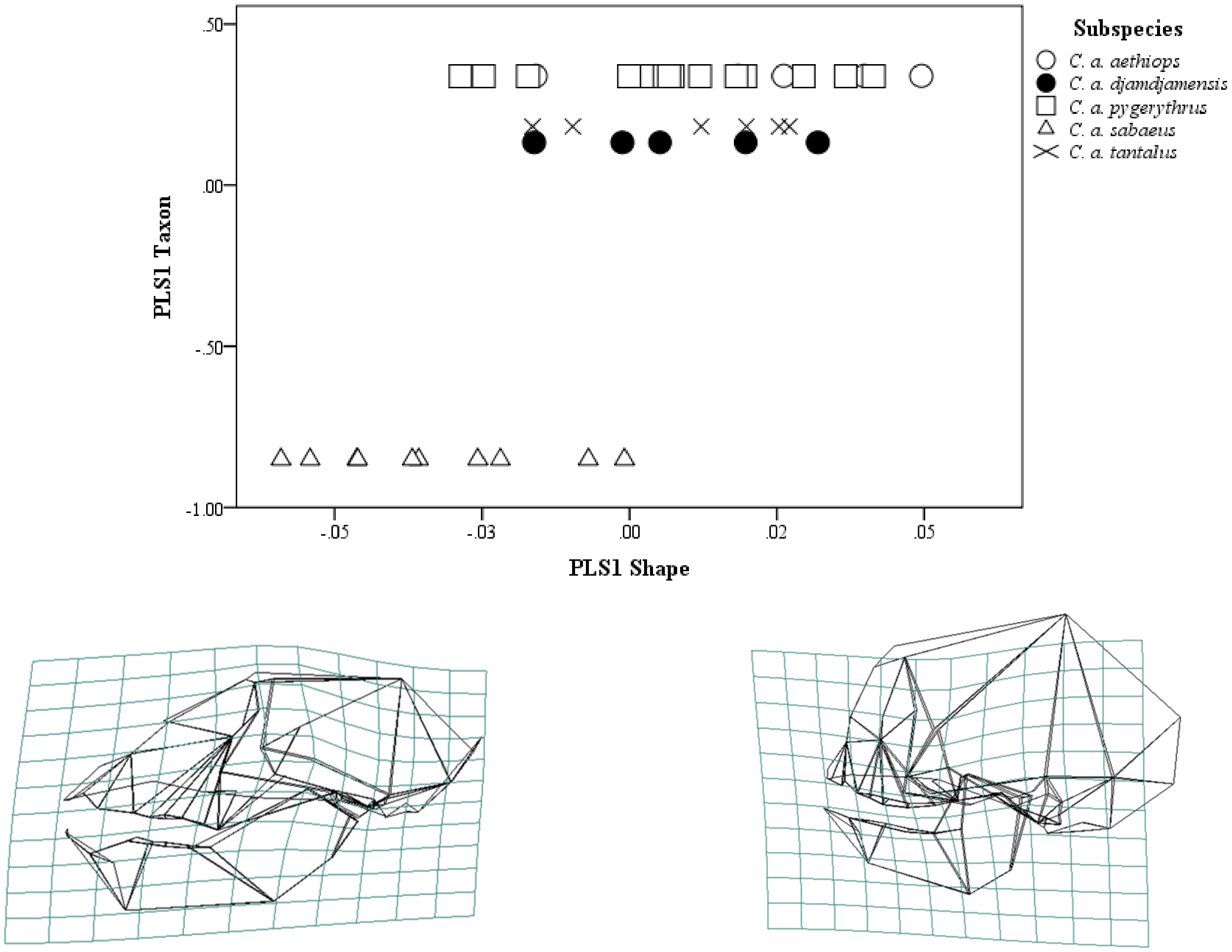


Figure 7.13. A scatter plot of scores for the first PLS between taxon and vervet shape. Wireframes show the morphological extremes of the axis of covariation (exaggerated by a factor of 3).

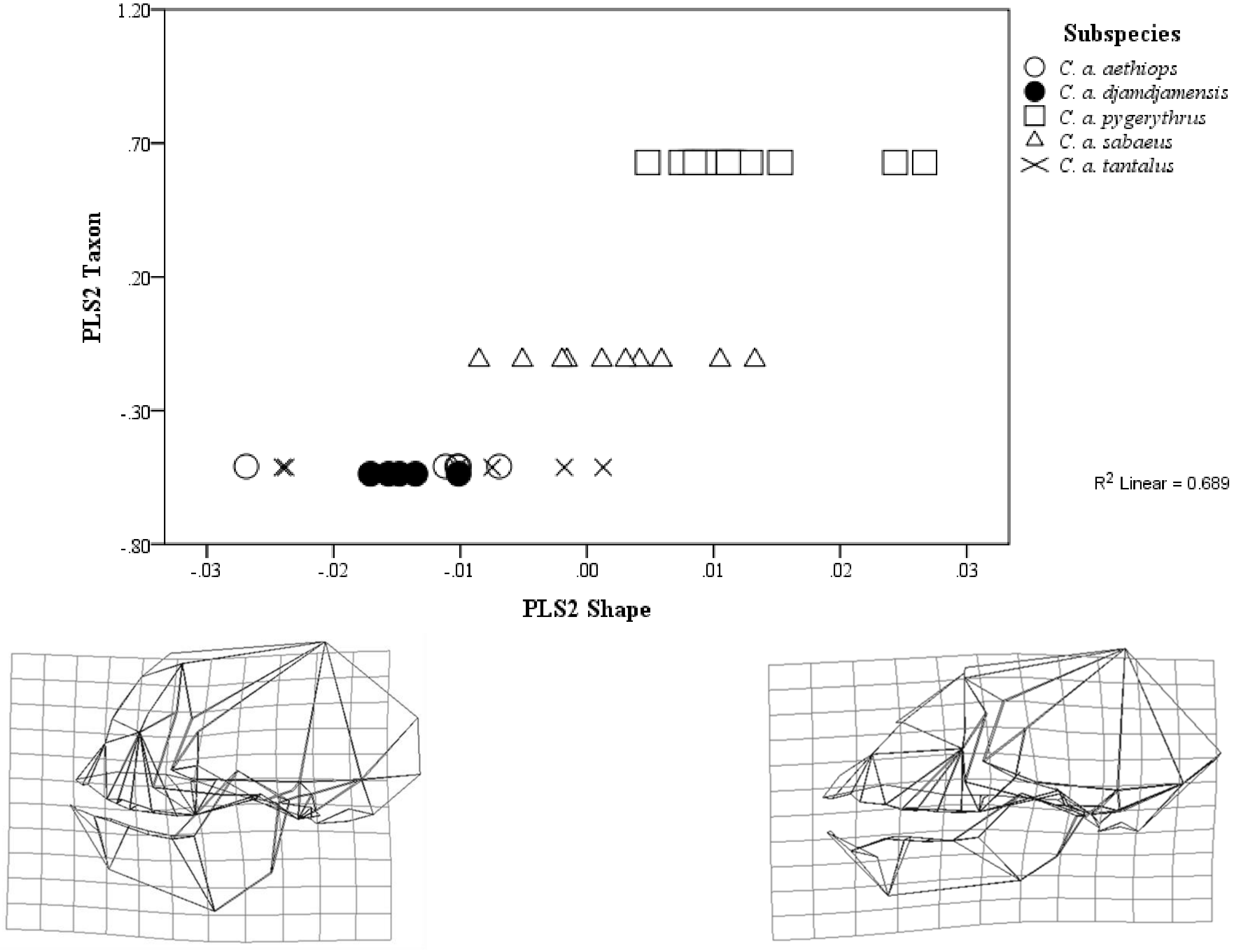


Figure 7.14. A scatter plot of scores for the second PLS between vervet taxon and vervet shape. Wireframes show the morphological extremes of the axis of covariation (exaggerated by a factor of 3).

5.3.7 Size-Controlled Taxon Analysis

Much of the shape variation is likely to be size-related (Chapter 2). To account for this the same analysis was carried out using allometrically controlled morphological shape.

Table 7.7. Singular values and pairwise correlations of PLS scores between vervet taxon and size-controlled shape blocks. For the whole PLS RV = 0.2600, p = 0.0016. For morphological specimens, n = 41. Significant p values are shown in bold.

	Singular value	**% Total Covariation**	**Correlation**	**P-value**
PLS1	0.008043	61.849	0.70247	**0.0095**
PLS2	0.004697	21.088	0.67742	**0.0078**
PLS3	0.003168	9.593	0.56188	**0.0433**
PLS4	0.002795	7.47	0.68655	**0.0027**

Size-controlled shape has a lower correlation with taxon suggesting allometric scaling is not part of the differentiation between subspecies (table 5.7). The PLS between allometry controlled shape and taxon does not result in a different pattern in the taxa but does increase the spread (figs. 5.15 & 5.16), demonstrating that size-variation is not a part of subspecific variation.

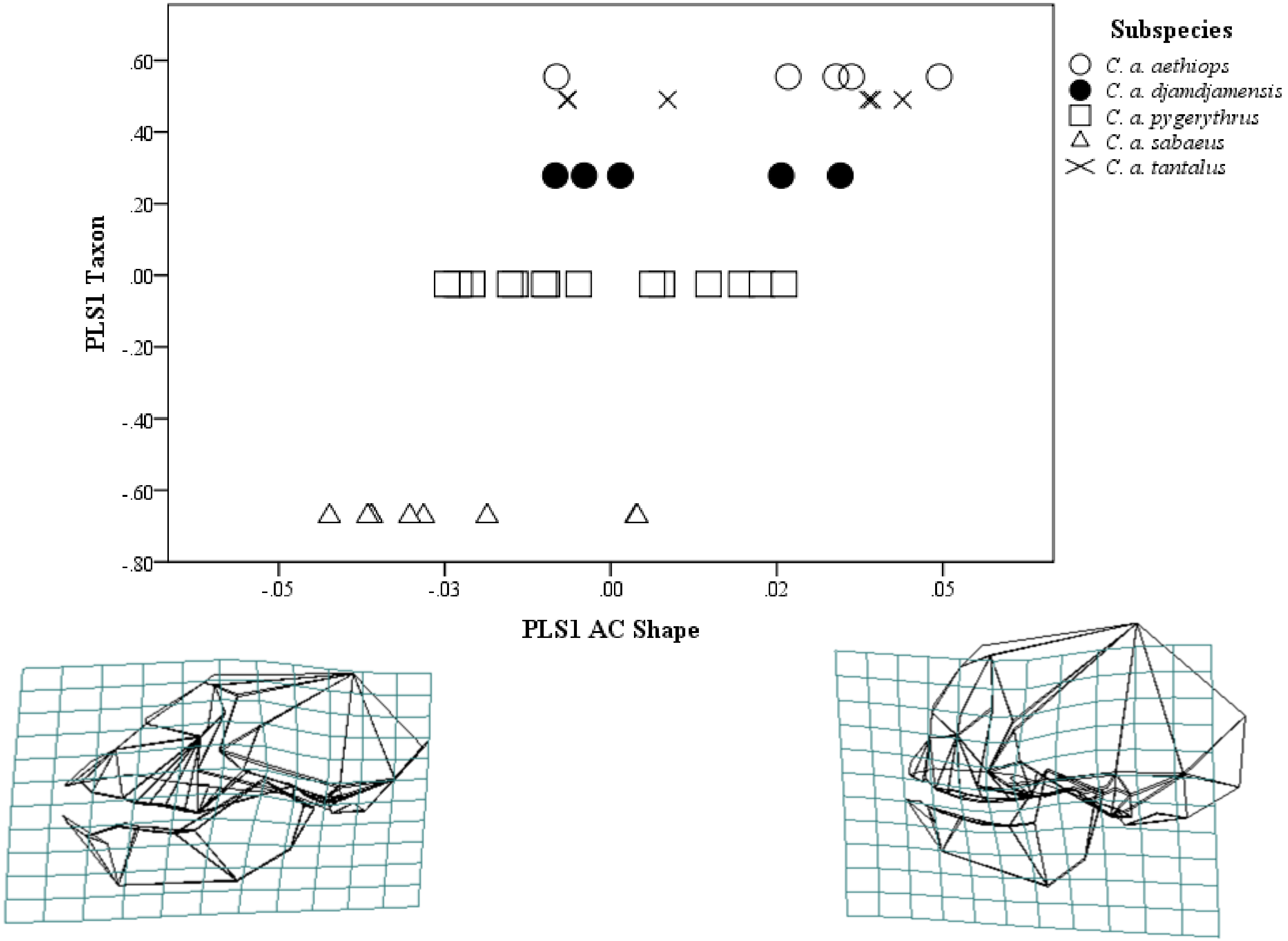


Figure 7.15. A scatter plot of scores for the first PLS between vervet taxon and size-controlled shape. Wireframes show the morphological extremes of the axis of covariation (exaggerated by a factor of 3)

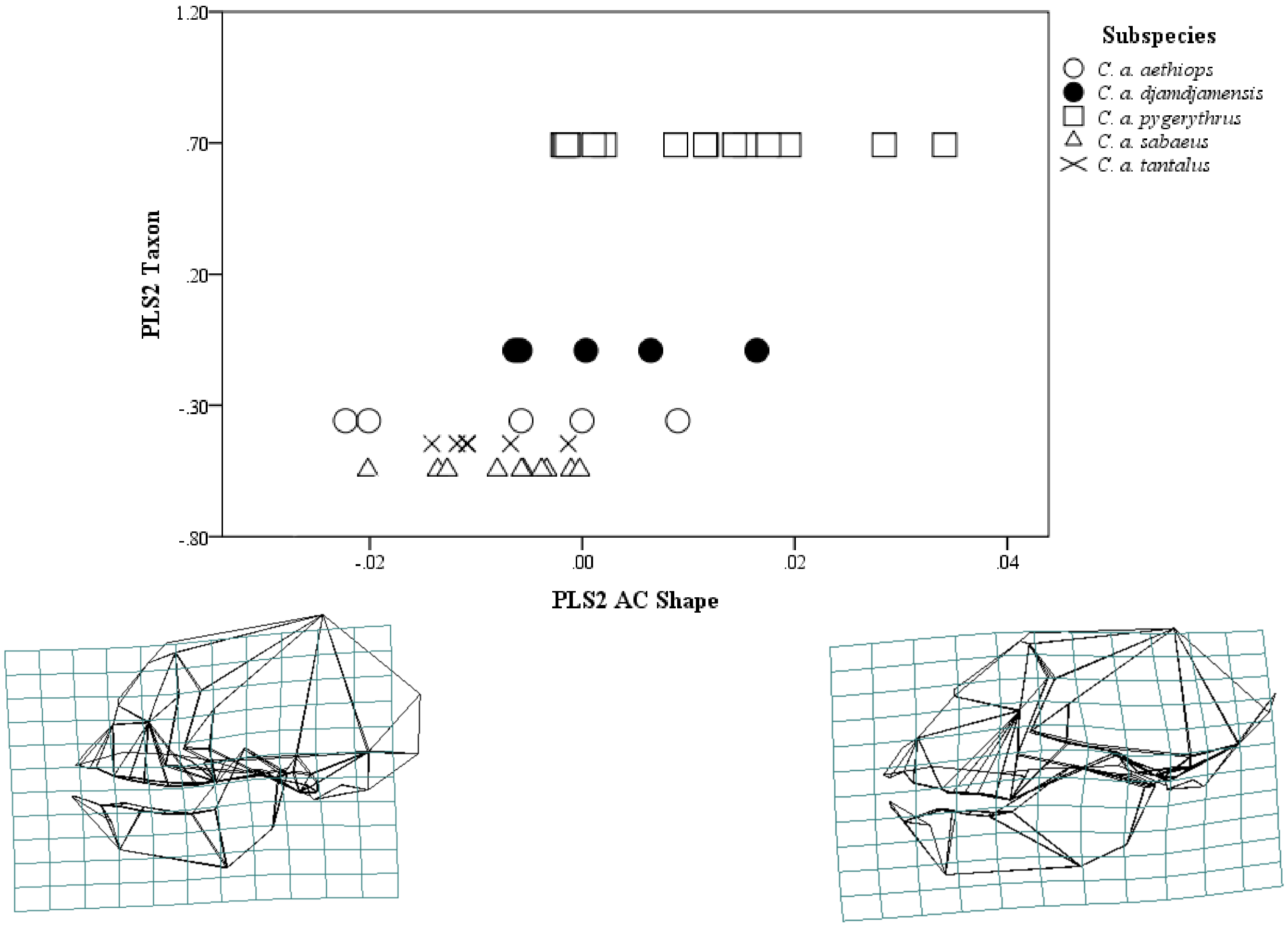


Figure 7.16. A scatter plot of scores for the first PLS between vervet taxon and size-controlled shape. Wireframes show the morphological extremes of the axis of covariation (exaggerated by a factor of 3)

5.4 DISCUSSION

5.4.1 Comparison of the Phylogenetic Structuring of the Vervet and Baboon

The baboon phylogeny used here is based on mtDNA and is thus less than ideal for quantifying the effect of phylogenetic relatedness in morphology, as morphology is coded for by nuclear DNA, which has a different mechanism and thus pattern of inheritance. However, an attempt has been made to reduce the error in using these data by creating an adjusted phylogeny where the northern yellow baboon population is reallocated to a group more likely to reflect its actual relatedness. This increases the effect of the phylogenetic signal as expected. It is likely however that there are discordances that we have not corrected for suggesting the true phylogenetic signal would be higher still. However, for testing the hypothesis of no differences between vervet and baboon signals the relative difference is of interest, and provided both signals are underestimated in to roughly the same degree conclusions can be made.

In the absence of a phylogeny for the vervets, taxon, a dummy variable describing subspecific affiliation, was used as a proxy. The quality of taxon as phylogenetic information was assessed by carrying out the taxon-shape partial least squares for baboons, and comparing it with the phylogeny-shape partial least squares. A markedly higher correlation was found between taxon and shape (RV = 0.3637) than between phylogeny and shape (0.2024 and 0.2125 for the unadjusted and adjusted phylogenies respectively) for baboons. If baboons are representative, this suggests that for vervets taxon may overestimate the phylogenetic signal. The shape-taxon RV value of 0.2940 is thus likely to be higher than the true phylogenetic-shape correlation. This value is lower than for baboons, suggesting that taxon and hence phylogeny is of lesser importance in describing the morphological divergence of vervet subspecies. Obviously, without an accurate phylogeny this cannot be stated for certain, but it seems likely that the vervet would be similar to the baboon in the relationship between taxon and phylogeny.

Thus while there is some uncertainty surrounding the reliability of the baboon phylogeny and the phylogenetic proxy for vervets, it seems clear that there is a higher phylogenetic signal in baboons than vervets. This is unexpected given initial predictions, which posited that vervets were less able to disperse, owing to smaller size (Bowman et al., 2002). Indeed observations recorded vervets as being unable to cross certain terrain types such as cultivated or very rocky ground (Shimada et al., 2002). It was predicted therefore that vervets would exhibit reduced gene flux in the present relative to baboons, and also in the Pleistocene when environmental constrictions that are proposed to have caused divergence in baboons (Zinner et al., 2009b) would have acted more strongly on vervets. One interpretation of this is that vervets do actually disperse more widely than baboons reducing the capacity for local differentiation. Certainly studies in different populations of *C. a. pygerythrus* suggested they were markedly similar between environments (Grobler and Matlala, 2002). However, given that this study looked within subspecies rather than between subspecies this is highly limited evidence. Indeed, between subspecies gene flow is high at a number of hybrid zones in baboons, such as the Awash between olive and hamadryas baboons (Nagel, 1973, Phillips-Conroy and Jolly, 1981) and at Amboseli between yellow and anubis baboons (Samuels and Altmann, 1986). While a hybrid zone at Lake Victoria between *C. a. pygerythrus* and *C. a. tantalus* has been reported from field observations for vervets (Kingdon, 1997) and at other borders (Grubb et al., 2003) detailed information has not been published, and the greater extent of hybridisation and gene flow between vervet subspecies remains unknown.

There appears to be little evidence to support greater gene flow in vervets than baboons as an explanation for the higher phylogenetic signal. An explanation for the low shape-taxon covariation may lie in differences in the timing and pattern of divergence between the two species. This study, found that *C. a. sabaeus* is the most different when shape and taxon are correlated. Indeed, the first PLS axis corresponding to the major difference between *C. a. sabaeus* and the other subspecies is higher at 63.1%, than the first PLS axis in the baboon (51%). Thus *C. a. sabaeus* are more divergent from the other subspecies than any of the baboon subspecies are from each other. This finding resounds with the provisional results of Hauser (personal communication) who found evidence of higher genetic variation in West Africa, the region to which *C. a. sabaeus* is endemic, as well as a basally divergent phylogenetic position for this taxon. This finding was also made by van der Kuyl et al. (1995). This is also concordant with the suggestion of Elton (2007) for a non-southern African origin. The timing of the origin of subspecific variation is difficult to establish as the fossil record is poor for guenons (Frost and Alemseged, 2007, Leakey, 1988). While a recent fossil of *C. aethiops* was found in Ethiopia dating from 0.5 Mya this yields little information about vervet origins and radiations. Genetic evidence from a study by Shimada et al. (2002) found subspecific divergence to be within the range of range of 1.6 – 0.4 Ma. However, this range is both broad, and owing to the study's omission of *C. a. sabaeus,* which appears to be the most basally divergent, unrepresentative.

Aside from genetic evidence, biogeography implies a vervet radiation from West Africa into East Africa and more recently southern Africa. This is apparent by observing subspecific ranges. *C. a. pygerythrus* is found from East Africa to the cape in South Africa. Baboons in the same environment are separated into an East African taxon, the yellow baboon, and a southern African taxon, the chacma, the Kinda baboon existing in Zambia between the two. The fact that the vervets have not undergone a comparable division, when they must certainly have been subject to the same isolating mechanisms as baboon, argues for a more recent colonisation of this environment, again in keeping with Elton (2007) and Hauser (personal communication). Indeed, yellow baboons are probably more recently found in East Africa given the fact that the oldest split is between the northern and southern taxa. The hybridization between olive and yellow baboons produces intermediate forms with most aberrant features such as supernumary teeth (Ackermann et al., 2006), suggesting a greater incompatibility of genomes than at other hybrid zones such as the Awash (Nagel, 1973, Phillips-Conroy and Jolly, 1981, Phillips-Conroy et al., 1991), Amboseli (Samuels and Altmann, 1986, Alberts and Altmann, 2001) or Kafue (Jolly et al., 2011).

Drift and divergence, which often follow a phylogenetic pattern, require time to accumulate. A more recent vervet colonisation of southern Africa is likely to give vervets a shallower pattern of diversification and might therefore explain the lower vervet morphology-taxon covariation. Vervets seems to exhibit their deepest phylogenetic split between two lineages, *C. a. aethiops*, existing approximately west of the Volta River, and another lineage comprising the other subspecies, to the west. Biogeography seems to suggest that the baboons have a longer history of being pan-African (apart from the deserts and rainforest) resulting in deeper phylogenetic splits. The major splits are between northern and southern taxa (Zinner et al., 2009b). However, even more recent splits such as that of the Guinea and olive baboon are marked. This West African subspecies exhibits a distinct morphology (Chapter 2), ontogeny (Jolly and Phillips-Conroy, 2006) and socioecological (Maestripieri et al., 2007, Jolly and Phillips-Conroy, 2006, Galat-Luong et al., 2006). This longer history of a wider geographic spread serves to promote diversification. Distance is a significant barrier to gene flux, and such reductions promote subspecific divergence, and give morphology a stronger phylogenetic structure. Vervets in contrast remained for longer in the tropics for much of that period, only recently colonising southern Africa.

While zygostructure is likely to be a key determinant of current phenotypic variation, this is not mutually exclusive with environmental adaptation. The environment is likely to underpinn baboon phylogenetically structured variation (Chapter 2). If the vervets have been restricted to the tropics until relatively recently, though this contains a variety of habitats from forest to savannah, this range misses the axis of variation in temperature or day length seasonality of the more temperate southern Africa (Anderson, 1982, Hill et al., 2003, Byrne et al., 1993).

5.4.2 Adjusted Phylogeny as a Control for Introgression

The purpose of the adjusted phylogeny was to control for recent introgression events which cause discrepancies between nuclear and mitochondrial DNA. While mtDNA is hereditary, the fact that it passes down the female line gives this macromolecule a different phylogenetic history from nuclear DNA, which codes for morphology. However, by using the mtDNA phylogeny and correcting it for likely introgression events this mismatch problem can be mitigated. In this study the northern populations of *P. h. cynocephalus*, which is likely to have acquired a northern mitochondrial haplogroup, was given the haplogroup of the southern population, better reflecting the ancestral condition before the confounding introgression event. This procedure did indeed increase the correlation between phylogeny and shape, although the effect of this is strikingly small. Similarly size-adjustment makes little difference to the correlation between phylogeny and shape. The two together do summate to produce the highest correlation but the difference is still ultimately a small one.

The slightness of the increase in the correlation between nonadjusted and adjusted phylogenies suggests that even though *P. h. cynocephalus* is on a side of the evolutionary division at odds with nuclear DNA relative to the northern taxa, it shares many affinities with these adjacent subspecies. This demonstrates the absence of a sharp split between northern and southern forms arguing for more clinal, gradistic change. This resounds with the success of modelling baboons as a single continuous cline (Chapter 2) and the clinal descriptions of other authors (Jolly, 1993). Specimens at hybrid zones are most similar in a given trait but within subspecies this gradual change across geography persists (Jolly, 2001, Jolly, 1993). This may initially sound at odds with the north-south divide being the major explanatory factor of baboon phylogenetic differences. However, the north-south divide creates an axis of variation, rather than maintain two discrete groups, neighbouring populations interbreed and so subspecies blend creating a clinal pattern of morphological variation.

5.4.3 Phylogeny, Geography and Diet: The Emerging Picture

It is evident that the important phylogenetic differences found here reveal similar patterns to spatial, environmental (Chapter 2) and dietary differences (Chapter 3). For vervets, an East-West pattern of clinal change in size was found in size (Chapter 2) as well as in allometry controlled shape (Elton et al., 2010). While this study has not had access to detailed phylogenetic information, the greatest morphological split when using taxon as a covariate is between *C. a. sabaeus* and the other subspecies. Existing genetic data put this difference in a phylogenetic context, and show that this corresponds to the variation between the most basally divergent subspecies and the others. Consequently this analysis suggests the existing size and shape cline may have a phylogenetic underpinning. Reduced gene flow and consequent divergence in genotype and phenotype can explain morphological variation without the need for invoking an environmental explanation (Kimura, 1969, Kimura, 1968). Certainly there are several polytypic species in Africa that owe their morphological distinctiveness to Pleistocene environmentally-mediated reductions in gene flow (Hewitt, 2004). However, while isolation can favour neutral differentiation is certainly aids adaptation to local conditions (Wright, 1932). As such, phylogenetic structuring is not incompatible with an adaptation explanation of morphological variation in the vervet or indeed the baboon.

In baboons allometrically controlled shape shows a north-south change (Chapter 2; Frost et al., 2003). Again this has a phylogenetic basis, as southern Africa is the site of origin of this taxon (Newman et al., 2004), with divergence into north Africa (Jolly, 1993). This axis corresponds to the morphological axis as shown spatially (Chapter 2) and in the phylogeny-morphology covariation (this chapter). While all African regions are different the steepest environmental axis is likely to be latitudinal; seasonality has been argued to be a reason for the large size of chacma baboons (Anderson, 1982) and day length has marked effects on socioecology and time budget (Hill et al., 2003). The alignment of latitudinal and phylogenetic variation makes it difficult to piece apart change owing to neutral change over the course of baboon radiation and local adaptation to different habitats. While the covariation between diet and morphology might suggest adaptation, diet would appear to be environmentally determined and morphology could be solely underpinned by population history. With the profusion of interacting variables at play, such bivariate models fail to dissociate complex interrelations and interactions. Evidently a more detailed model incorporating all of these variables is required to get closer to revealing the causal factors in the subspecific morphological radiation of these two African primates.

5.4.4 Conclusion

This study has found evidence to suggest that baboons are more phylogenetically structured in morphology than vervets. This is likely to be because vervets have more recently colonised southern Africa from West Africa, and consequently have only recently been subject to a reduction in gene flux via distance. Baboons have an historically deeper history of existing throughout sub-Saharan africa and have diversified more fully over that longer time period. Additionally, while not homogenous, tropical Africa is without the climatic variation in seasonality and photoperiod seen in the north-south axis. Baboons have thus been exposed to divergent evnironments and potentially selective pressures for longer. However, though this study has shown phylogenetic structure, this study lacks the capability to determine if this morphological variation is the result of neutral genetic drift or adaptation to local conditions.

CHAPTER 8. CONTRIBUTIONS TO MORPHOLOGICAL VARIATION

6.1 INTRODUCTION

6.1.0 Overview

The correlation between environmental and morphological variation has been established in baboons (Chapter 2) and vervets (Cardini et al., 2007), as has the link between dietary and morphological variation for baboons (Chapters 3 & 4). However, the precise interrelation of these potentially correlated variables is unknown. The effect of the environment may be direct, with this exerting a selection pressure and thus structuring morphological variation in line with environmental variation. Alternatively, it is possible that these abiotic forces act indirectly on the species. Vegetation is profoundly responsive to abiotic variation, such as rainfall and temperature (Dunbar, 1990, Bronikowski and Webb, 1996, Bronikowski and Altmann, 1996). It is possible therefore that environment has an influence on biotic variables such as food abundance and quality in determining intraspecific variation (Ho et al., 2010). Both direct and indirect adaptationist explanations of morphological variation may be aided by reductions in gene flow related to phylogeny (Chapter 5). Alternatively, most of the morphological variation could be neutral relating exclusively to drift in reproductively restricted populations.

Path analysis is an excellent way of teasing apart interrelated variables. This methods splits a correlation into its direct and indirect components (Sokal and Rohlf, 1995, Wright, 1921), shedding light on the interrelation of factors and helping to get at ultimate causation. An additional benefit to this method is that it serves to contextualise the correlations, as all the factors are presented in the same model, drawing attention to high correlations and strong paths. One aim of this chapter is to quantify the direct and indirect (via diet) effects of environment and geography and so see which is the stronger path and, by implication, selection pressure. This chapter also examines each correlation for outlying subspecies that potentially skew the trend. Comparison of the coefficients reveals the relative effects of environment, space, diet and phylogeny for the two subspecies, and gets at the very heart of the putative drivers of subspecific divergence in these two primates.

6.1.1 Temperature and Morphology

Animals are subject to physical laws that determine the physiological implications of size and shape (Schmidt-Nielsen, 1984). An animal's surface area to volume ratio determines the capacity for heat loss or gain, along with the relative difference between body and ambient (Scholander, 1955). The same ratio determines the rate of water loss from the respiratory tissues. In environments where heat conversation/dissipation or water conservation is important, abiotic factors are likely to exert a strong selective pressure. Indeed the classic explanation of Bergman's and Allan's rules is couched in terms of optimal surface area to body mass ratio to aid thermoregulation (Millien et al., 2006, Chapter 2). This view still has it vocal adherents (Pincheira-Donoso, 2010). Size and shape dictate the thermoneutral zone, which describes the temperature below which an endotherm needs to upregulate its metabolism to maintain core body temperature, and below which an animal needs actively to cool itself, through sweating, panting or vascular changes (Scholander, 1955, Porter and Kearney, 2009). Changes to size and shape therefore change this thermoneutral zone and thus reduce metabolic costs. Meta-analyses suggest size variation is indeed related to temperature variation in birds (Ashton, 2002) and mammals (Ashton et al., 2000). Indeed experimental evidence shows that cold reared animals grow larger, providing causal rather than correlational evidence for this size temperature relationship. For instance *Drosophila* develop larger wings, eyes and legs as a result of increased cell size when reared at low temperature (Azevedo et al., 2002). Indeed this response is widespread in ectotherms (Walters and Hassall, 2006). Ectotherms however cannot metabolically alter their body temperature, while endotherms can. Nevertheless, there is a metabolic costs to heat generation in endotherms, and so changing surface area to volume ratio is likely to represent a considerable energy saving and would thus be highly adaptive (Mayr, 1956). Experimental work on mice has demonstrated this, by showing that cold reared mice grew shorter limbs and had stockier bodies than warm reared mice; a finding in line with lower surface area and greater heat conservation (Serrat et al., 2008). While not size related this is certainly thermoregulatory corresponding to Allen's rule, which is found to hold in numerous taxa (see Chapter 2), for instance in human height (Ruff, 1994) and in bill lengths for various birds (Symonds and Tattersall, 2010).

While temperature has an obvious interaction with latitude, putatively accounting for Bergman's and Allen's rules, it is also related to elevation, as temperature decreases with altitude. A morphological axis relating to cranial base flexion was found in mice with elevation at Yellowstone Park (Grieco and Rizk, 2010). This was quite unrelated to size. Humidity also decreases with altitude and this effect in concert with low temperature was found to be an important determinant of wing length in North American birds (James, 1970) and size in bobcats (Wigginton and Dobson, 1999). Similarly moisture was found to be a significant size predictor in bats (Burnett, 1983).

However, animals may adapt by modulating factors other than size and shape. As mentioned endotherms can upregulate their metabolisms, to buffer themselves from the environment. However, this has an energetic cost (Scholander, 1955, Porter and Kearney, 2009), and so often insulation such as fur or fat is used to conserve heat without an energetic cost. Both these are facultatively variable, with piloerection conferring additional heat conservation (Scholander, 1955) and vasculature changes to bringing the blood to the surface for cooling or retaining it in the core for heat conservation (Scholander, 1955). Additionally animals have behavioural response such as basking to warm up (Scholander, 1955), or huddling (Alberts, 1978), or seeking shade and reducing activity when it is hot (Hill et al., 2004). Moreover, as was suggested by Rodriguez et al., (2006) temperature may exert itself when below a certain threshold, as southern European animals where temperatures are more temperate were not found to have a size-temperature relationship.

6.1.2 Primary Productivity and Morphology

Temperature and other physical parameters exert their effect not only directly on animals but directly on the biotic component of their environment. Ho et al.(2010) found that Bergmann's rule was underpinned by dietary quality in three invertebrate taxa. Mammalian examples include bats, where primary productivity determines size (Burnett, 1983), and carnivores, where primary productivity had a greater explanatory power of size variation than latitude or temperature (Rosenzweig, 1968). In these cases temperature was a lesser explanatory variable than primary productivity. However, in a study on mountain pika, cranial size decreased with altitude, in contrast to thermoregulatory expectations. However, given the reduced food availability at altitude this provides clear evidence for a primary productivity explanation (Liao et al., 2006). For a number of middle eastern animals primary productivity was the greater determinant of body size (Yom-Tov and Geffen, 2006). The argument for resources-based size variation can be advanced through studies of insular versus mainland variation (Lomolino, 2005, Lomolino, 1985, Millien et al., 2006). Large animals get smaller on islands owing to diminished resources and selection for less growth. Palkovacs (2003) framed this in life history terms by suggesting that large animals benefitted by bringing forward reproduction to an earlier ontogenetic stage: the scarcity of resources shifts the balance between investing resources in reproduction versus growth in favour of the former.

Both resource abundance and quality appear to be correlated with morphological variation. However, correlation does not prove causation. Indeed it is impossible to directly observe morphology responding to diet over evolutionary time. Nevertheless experiments can provide evidence for how animals are likely to respond over evolutionary time. Rodents fed on poor (i.e. highly fibrous) food develop larger guts (Hammond and Wunder, 1991, Hammond, 1993) as well as absolute size (Green and Millar, 1987). This is adaptive as larger guts and larger size increase food retention time enabling greater extraction of energy (Demment and van Soest, 1985), the so called Jarman-Bell principle (Geist, 1974). While in this case this may be phenotypic plasticity it is this variation that natural selection canalises resulting in genetic differences in response to environment (Mayr, 1963).

In primates a large interspecific comparison has found larger species tend to have a poorer dietary quality (Sailer et al., 1985) in line with Jarman-Bell principal. Recently digestive adaptations has been shown to be more important in retention time and thus the ability to eat high fibre foods than size (Clauss et al., 2008). However, for animals with generalist digestive anatomy, such as the vervet and baboon, lacking sacculated stomachs for example, the Jarman-Bell principle is likely to apply.

6.1.4 Seasonality and Morphology

Of course neither temperature, nor primary productivity are uniform throughout the year and most environments exhibit some seasonal variation. Temperate environments have a cold winter and warm summer, with tropical savannah environments exhibiting rainy and dry periods (Alberts and Altmann, 2006). Warm and wet conditions suit plant growth. As such primary productivity and hence food availability is increased after the rains or with increasing temperatures and photoperiod in temperate environments. This fluctuation between food abundance and scarcity results in animals having to rely on their reserves, such as an exogenous food cache or endogenous fat stores, or reducing metabolic needs, as in the case of seasonal torpor (Millar and Hickling, 1990). Ruling out caching, large size enables animals to survive or buffer themselves from seasonal food shortages (Lindstedt and Boyce, 1985, Boyce, 1978, Lindsey, 1966). Proving this is difficult because often the most seasonal environments are often colder, and thus have lower annual temperatures, and thus qualify for a Bergmannian thermoregulation explanation.

Storing resources is one strategy, switching to less favourable resources is another (Chapter 3). Numerous animals have fallback foods that are less preferred but and lower quality but that enable survival through periods of food scarcity (Marshall et al., 2009). Indeed these are thought to represent a major selection pressure on morphology and behaviour. Baboons have been shown to have morphology that varies with resources type. In baboons the main axis of dietary variation was between high levels of subterranean food eating or low levels and frugivory (Chapter 4). There is good evidence to suggest that this dietary difference is mediated by the environment. Subterranean foods are by definition storage organs and so they are found in very seasonal environments where there are periods of low rainfall (Dominy et al., 2008). These are especially abundant in southern Africa, but also East African Savannah; the environments of the yellow and chacma baboons. In West Africa in particular the diet is much more frugivorous (Culot, 2003).

6.1.5 Allocation of Resources and Growth

The presence or absence of food resources can cause morphological adaptations such as large size for food reserves or physiological changes relating to digestion. However, a profound effect of resource presence/absence is the amount of growth and somatic versus reproductive investment. Life history, as touched on with the island rule, is responsive to the presence or absence of resources. As discussed limiting resources, per capita, favours decreased growth and earlier investment of energetic resources into reproductive effort. Mortality risk is a key determinant the timing of reproduction, as extensive growth is maladaptive when the chances of not surviving to reproduce is high (Charnov, 1993). Animals with low predation risk are likely to grow more and reach larger sizes than high predation risk animals, assuming a constant rate of growth. However, growth rate is not constant. Rapid growth that outstrips resource intake results in increased starvation risk (Janson and van Schaik, 1993). An animal in a resource poor habitat must grow slowly to avoid this. This is definitely the case in the study taxa. Garbage-eating baboons grow faster, stopped growing earlier, and reached a higher weight (Strum, 1991). Vervets in environments with increased resources grow faster (Whitten and Turner, 2009). Hence growth rate is determined by resources and growth time is determined by mortality-influenced trade-off between somatic growth and reproduction. Adult morphology is the endpoint of growth and thus reflects variations in the trade-off between these factors.

6.1.5 Environmental Variation and Reproduction

The timing and frequency of reproduction are major life history features. Mammals generally reproduce seasonally because of the advantage of having young born into an environment in which food resources are at a maximum (Bronson, 2009). Indeed for savannah ungulates rainfall is a strong correlate with and likely determinant of seasonal breeding as this is determine the primary productivity (Ogutu et al., 2008). Primates have seasonality in births in general (Lancaster and Lee, 1965), typically responding to photoperiod, or food abundance as the cue (Di Bitetti and Janson, 2000). However there is considerable variation in this (Lancaster and Lee, 1965). Indeed even within the genus *Macaca* there are some seasonal and aseasonal species

(Smith, 1984) suggesting that this is a flexible rather than phylogenetically controlled trait.

There are two aspects to seasonal reproduction (Janson and Verdolin, 2005): the height and width of the peak. Clearly there is a continuum between aseasonal reproduction, from a straight line, with no birth peaks, to a single, tall narrow peak, representing highly synchronous birth. Vervets are considered seasonal (Else et al., 1986, Butynski, 1988) and baboons are not (Bercovitch and Harding, 1993, Alberts and Altmann, 2006). For baboons certain populations exhibit slight peaks in birth related to rainfall (Wasser, 1996). Furthermore, baboon interbirth intervals are reduced when rainfall, and hence food availability, is high (Hill and Dunbar, 2002). In the absence of rainfall when food resources are scarce conceptions will cease (Wasser, 1996, Beehner et al., 2006b). Additionally baboons conceive when conditions are most favourable (Bercovitch and Harding, 1993), though they do not necessarily carry this pregnancy. Indeed Wasser (1996) stated that baboons have a "reproductive filter." Baboons then appear to be more facultative in reproduction, not calibrating reproduction to an annual cycle but rather attuning to variation outside the annual cycle. Indeed in environments with high interannual variation this is a sensible strategy. Mast fruiting in South East Asia is interannually variable, and apes in this environment display aseasonal reproduction (Janson and Verdolin, 2005).

Vervets, though are capable of reproducing throughout the year (Fairbanks and McGuire, 1995), typically exhibit a well-defined birth season (Butynski, 1988). Much of the reason for the tightness of this peak relates to predator-swamping, and thus reducing predation risk per capita for infants (Di Bitetti and Janson, 2000). Additionally females with infants outside the birthing season suffer by having their infant taken by other females in the group. This causes stress, and occasionally death, to the infant (Kavanagh, 1977). Variation between adjacent populations in the timing of the birth season, demonstrates that these factors account for the narrowness of the peak. However, the timing is broadly similar and reproduction is modulated by an internal clock taking into account environmental as well as social cues (Else et al., 1986, Baldellou and Adan, 1997, Lee, 1984).

Baboons have broken out of the seasonal reproduction characteristic of most cercopithecines. This liberation means they are able to more efficiently invest available resources in growth and reproduction. Vervets are constrained by ecological and social factors forcing them to reproduce at a certain time of the year. While this is optimised, it cannot be as adaptive and in line with environmental variation as with baboons. The baboon therefore is likely to exhibit a greater correlation between life history variation and the environment than the vervet. Morphology, as the end product of growth, may therefore show a similarly high covariation with environmental variation.

6.1.7 Path Analysis

Path analysis is a method devised by Sewell Wright (1921) to partition the direct and indirect components of a correlation (see Chapter 4). This is useful when one variable is likely to act via another variable, and when numerous variables are intercorrelated (Sokal and Rohlf, 1995).   The high interrelation among variables is common in biology and this method is widely used in a range of biological systems. Examples include determining the factors that influence the growth of populations, such as detritus type and productivity in mosquitoes (Yee et al., 2007), demographic changes, such as environmental factors determining the composition of bumble bee colonies (Duchateau et al., 2004), as well as above-species level variation such as the parameters affecting land snail species richness (Cowie, 1995) or pond life (Ripley and Simovich, 2009). Primatological examples include a meta analysis to establish the socioecology (group size, female dispersal etc) and anatomy (body mass and neocortex ratio) and grooming time (Lehmann et al., 2007) see also Seuer et al. (2011)). This method has also been used to assess the magnitude of various biotic and abiotic variables on morphology.   Examples include determining the effect of factors affecting cranial and mandibular shape in mice (Caumul and Polly, 2005) and plastron shape in turtles (Angielczyk et al., 2010). In both these cases environment, putative function and evolutionary history were included in the model.

6.1.8 Aims

The aim of this chapter is to determine the association between the factors that have so far been considered separately as correlates in baboon and vervet morphological variation. This will be done by incorporating them in a path model to dissociate the correlations and establish the relative importance of these factors. Environment has been shown to have some correlation with morphology, as has diet. However, these two factors are clearly not independent as the environment determines the abundance and type of food resources available. As such this chapter will determine which of two hypotheses is best reflects reality. These are I) that the environment is correlated with morphological variation directly versus II) that environmental variation is correlated with dietary variation which in turn is correlated with morphological variation: the link between environment and morphology is indirect. Thus there are two possible causal paths, a direct and indirect route. Previous assumptions about the quality of dietary and environmental variation still apply, though data are likely to be sufficient in scope given previous significant findings to answer the question.

This path model will also incorporate spatial variation and phylogeny as factors, as both population history and geographic distance have a clear influence on morphological variation. To some extent the correlation coefficients of a path analysis are dependent on the model employed. However, given the nature of the data there are few meaningful models, and the model chosen is justified.

A second aim of this study is to compare the two path models of the vervet and baboon to test the null hypothesis that the two have subspecific variation determined by the same evolutionary forces. Here the factors described, environment, diet, spatial variation and phylogeny are assumed to reflect in their correlations the importance of these forces in structuring subspecific variation. Crudely similar path coefficients therefore would suggest similar levels of environmental influence, for example, while different values might suggest unique responses to evolutionary forces.

6.2 METHOD

6.2.1 Path Analysis

Path analysis was used to visualise the correlations between factors (Caumul and Polly, 2005, Plavcan and Schaik, 1997, Wright, 1921). This method partitions the effects of correlated variables (Sokal and Rohlf, 1995) into their direct (exclusive) and indirect (via another variable) component, such that a correlation between two variables is the product of the path coefficients. Values depend on the arrangement of the path model which is an *a priori* expectation (see 6.2.3 Justification for the Model).

Because the data used were multivariate, partial least squares was used (Rohlf and Corti, 2000) to obtain correlation (RW) coefficients between blocks of variables. Blocks with variables of different units were standardised to having a mean of zero and a variance of one using NTSys. The partial least squares was carried out using MorphoJ (Klingenberg, 2011). These RV values were used to calculate the path coefficients (Sokal and Rohlf, 1995). Plots of the partial least squares axes were used to visualise the relationships underlying these values and to test for outliers.

6.2.2 Model Variables

The following variables are used in the path analysis:

Shape: the landmark data for specimens associated with diet and haplogroup (Chapter 4).

Size-Controlled Shape: the landmark data for specimens after regressing out size for each subspecies.

Diet: the proportion of fruit, leaves, subterranean items, flower, animal and other in the diet (Chapter 4).

Environment: comprising mean temperature, seasonality index, mean NDVI, standard deviation of NDVI and altitude (Chapter 2).

Taxon: dummy variables for the six subspecies

Phylogeny: principal coordinates expressing the major axes of phylogenetic variation were taken from a phylogenetic distance matrix derived from the literature.

Spatial: the terms of the expanded polynomial of longitude (x) and latitude (y) found to be significant in trend surface analysis of previous chapters. These are:

Baboon shape: $y\ x^2\ xy\ y^2\ x^3\ x^2y\ y^3$

Vervet shape: $x\ x^2\ x^3\ y^3\ xy\ x^2y\ xy^2$

6.2.3 Justification for Model

Path analysis is a method of dissecting a correlation into its constituent parts according to certain putative paths. The path coefficients are therefore entirely dependent on the topology of the model. Consequently *a priori* expectations are needed about which variables are likely to be causally related. The environmental and geographical variables (i.e. spatial position in terms of latitude and longitude) are highly likely to be correlated, not least because temperature is to a large extent latitudinal. Importantly however, envionrment and geography are both likely to have an impact on the flora and hence, given the vegetative diet of the two study species, on the diets. However, both these variables might putatively act directly on the morphological variation itself. Thus the model chosen contains direct paths from environment and geography to shape as well as indirect paths via diet. Phylogeny is unlikely to be causally related to diet or current environmental conditions. Of course it could be correlated with them and geography. To some extent all possible variables are interrelated. However, path analyses are tradeoffs between representing a complex reality and creating an interpretable model.

6.3 RESULTS

6.3.1 Baboon Path Analyses

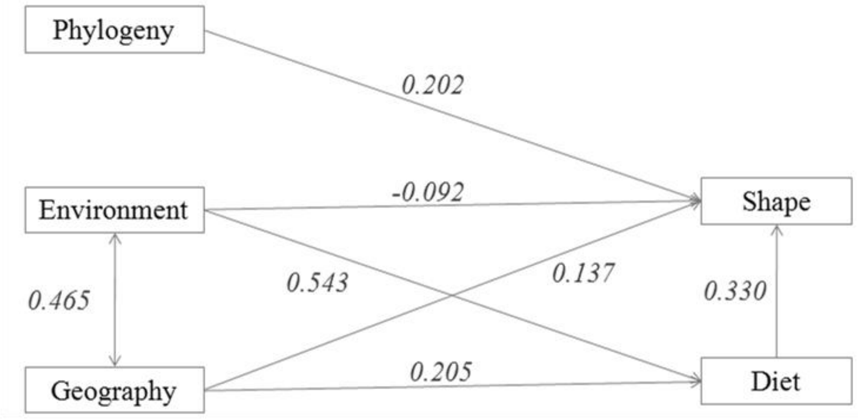


Figure 8.1. A path analysis model showing a priori causal relationships and partial correlations between the factors related to baboon morphological variation.

The strongest factor correlated with shape is diet (fig. 6.1), followed by mtDNA phylogeny. Environment has a poor correlation with shape directly (-0.092) but via the diet pathway this is rather higher (0.543 x 0.330 = 0.179). Geography is less highly correlated with shape than this (0.137) but its direct effect is higher than the path through diet (0.205 x 0.330 = 0.068). Both the environmental and geographic blocks are highly correlated (0.465).

Bivariate relationships were visualised to determine if any subspecies was skewing the correlations.

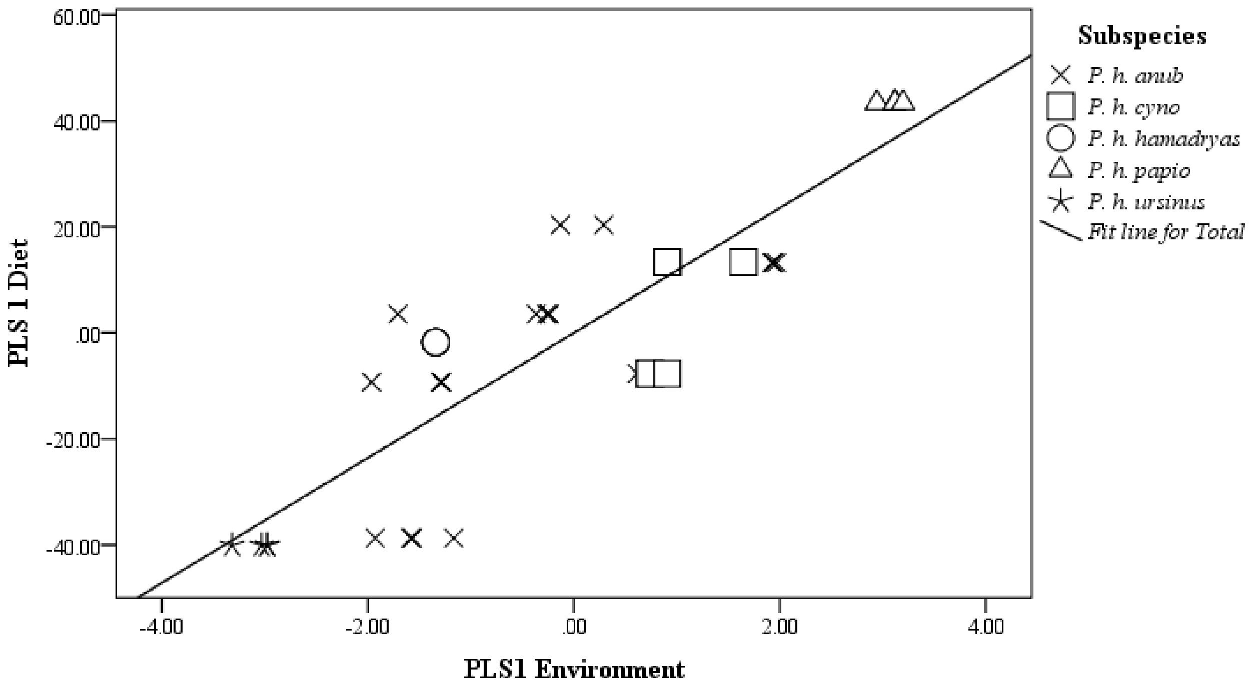
6.3.2 Environmental-Dietary Covariation

Table 8.1. Singular values and pairwise correlations of PLS scores between the baboon dietary and environmental blocks. For the whole PLS RV =0.6327, p < 0.0001. For morphological specimens, n = 45, and for associated dietary data n =12. Significant p values are shown in bold.

	Singular value	**% Total Covariance**	**Correlation**	**P-value**
PLS1	41.0838	94.884	0.86677	**<.0001**
PLS2	9.27048	4.831	0.5898	**0.0039**
PLS3	2.16749	0.264	0.32677	0.2521
PLS4	0.55195	0.017	0.27701	0.8366
PLS5	0.23937	0.003	0.05503	0.5671
PLS6	0.0026	0.000	0.01237	0.6472

The block of baboon dietary variation is significantly correlated with the block of environmental variables (RV = 0.6327, p < 0.0001, table 6.1). The first PLS accounts for virtually all of the covariation, and is highly significant (table 6.1). The scatter plot of the first PLS scores reveal all subspecies to be approximately on the same trend line (fig. 6.2). The axis of variation is between high levels of frugivory corresponding to values to high temperature and seasonality and rainfall, versus subterranean food eating and folivory at locations of high altitude. The second dietary-environmental PLS axis (fig. 6.3) is less strong with considerable scatter. This axis separates subterranean foods from leaves, with the former corresponding to high seasonality index values, versus folivorous diets at low precipitation environments.

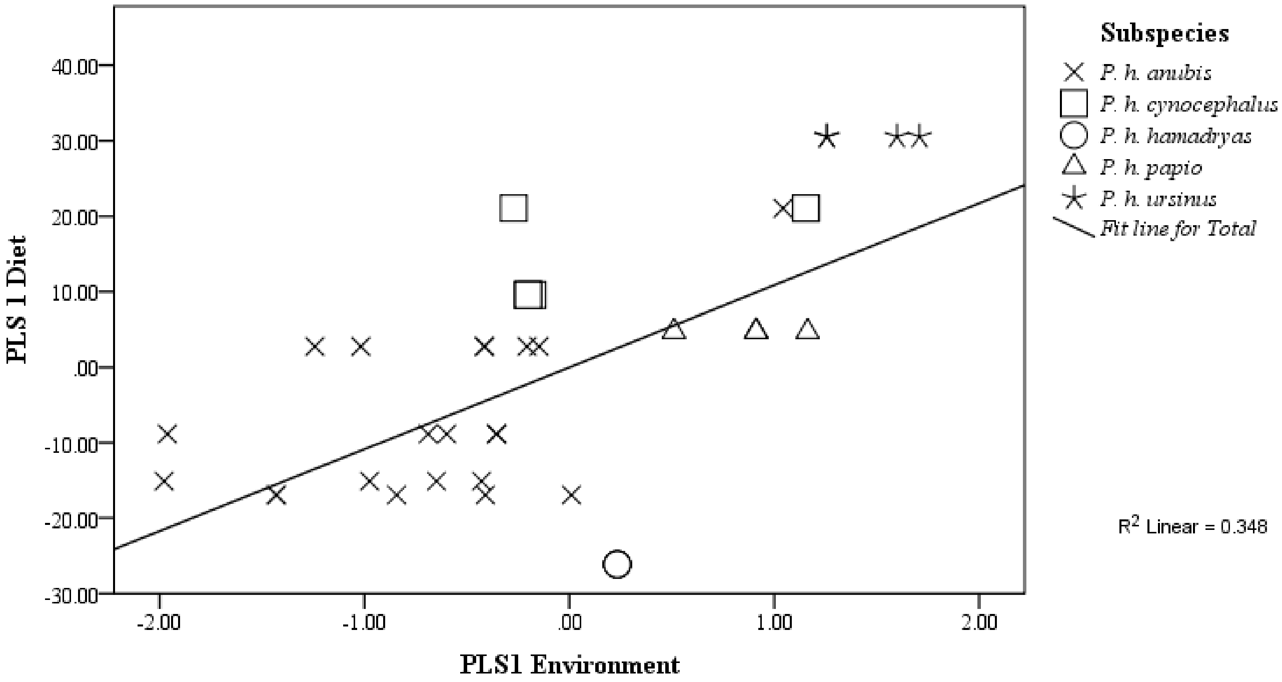
	PLS1
Fruit	0.80
Subterranean	-0.41
Leaves	-0.44
Flower	-0.01
Animal	-0.02
Other	0.08



	PLS1
Mean Temperature	0.55
Seasonality Index	0.40
Mean NDVI	0.21
SD NDVI	0.41
Altitude	-0.42
Mean Precipitation	0.38

Figure 8.2. A scatter plot of scores for the first PLS between diet and environment. Loadings are given adjacent to the axis.

	PLS2
Fruit	-0.03
Subterranean	0.68
Leaves	-0.72
Flower	0.14
Animal	-0.03
Other	-0.05



	PLS2
Mean Temperature	-0.19
Seasonality Index	0.46
Mean NDVI	-0.27
SD NDVI	0.21
Altitude	-0.37
Mean Precipitation	-0.70

Figure 8.3. A scatter plot of scores for the second PLS between diet and environment. Loadings are given to aid the interpretation of the two axes

6.3.2 Environmental-Shape Covariation

The relationship between the environmental and shape blocks was quantified and visualised.

Table 8.2. Singular values and pairwise correlations of PLS scores between the baboon shape and environmental blocks. For the whole PLS RV = 0.2122, p = 0.0104. For morphological specimens, n = 45, and for associated dietary data n =12. Significant p values are shown in bold.

	Singular value	**% Total Covariation**	**Correlation**	**P-value**
PLS1	0.02172891	63.703	0.59554	**0.0368**
PLS2	0.01244105	20.883	0.81198	**0.0281**
PLS3	0.00736664	7.322	0.82353	0.0598
PLS4	0.00613107	5.072	0.65294	**0.0028**
PLS5	0.00381496	1.964	0.62655	0.1774
PLS6	0.00279903	1.057	0.67237	0.173

The correlation between environment and shape is significant (RV=0.2122, p=0.0104, table 6.2). The first two partial least squares axis account for the majority of the covariation and are both significant (table 6.2).

The correlation between environment and shape is less strong than that of environment and diet, as shown by the scatter (fig. 6.4). The environmental axis runs between high altitude and high mean temperature and seasonality. The high altitude corresponds to an elongated klinorhynch shape and the high temperature a shorter muzzled airorhynch one.

	PLS1
Mean Temperature	0.52
Seasonality Index	0.44
Mean NDVI	0.19
SD NDVI	0.44
Altitude	-0.29
Mean Precipitation	0.47

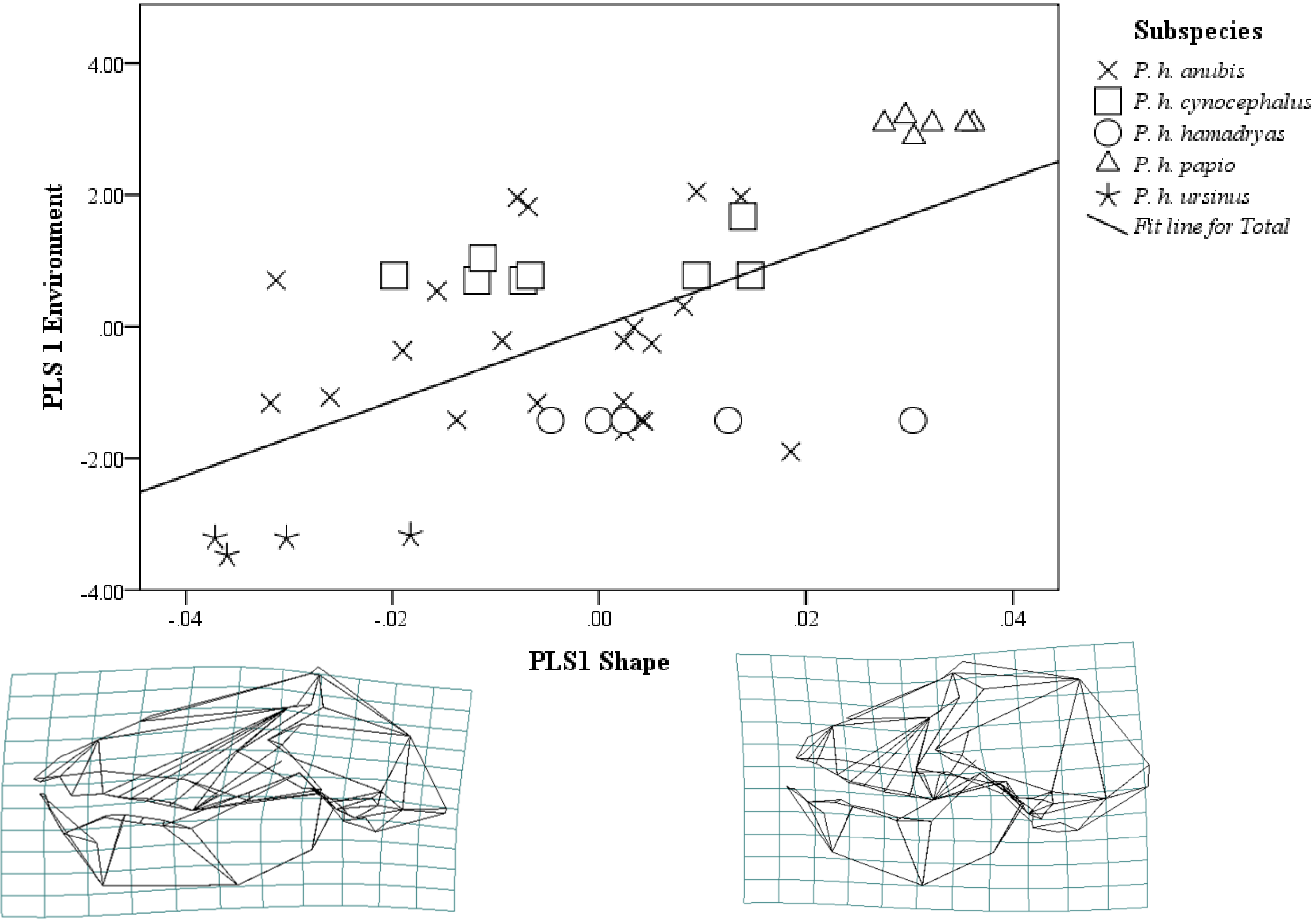


Figure 8.4. A scatter plot of scores for the first PLS between baboon environment and shape. Wireframes show the morphological extremes of the axis of covariation (exaggerated by a factor of 3). Loadings are given in the table adjacent to the environmental axis.

6.3.3 Geographic and Morphological Covariation

The terms of the trend surface analysis (Chapter 2), constituting the geographic block, and their relationship with shape was graphed and visualised.

Table 8.3. Singular values and pairwise correlations of PLS scores between the dietary and shape blocks. For the whole PLS RV =0.3093, p < 0.0001. For morphological specimens, n = 45, and for associated dietary data n =12. Significant p values are shown in bold.

	Singular value	**% Total Covariance**	**Correlation**	**P-value**
PLS1	0.02833	61.704	0.69801	**0.0004**
PLS2	0.02031	31.692	0.81844	**0.0001**
PLS3	0.00878	5.929	0.77502	**0.0135**
PLS4	0.00278	0.593	0.77171	**0.0004**
PLS5	0.00091	0.063	0.77571	0.0973
PLS6	0.0005	0.019	0.65857	**0.0351**
PLS7	9.9E-05	0.001	0.63283	0.9322

Shape is significantly correlated with geographic variation in latitude and longitude (RV = 0.3093, p < 0.0001, table 6.3) and the first four axes are significant (table 6.3).

The first PLS axis reveals a covariation between geography and shape, largely made up of the variation between the chacma baboon and the other subspecies (fig. 6.5). The shorter rostrum and larger neurocranium corresponds to the northern subspecies while the longer rostrum the southerly.

Spatial Term	**PLS1**
y	0.12
x^2	0.44
y^2	-0.05
x^3	-0.52
x^2y	0.49
xy^2	-0.52
y^3	-0.07

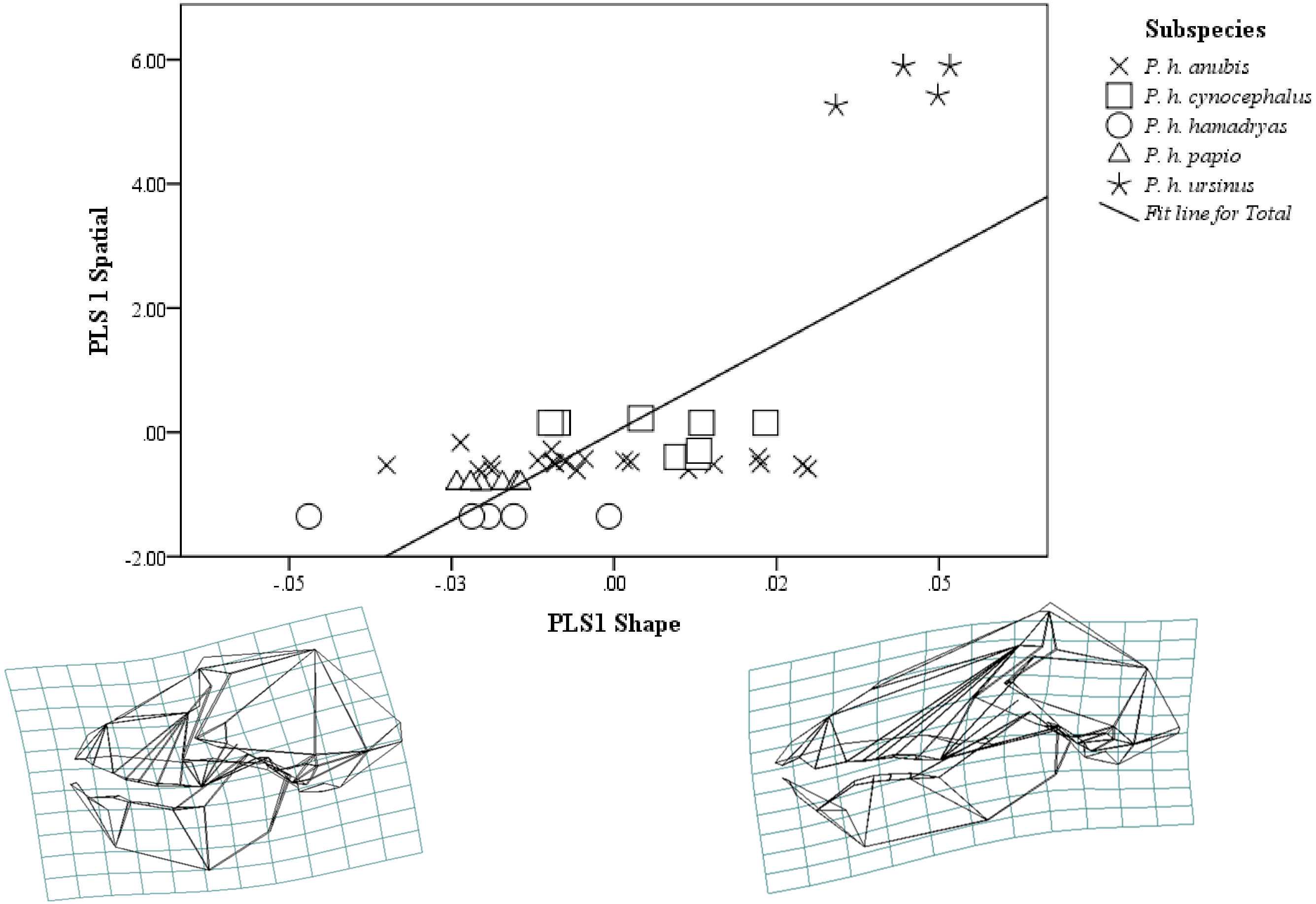


Figure 8.5. A scatter plot of PLS scores for the first PLS axis between phylogeny and baboon shape. Wireframes show the morphological extremes of the axis of covariation (exaggerated by a factor of 3). Loadings are given in the table adjacent to the spatial axis.

6.3.4 Baboon Size-Controlled Path Analysis

Shape contains a size related components, the pattern of which varies between subspecies. Consequently, size-controlled shape is likely to reveal different relationships.

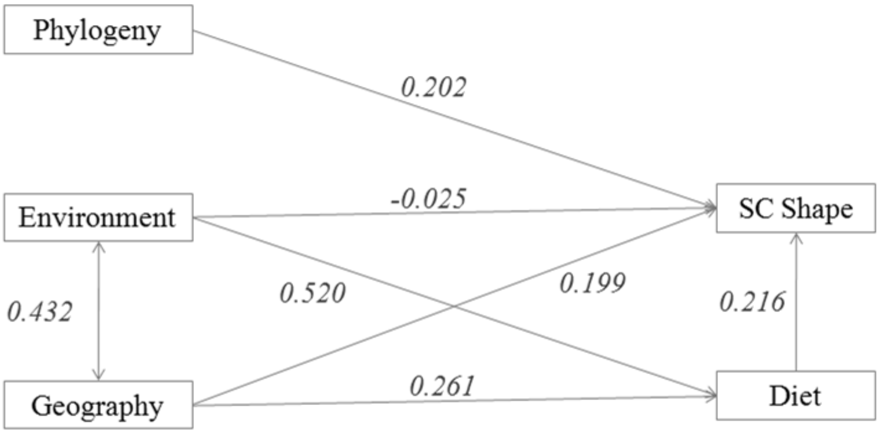


Figure 8.6. A path analysis model showing a priori causal relationships and partial correlations between the factors related to size-controlled shape for baboons.

Controlling for size shows broadly the same path coefficients as full shape (fig. 6.6). The biggest change is the reduction in the correlation between diet and shape (0.330 => 0.216). There is a slight increase in the amount of variation explained by geography.

6.3.5 Vervet Path Analyses

The path model for vervets was constructed. This used the same variables as those for baboons, with the exception that taxon is used instead of phylogeny, as no suitable information is available for all vervet subspecies.

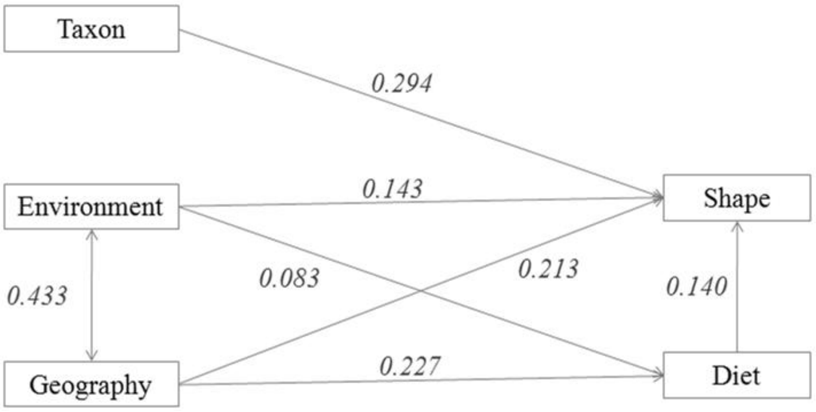


Figure 8.7. A path analysis model showing a priori causal relationships and partial correlations between the factors related to shape for vervets.

Taxon has the strongest correlation with shape (fig. 6.7). This is lower than phylogeny-shape covariation in baboons. Shape is secondarily most correlated with geography.

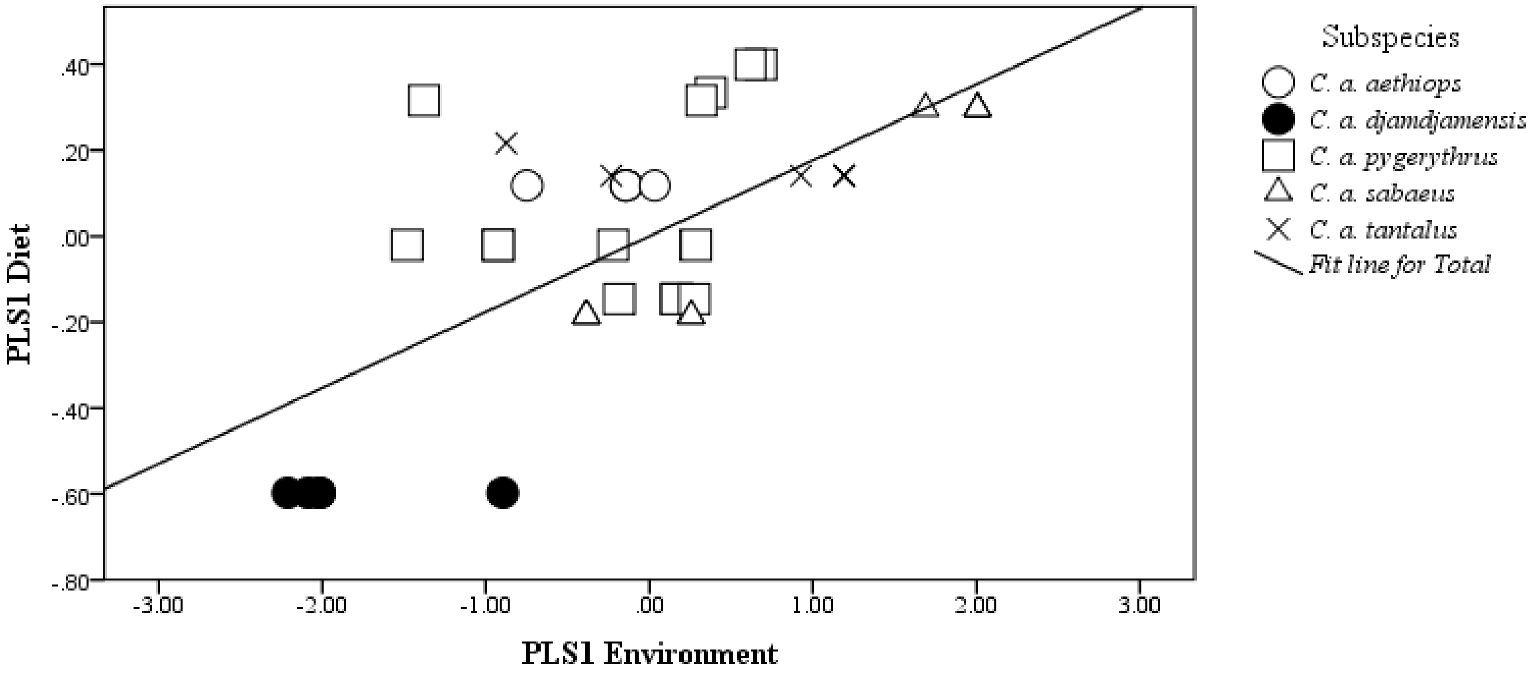
6.3.6 Vervet Environmental-Dietary Covariation

Table 8.4. Singular values and pairwise correlations of PLS scores between the dietary and environmental blocks for vervets. For the whole PLS RV =0.1817, p = 0.0078. For morphological specimens, n = 41, and for associated dietary data n =12. Significant p values are shown in bold.

	Singular value	**% Total Covariance**	**Correlation**	**P-value**
PLS1	0.22713796	82.363	0.69173	**0.0153**
PLS2	0.08337815	11.098	0.4571	**0.0301**
PLS3	0.0552066	4.866	0.40387	**0.0006**
PLS4	0.03189209	1.624	0.49448	**0.0001**
PLS5	0.00554548	0.049	0.23729	0.1702
PLS6	0.00033323	0	0.24127	**0.0148**

The PLS between diet and environment is significant (RV = 0.1817, p = 0.0078). The first PLS accounts for virtually all of the covariation, and is highly significant (table 6.4).

	PLS1
Fruit	0.63
Leaves	-0.74
Flower	-0.06
Animal	0.20
Sap	0.05
Other	-0.04



	PLS1
Mean Temperature	0.43
Seasonality Index	0.14
Mean NDVI	0.15
SD NDVI	0.52
Altitude	-0.60
Mean Precipitation	0.36

Figure 8.8. A scatter plot of scores for the first PLS between vervet environment and diet. Tables showing the loadings are given beside the appropriate axes.

The environment diet PLS equates leaf eating with altitude and fruit eaging with high seasonality and mean temperaterues (fig. 6.8). Much of this is evidently driven by the *C. a. djamdjamensis*.

6.3.7 Vervet Size-Corrected Path Analysis

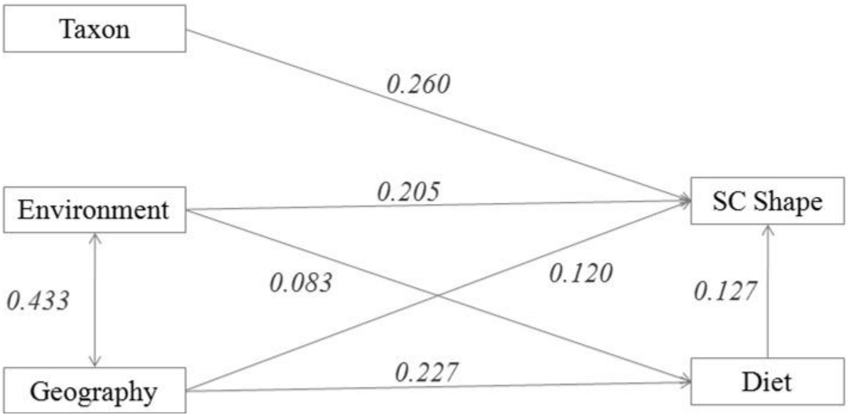


Figure 8.9. A path analysis model showing a priori causal relationships and partial correlations between the factors related to size-controlled shape for vervets.

Size correction reveals a slight reduction in the diet-shape and taxon-shape covariation, with more substation decreases in both environment-shape and geography-shape (fig. 6.9).

6.4 DISCUSSION

6.4.1 Baboon Environment

Subspecific variation can be structured by the features of the physical environment (Millien et al., 2006), such as temperature and rainfall, directly, or else by the effect of these variables on the biotic environment (Ho et al., 2010, Burnett, 1983, Liao et al., 2006), chiefly the availability of food resources. This study revealed that baboon morphology is correlated with the physical environment. However, the path analysis reveals that little of this correlation is direct but rather consists of an indirect component via diet. This suggests food resources play a major role in structuring baboon subspecific variation.

The pattern of diet-environment covariation matches expectations. The first axis of this covariation is between fruvigory versus subterranean food and leaf eating. The former diet corresponds to low altitude and but high temperature and seasonality, while the latter is associated with the opposite condition. The second axis also features subterranean foods, this time associating them with high seasonality. Here subterranean food eating is contrasted with leaf eating, found in low precipitation environments. It seems a contradiction that seasonality is associated with fruit in one PLS, and with subterranean foods in another. However this suggests that both environments are actually highly seasonal, indeed more so than the intervening environments, and the linear first axis cannot express this pattern.

Overall these findings resound with the conclusions of Chapter 4. In both plots chacma baboons are placed at the subterranean food eating extreme. This subspecies inhabits the whole of southern Africa, but has populations, included in the analysis, that exist at high altitude in the Drakensbergs (Whiten et al., 1991a). Here in particular fruit is scarcer than in other habitats. This environment exhibits high temperature seasonality (Anderson, 1982, Barton et al., 1996). The Guinea baboon in contrast is highly frugivorous (Culot, 2003) and inhabits warm tropical environments of West Africa, where fruit is more plentiful and consequently makes up a higher proportion of the diet. This environment is also highly seasonal but in terms of rainfall (Anderson and McGrew, 1984). The olive baboon shows a high scatter, reflecting the fact that it is found more widely over an array of environments. The hamadryas baboon is represented by a single point, appearing towards the higher altitude less fruit eating extreme, relating to its Ethiopian habitat and less frugivorous diet (Zinner et al., 2001).

The axis between physical environmental terms and morphology produced much the same axis as between diet and environment. However, this correlation is not so strong. The scatter is high for all subspecies rather than a single outlying population. A scenario of morphological variation following environmental variation, corresponding to Bergman's or Allan's rule would no doubt show a higher correlation. However this finding agrees with that of Chapter 2, where environmental terms proved poor when included in the partial regression. In Chapter 2 this was argued to be because the similar morphologies might arise in adaptive response to two very different environmental conditions. For instance the chacma may be large for thermoregulatory reasons, in the face of poor resources while the olive baboon may be large because of greater abundance of resources. Light may be shed on this by considering life history variation.

6.4.2 Life History Variation

Adult morphology is the endpoint of growth, the amount of which is determined by a trade-off between growth/maintenance and reproduction (Hennemann, 1983). This in turn is related to mortality risk, with high levels favouring earlier reproductive maturity (Charnov, 1993). The rate of growth is determined by resource availability (Janson and van Schaik, 1993), comprising how much food the environment supports and how much an individual has access to depending on intragroup competition (Bettridge et al., 2010, Barton et al., 1996). Between adult morphology and environmental variation therefore lies a range of ecological and life history parameters. This study lacks detailed information on the timing of life history events (Lee, 1996, Leigh and Bernstein, 2006, Swedell and Leigh, 2006), ecological factors such as predation risk (Hill and Weingrill, 2007), and social information such as group size (Barton et al., 1996, Barton, 1989, Henzi and Barrett, 2005). All of these factors exert an effect on the adaptive investment of food resources into growth and thus adult form. Nevertheless, armed with this knowledge and the morphological variation here described, some predictions can be made. If resources are more plentiful in central Africa faster growth would be expected (Janson and van Schaik, 1993). Indeed the large baboons of Central Africa have a faster growth rate than those of the Savannah (Rowell, 1964, Rowell, 1966). Conversely, reduced and seasonal resources in South Africa (Anderson, 1982) could not keep pace with fast growth and early maturation (Janson and van Schaik, 1993). The male chacma baboon takes an extra year to reach maturity than the yellow baboon (Beehner et al., 2009), although this habitat was more northerly than the rest of the subspecies. Thus, there is tentative evidence that life history variation may be the missing link between morphological and environmental variation.

Nevertheless, the strong dietary covariation implies morphological responsiveness to food resources. Given the absence of biomechanical adaptation (Chapter 4), morphology-diet covariation is more likely to be underpinned by the quality this resource type. Subterranean foods are fibrous, poor quality, and chiefly eaten in the absence of other foods (Norton et al., 1987, Rhine et al., 1989, Chapter 3). Fruits in contrast are richer in energy, and easier to process , with baboons eating more fruit spending less of their time budget on foraging (Hill and Dunbar, 2002).   Baboon morphological variation may align with diet through growth-reproduction trade-offs.

6.4.3 Vervet-Baboon Comparison

Vervets are markedly different from baboons with regard to their morphological covariation with the environment. Dietary variation does not align with subspecific variation. Indeed vervets exhibit smaller dietary variation and exhibit a tighter dietary niche with less flexibility. They also stick to a small number of staple foods (Harrison 1984; Whitten 1988; Lee and Hauser; 1998; Alberts et al.2005). Environment has a larger direct effect than via diet. This suggests that vervet subspecific variation is not driven by environment’s effect on diet as is potentially the case with baboons, but by environment directly, although to a much smaller degree.

One crucial difference in environmental responsiveness of the vervet and baboon concerns birthing seasonality. Vervets reproduce seasonally within a sharply defined period, unlike baboons (Kavanagh, 1983, Else et al., 1986, Butynski, 1988). Both respond to environmental variation, but in a different manner. Vervets respond to annual seasonal variation, reproducing when resources are most abundant (Butynski, 1988). Baboons are reproductively responsive to the environment, with interbirth intervals relating to rainfall (Hill and Dunbar, 2002), and the chances of conception increasing with food resources (Bercovitch and Harding, 1993). However, crucially this does not relate to annual availability in resources, but resources in general, irrespective of season. Baboons are much more fine-tuned to the environment, birthing when conditions are optimum. While conceptions may occur when resources are abundant, this may not lead to parturition (Bercovitch and Harding, 1993). This reproductive filter (Wasser, 1996), and aseasonal reproduction means that baboons are liberated from the annual cycle and are therefore better at converting food resources into reproductive investment. Vervets, are constrained by seasonal reproduction, and a sharp birth period for predatory and social reasons

(Kavanagh, 1983), potentially reducing the link between variation in the physical environment and growth, and hence morphology. Additionally vervets have generally lower diversity in food resources. Baboons however, as a result of their flexibility and plasticity, better exploit food resources and this potentially underlies the high correlation between dietary and morphological variation.

6.4.4 Conclusion

Baboons respond to dietary variation more than any other factor. This in turn is strongly mediated by the physical conditions of the environment such as rainfall and temperature. Baboon morphological variation is likely to be underpinned by different factors, relating to increased resources permitting a higher rate of growth, versus low resources forcing slow growth rate, but extended duration to acquire large size for seasonal buffering. Similar morphologies arise out of different environmental conditions. Additionally dietary covariation with shape is strong. As this variation is between poor and high quality foods, this further makes the case for morphological variation respond to life history trade-offs affecting levels of growth.

Vervets, in contrast to baboons, have relatively little dietary responsiveness to morphological variation. Additionally they are less responsive to the environment than baboons in absolute terms. Seasonal reproduction and a constricted reproductive window, for mortality-reducing predation and social reasons, may erode the covariation between environment, diet and subspecific morphological variation. In contrast the baboon’s high flexibility and ability to better exploit environmental variation creates a strong diet-shape covariation.

CHAPTER 9. FINAL CONCLUSIONS ON THE MODE OF SUBSPECIFIC RADIATIONS

7.1 OVERVIEW

This thesis has thus far compared and contrasted the pattern and underlying features of subspecific divergence in two widespread, sympatric African monkeys. The purpose of this chapter is twofold. First, this chapter will bring the separate findings together, and integrate these into a coherent picture of what evolutionary forces have been most active in subspecific divergence of the two study taxa. Second, this chapter will characterise the subspecific divergence in general by testing a number of hypotheses. These chiefly concern whether the environment is an overarching force that acts in spite of stochastic events and specific differences, or whether those differences that already exist between the taxa interact with the environment in different ways causing differing patterns of divergence. Additionally, the environment might be of lesser importance than stochastic effects, with morphological variation being largely the product of chance population-history events, such as founder events, bottlenecks and periodic restrictions in gene flux.

7.2 HYPOTHESES OF SUBSPECIFIC RADIATION

Both the baboon (Jolly, 1993, Jolly, 2001) and the vervet (Fedigan and Fedigan, 1988, Elton, 2007) have undergone a radiation from some ancestral form into the polytypic, geographically widespread species seen today. This thesis has sought to describe, and in so doing, highlight the potential underlying forces that have sculpted this variation. This has been done by looking at the various factors, such as physical conditions and diet, that correlate with present day subspecific diversity and describing whether the pattern and magnitude of correlation is similar or different. This is useful as it implicates actual biotic or abiotic forces. However there is a more fundamental level of characterising these subspecific radiations in terms of the extent to which diversification has arisen through an adaptive process of natural selection, or neutral drift and or prevailing differences in ancestral state. These represent three extremes in which environment, used here in its broadest sense, and stochastic effects can result in subspecific diversification (summarised in table 7.1 and graphically represented in figure 7.1).

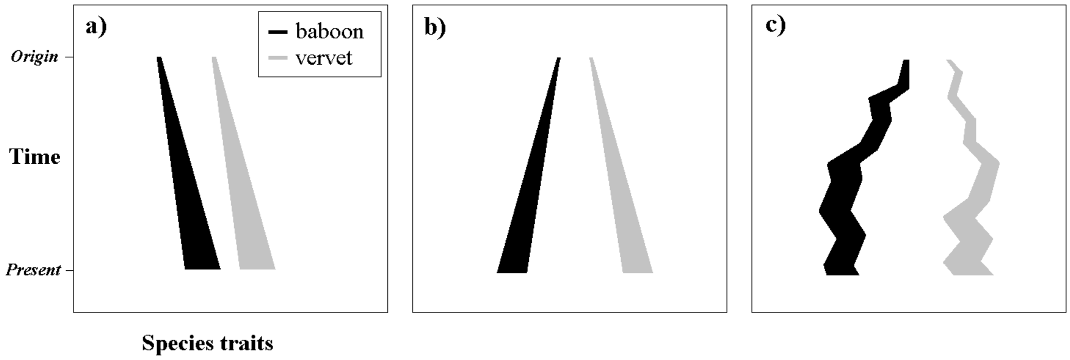


Figure 9.1. Three models for the pattern of specific divergence and subspecific radiation in two species from their origin to the present day. Two sympatric subspecies may either ***a)*** *exhibit the same trajectory of intraspecific divergence as a result of the same overarching environmental pressures (hypothesis 1, table 7.1),* ***b)*** *exhibit different trajectories of intraspecific divergence as a result of overarching environmental pressures exerting their effects on the two species in a different way (hypothesis 2, table 7.1) or* ***c)*** *exhibit different trajectories as a result of stochastic effects creating a random or Brownian divergence (hypothesis 3, table 7.1).*

First, given the general similarity of the study taxa, for instance in habitat, social structure, and a shared African environment (Chapter 1), it could be justifiably hypothesised that the pattern of subspecific divergence and magnitudes of environmental correlates would be correspondingly similar. Such an hypothesis is necessarily based on divergence being adaptive, with the environment exerting a strong and similar selection pressure on the two species. Here stochastic effects such as drift (Wright, 1931) and founder events exert a small effect relative to natural selection caused by the broader environment. Similar selection pressures act from the beginning in the same manner in spite of differences in the ancestral state of the two species. This is illustrated graphically in fig. 7.1a, where divergence is represented as a broadening line, or wedge, from an ancestral point to the modern spread of subspecific phenotypes. The similarity of subspecific divergence is represented by the identical gradient of the wedge-shaped divergences. The underlying force here is the environment (in its broad sense incorporating biotic and abiotic factors), which being the same for the two species exerts itself in the same way. A useful analogy is of the trajectory of two balls dropped, a fixed distance apart, on an inclined table (Goldberg et al., 2007). The spheres will describe the same trajectory irrespective of where they are dropped. Initial differences are immaterial next to the force of the environment, represented by gravity and the incline of the surface. Stochastic or chance effects are negligible.

There is considerable empirical evidence of convergent adaptation in animal radiations, in the face of different starting conditions. Similarities in placental and marsupial mammal radiations are extensive (Springer et al., 1997) despite fundamental differences in reproductive physiology. These correspondences provide evidence for certain environmental niches into which natural selection drives animals, resulting in convergent forms irrespective of ancestry. Ecomorphological analogues include marsupial moles and placental moles, the ant-eating numbat and aardvark, the flying squirrel and the almost indistinguishable sugar glider, as well as the wolf and the recently extinct thylacine or Tasmanian tiger (Springer et al., 1997).

Convergence in subspecific radiations is understudied, presumably owing to the subtlety of the differences involved. Nevertheless there is some evidence of convergent adaptation in independent colonisation events within species, suggesting adaptiveness to subspecific variation. For instance in a study of birds of the genus *Zosterops*, a clade which has independently colonised numerous islands, the pattern of mainland-island change was consistent in several cases (Clegg et al., 2002). The colonisation of North American by sparrows quickly resulted in a pattern of large animals in the north and small ones in the south, corresponding to the existing size cline of several other species (James, 1991). Sparrows similarly fell in line with existing birds on New Zealand (Baker, 1980) and opossums introduced to New Zealand quickly began to exhibit size variation corresponding to that of the animals on Australia itself (Millien et al., 2006).

However, general size trends may obfuscate more subtle and unique morphological differentiation. The study by Clegg et al. (2002) reported some evidence of shape differentiation that was unique to each colonisation. Indeed a study of pipistrelle bats found that each of three colonisations produced separate skull morphologies (Evin et al., Accepted). There are two explanations for this. One is local adaptation, where differential selection pressures create differences in morphology. Alternatively chance and founder effects (stochastic events) cause differentiation.

Indeed, many radiations take place that are entirely unique and lack any analogy with other radiations; there are more unique animals than convergent ones. This is not to deny the role of natural selection as a deterministic force, but rather that it might not always drive animals to evolve down the same path, either because of the environments are different, or if they are the same because of differences in starting points.

Table 9.1. A summary of three hypotheses representing extreme forms of subspecific variation.

Hypotheses	Description
Hypothesis 1	The overarching similarity of environment causes the same pattern and magnitude of correlates in subspecific divergence
Hypothesis 2	Overarching environments act differently on the two species because of their initial differences, causing differences in pattern and magnitude of correlates in subspecific divergence
Hypothesis 3	Environment is a minor factor relative to stochastic differences in subspecific divergence

Hypothesis 1 is a model where the environmental selective pressures push disparate animals down the same path of divergence. However, some of the evidence above suggests a model is required where there is an interaction between the environment and differences in starting condition. In the case of vervets and baboons these differences are significant, and selection might therefore act in quite different ways, resulting in different patterns of subspecific diversity. The importance of starting conditions can best be expressed by an adaptive landscape model (Wright, 1932, Chapter 1). This approach uses a conceptual landscape where peaks represent adaptive states. Natural selection acts to push an animal up an adaptive peak, lifting it out of a maladaptive trough. The first hypothesis can be represented as a landscape with a single adaptive peak. Natural selection acts to drive both taxa up this single peak wherever they start on the landscape because it is the only path available. However, in a landscape with multiple peaks, starting position, representing ancestral condition, is crucial to the trajectory taken. The further away the species start the less likely they are to ascend the same adaptive peak. Hypothesis 2 is shown graphically in fig. 7.1b. In terms of the ball and surface analogy, this time while the plane is sloped there is also a watershed inclined from the middle. Dropping the two species either side of this watershed results in divergent patterns of divergence (fig. 7.1b).

The first and second hypotheses are both adaptationist. While adaptation can arise through chance preadaptation (Gould and Vrba, 1982), it more often arises as a result of natural selection favouring those traits that suit an animal to its environment. However, genetic drift and mutation also play a role in shaping genotype and phenotype (Wright, 1931, Clegg et al., 2002). This neutralist evolutionary paradigm is based on the observation that genetic changes tend to be regular, irrespective of evolutionary change (Kimura, 1968, Kimura, 1969). So called “living fossils” that exhibit a long evolutionary history of morphological stasis show as much genetic change as rapidly evolving lineages. This suggests most genetic change is neutral with respect to phenotype and fitness. However, though there are instances of phenotype remaining stable over time, there are also instances of phenotype evolving according to drift. It seems to be dependent on whether stabilising selection is acting on morphology or not. For instance, in cardueline finches morphological variation could not be described by drift alone. In this case there was actually less morphological variation than drift would predict (Björklund, 1994). This suggests stabilising selection acting against drift to maintain certain phenotypes. Given much of the morphological variation was related to bill morphology which has a clear trophic role, it is likely that natural selection prevents genetic drift from realising certain mechanically disadvantageous phenotypes. That said, in the absence of stabilising selection, such as when a phenotype lacks so circumscribed a function, drift is free to occur. Genetic drift alone was able to explain morphological variation in body lengths and proportions of the lizard *Anolis sagrei* (Kolbe et al., 2007). Morphological variation in the skulls of small bodied tamarins and the *Fusicollis* group was consistent with a model of genetic drift alone and no selection (Ackermann and Cheverud, 2002), though not in the *Nigricollis* group. Indeed drift was also shown to be the major factor in modern human variation (Ackermann and Cheverud, 2004). Drift therefore is certainly of considerably evolutionary importance, though its magnitude remains equivocal. Consequently the third hypothesis of specific divergence in subspecific radiation is a neutralist theory that posits all the observed morphological variation is the result of drift.

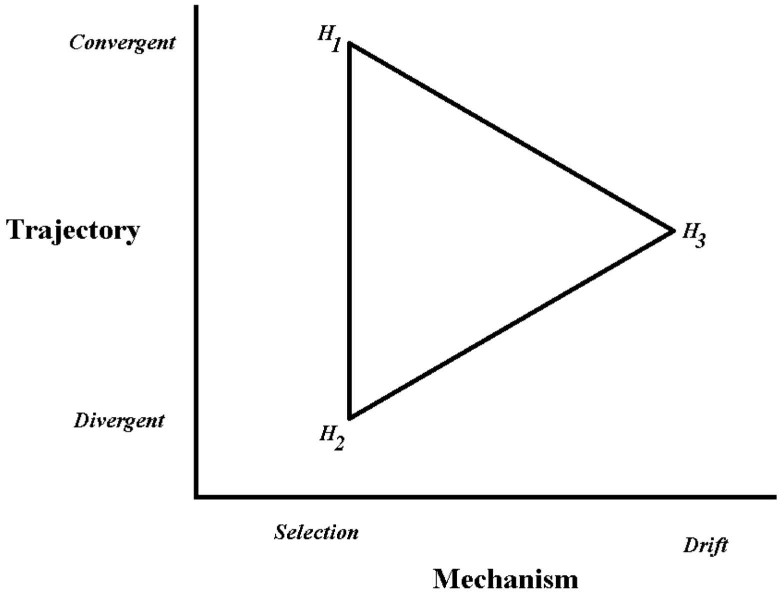


Figure 9.2. A conceptual model demonstrating the features of the three hypotheses in table 7.1 and fig. 7.1. The three hypotheses represent extremes, and so the true pattern of divergence can fall anywhere within triangle delineated by these three points. The x-axis shows the mechanism by which subspecific divergence may arise, namely through natural selection or drift. The y-axis shows the trajectory of the two study taxa which may either be convergent or divergent in their pattern of subspecific radiation.

So far three models have been proposed as hypotheses to explain the way in which the two subspecies might have subspecficially radiated. Reality is likely to be somewhere within the space demarcated by these three extremes. As there are two underlying features, selection versus drift and divergent versus convergent radiation, this may be conceptualised as a triangle in a space defined by those two axes (fig. 7.2). In order to determine the true position the specific starting points, their interaction or not with divergence and the likely underpinning (selection or drift) must be discussed.

7.3 DIFFERENCES IN SPECIFIC CHARACTERISTICS

Of interest to all hypotheses, but in particular hypothesis 2, is the initial difference in species characteristics before the radiation into current subspecific forms, namely the last common ancestor of all existing vervet subspecies and the last common ancestor of all baboon subspecies. It should be stated for clarification that the last common ancestor of both taxa is not of concern when considering differences in the two subspecific radiations. Consideration of these ancestral starting points is crucial for recreating the evolutionary raw material on which natural selection could act, in order to address whether natural selection is likely have exerted a similar effect. Potentially animals that are significantly different cannot be affected by natural selection in the same way and will follow unique trajectories (illustrated in fig. 7.1b). Hence consideration of the differences in staring point is crucial to see if this interacts with the environment to cause differences in the pattern of divergence.

The precise features of the two pre-divergence ancestral conditions are unknowable. However, though considerable variation has emerged from these two progenitors, the ancestral state is unlikely to be very different from the modern state owing to the rather shallow time depth and thus limited scope for change. Certainly the disparity between modern and past specific characteristics are necessarily small in magnitude relative to the differences between the two species.

Table 9.2. A summary of the differences in specific characteristics of baboons and vervets.

	Baboons	**Vervets**	**Reference**
Site of Evolution	South Africa	West Africa	*(Fedigan and Fedigan, 1988 Hauser, personal communication, Chapter 6, Elton, 2007)*
Size	10-30 kg	3-4 kg	*(Bolter and Zihlman, 2003, Fleagle, 1988)*
Flexibility			
• Reproduction	Aseasonal	Seasonal	*(Butynski, 1988, Alberts and Altmann, 2006)*
• Habitat use	Wide	Less wide (lesser savannah use, absent from montane environment)	*(Kingdon, 1997, Alberts and Altmann, 2006)*
• Diet	Wide diet, opportunistic, eclectic	Diet half as wide over the year, and narrower at any one point.	*(Altmann, 1998, Barrett, 2005, Alberts and Altmann, 2006)*
• Social System	Variable	Invariable	*(Kummer, 1968, Schreier and Swedell, 2009, Maestripieri et al., 2007, Fedigan and Fedigan, 1988)*

While there are difference between vervets and baboons (table 7.2), they are generally similar (Chapter 1). Both are found south of the Sahara to the Cape and from the west coast of Africa to the east (Kingdon, 1997). They both avoid only true desert and high rainforest, living in savannah and forest mosaic. They both live in groups with male dispersal and female philopatry (Isbell et al., 1993, Alberts and Altmann, 1995) with sexual dimorphism (Fleagle, 1988) and a similar time budget requirements (Dunbar, 1992, Harrison, 1985, Hill, 1999, Willems and Hill, 2010).

Physiology and anatomy are largely similar owing to a recent divergence, circa 10 Mya (Tosi et al., 2005).

However, these broad similarities mask numerous differences. In particular, the site of origin of extant forms is different for vervets and baboons. The ancestor of modern vervets arose in West Africa (table 7.2, Chapter 5) in contrast with baboons which arose in southern Africa. This hypothesis is supported by three lines of evidence. First, vervets are absent from the southern African fossil record in spite of good preservation of papionins in this region (Elton, 2007). Second, provisional genetic data suggest the most basally divergent and genetically diverse subspecies is the *C. a. sabaeus* (Hauser, personal communication). Third, this study finds the greatest morphological distance between *C. a. sabaeus* (Chapter 6). Baboons in contrast, are well represented in southern Africa (Delson et al., 2000), and genetics put the greatest split between a north and south group (Zinner et al., 2009b). The consensus therefore is for a southern African origin.

Difference in site of origin is likely to fundamentally affect the way natural selection has acted on the two study species. In broad terms the vervet progenitor was adapted to the features of West Africa, an equatorial, comparatively wet, consistently warm environment with low temperature seasonality (Rubel and Kottek, 2010). This environment is productive and fruit rich (Culot, 2003). The ancestral baboon is more likely to be adapted to the features of southern Africa, which is an arid (Rubel and Kottek, 2010) and seasonal environment (Anderson, 1982). Thus the ancestor of vervets probably had adaptations quite different from the ancestor of modern baboons. Subsequently radiations based on these different starting points could potentially trace different evolutionary trajectories. In the parlance of Sewell Wright (1932) both the differences between subspecies mean they have quite different adaptive landscapes.

The second major difference between baboons and vervets is a striking difference in size (table 7.2). Baboons range between 10-30 kg while at 3-4 kg vervets are much smaller (Bolter and Zihlman, 2003, Fleagle, 1988). Baboons are posited to have got larger in recent times, with Kinda baboons representing something closer to the ancestral state (Leigh, 2006). Certainly fossil baboons such as *P. izodi* are small, and the large size of the chacma and olive baboon are probably derived.

The most basally derived vervet is *C. a. sabaeus*, which is actually the largest vervet subspecies. Whether this size increase is retention of the ancestral size or is a derived character is difficult to say. However, even assuming a baboon progenitor at the smaller end of the current size spectrum and a vervet towards the larger end, the size difference at that point would still have been marked. Size has numerous implications for metabolism, life history and predation (Peters, 1983). Smaller animals have proportionally higher metabolisms and thus require more calories (Demment, 1983, Demment and van Soest, 1985). As such natural selection is less likely to be able to drive a small animal, such as a vervet monkey, down a resource-poor dietary strategy, such as corm and tuber eating, if there is some limit on an increase in body mass. Smaller size also means that animals are less buffered from the environment, as they have physically smaller energy reserves, as well as a disproportionately higher metabolism (Boyce, 1978, Lindstedt and Boyce, 1985).

Vervets have 16 predators while baboons have only four (Struhsaker, 1967b). This obviously changes the predation risk, which is a major determinant of socioecology. Predation risk is argued to be at the heart of group living (Hill and Lee, 1998) and time budget (Willems and Hill, 2009, Hill and Lee, 1998). This heightened predation-risk might therefore act as an evolutionary constraint to entering certain niches. Certainly vervets spend less time in the savannah and are more tied to trees, which are refugial habitats (Altmann and Altmann, 1970). Additionally, smaller size means smaller muscles and correspondingly smaller power. Vervet struggle to uproot the subterranean foods that baboons manage to uproot with relative ease, making a considerable proportion of their diet (Altmann, 1998).

Both vervets and baboons are highly flexible monkeys (Altmann and Altmann, 1970, Fedigan and Fedigan, 1988). Indeed it is this flexibility that has enabled them to colonise so much of sub-Saharan Africa and explains their status as being of little conservation concern (IUCN, 2010). However, of the two species the baboon is the more flexible in a variety of ways. One enduring life history difference is in the time of reproduction. Vervets are constrained to mate and reproduce at the same point in the year (Baldellou and Adan, 1997). For vervets this is an hormonal change caused by changes in the physical environment such as temperature (Baldellou and Adan, 1997). This is one strategy employed by guenons of ensuring young are born when conditions are most favourable (Butynski, 1988). An additional advantage to birthing synchrony is the anti-predator benefit it confers, with large numbers of young reducing the predation risk per offspring given a finite number of predators (Ims, 1990, Janson and Verdolin, 2005). An additional reason might be to avoid allomothering (Kavanagh, 1977), in the sense of harmful infant transfer (Kohda, 1985), where females deprive the mother of her infant, leading to infant stress, and in some cases death. Such a social selective pressure is likely to act against a female who births out of season.

Baboons do not have a fixed mating season, with young being born throughout the year (Alberts and Altmann, 2006). Possibly as baboons have fewer predators (Struhsaker, 1967a), owing to their larger size as discussed, birthing synchrony is of relatively little importance. However, perhaps time of year is fundamentally less important for baboon infant survival. That is not to say baboon reproduction is unrelated to the environment: interbirth interval is related to temperature (Hill and Dunbar, 2002). However, this is not directly causal and mediated by hormones as in vervets, but rather is underpinned by the fact that temperature relates to resources and energy expenditure. As such baboons do not need to time birthing according to the fruiting of some potential food tree. Rather baboons have the flexibility to respond to interannual variation by enabling them to exploit an environmental windfall, and cut their losses in a bad year. Indeed inter-birth interval is related more to position in the dominance hierarchy (Smuts and Nicolson, 1989), no doubt owing to the greater foraging access enjoyed by high ranking individuals. As such personal condition matters more than seasonal conditions for baboons.

The general difference therefore is that vervets exhibit a strategy of following the predictable seasonal variation in resources, with their fixed mating system, while baboons are flexible in reproduction, and thus can invest in offspring whenever the environment favours it (Bercovitch and Harding, 1993, Wasser, 1996). Baboons are no doubt aided in this by their greater dietary generalism, taking advantage of windfall events, as the fruiting of a particular tree or some insect superabundance event (Chapter 3). This enables them to convert more of the available resources into growth or reproductive effort. Vervets in contrast track resources specialising on a few foods over the year (Chapter 3). Indeed this results in the oft cited crash in populations during the dry period in Amboseli (Samuels and Altmann, 1991). The baboon dietary strategy enables them to have this flexible life history strategy that to some degree buffers them from their environment when conditions deteriorate (Alberts and Altmann, 2006), but allows them to make the utmost of conditions when they are favourable (Bercovitch and Harding, 1993).

Baboons show more considerable environmental responsiveness and consequently variation in their social system than vervets. While most baboon subspecies exhibit female philopatry and male dispersal, as does the vervet, the hamadryas baboon has the opposite system (Kummer, 1968). Moreover, this subspecies does not have multimale groups but small units with a single male. These solitaries dominate a harem of females (Kummer, 1968), which they herd, keeping them within the group by agonistically punishing those which stray. The Guinea baboon shows tendencies towards this end of the spectrum of social behaviour, with one male units that build up into larger association for sleeping and travelling (Maestripieri et al., 2007, Galat-Luong et al., 2006). Crucially however Guinea baboons do not herd females and males tolerate other males (Maestripieri et al., 2007, Galat-Luong et al., 2006). Whether these social system differences are “flexible” or not is hard to say. It is possible that they are under strict genetic control, as hamadryas-olive baboon hybrids showing intermediacy in these traits (Bergman et al., 2008). The ancestral condition was probably one corresponding to multi-male groups, with one male units being a derived feature. However, it is likely that the ancestral baboon had more social flexibility than the vervet, some of which has now become fixed as described.

7. 4 SUMMARY OF THE FEATURES OF THE TWO SUBSPECIFIC RADIATIONS

So far the probable starting conditions before subspecific divergence have been considered. It is on these features that natural selection might have acted to give rise to the current pattern of intraspecific variation. The next step is to summarise the major features of the two radiations from work in the previous chapters. Doing so will enable the integration of this information with that of the previous section and will enable testing of the three hypotheses. This in turn will enable a categorical decision on the processes that have shaped the current intraspecific diversity. To that end Chapters 3, 4, 5 and 6 have revealed numerous differences in the pattern of intraspecific variation (summarised in table 7.3).

Table 9.3. A summary of the features of subspecific variation for the vervet and the baboon.

	Baboons	**Vervets**	**Source**
Clinal variation	Size-related. North-South clinal component. Small in West Africa	Size-unrelated Largely East West Large in West Africa	(Cardini et al., 2007 Chapter 2)
Phylogeny	Northern and southern clade	Divisions smaller.	(Zinner et al., 2009b Chapter 6)
Diet	Significant difference and correlated with morphology	Nonsignificant differences, uncorrelated with morphology	(Chapter 3, 4)
Environment	Acting on diet	Acting directly	(Chapter 6)

7.4.1 Clinal Variation

Both vervets and baboons exhibit clinal variation (Chapter 2Grubb et al., 2003, Jolly, 1993, Cardini et al., 2007). While there are slightly steeper gradients of change from one subspecies to the next, on the whole the pattern of change is continuous in these taxa. The contours of this clinal variation in baboons have been mapped and compared with that of vervets (Chapter 2). To some extent vervets and baboons are similar: animals in East Africa are small while animals in West Africa are large. However, this similarity breaks down, with vervets having large animals in West Africa corresponding to the *C. a. sabaeus* subspecies, while baboons have small animals in this region corresponding to *P. h. papio*. Shape in both cases follows size, although crucially with baboons there is a north-south component reflecting the change from northern to southern taxa. Dissociation of size and shape reveals that this east-west trend is largely the product of allometric scaling. Controlling for size reveals a north south clinal change, agreeing with earlier work by Frost et al.(2003), and suggesting a phylogenetic underpinning to this pattern. For vervets allometry appears to be a very small part of the differences between subspecies (Elton et al., 2010). The removal of size does little to erode the difference between subspecies, in stark contrast to baboons. Baboons and vervets thus display different patterns and underlying relationships with size suggesting their pattern of morphological variation is rather different.

7.4.2Phylogeny

Phylogeny was discovered to be a greater explanatory factor in baboon morphological variation than in vervets, even with size correction (Chapter 5, 6). Given the probably more limited capacity for dispersal in vervets this is surprising. While using taxon for vervets is an abstraction of a more complex but unavailable phylogeny, using taxon for baboons revealed that this probably overestimated true phylogeny. As such it can reasonably be concluded that phylogeny is a greater explanatory variable in baboons. Chapter 5 suggests that vervets have a shorter history of their pan- African distribution unlike baboons and so deep splits have not had time to arise.

In baboons the deepest split was on a north south axis of variation corresponding to the split. Nevertheless, this is not a steep division. Hybridisation occurs between yellow and olive baboons which are putatively on opposite sides of this split. Additionally, phylogenetic correction of yellow baboons, to counter the effects of putative mtDNA introgression, does not greatly increase the explanatory power of phylogeny.

7.4.3 Diet

The two subspecies differ markedly in their relationship with diet (Chapter 3, 4). Baboons exhibit a significant subspecific difference in the amount of subterranean foods in the diets of olive and chacma baboons. It is likely a larger sample size would reveal more significant differences, as the Guinea baboon in particular is highly frugivorous (Chapter 3). This correlated significantly and well with an axis of morphological variation (Chapter 4). Vervets, in contrast, were found to exhibit no subspecific dietary differences and no significant morphological correlation with diet was found.

Vervets have a smaller dietary niche width and do not eat the subterranean foods that are central to the variation in baboon morphology (Chapter 3). It is possible that vervets therefore lack the dietary differentiation of baboons simply because of this. However, vervets do not avoid this food out of choice: their smaller size leaves them without the capacity to eat such foods. One potential split, that was not statistical owing to the single datum for this species, is between the djam-djam and other vervets. This species is highly folivorous, eating as much as 80% leaves. It is likely therefore that any differentiation exists as an axis between this and the more frugivorous other subspecies. This represents a completely different axis and evolutionary trajectory from that seen in baboons.

7.4.4 Environment

Environment correlates with shape, though for baboons partial regression reveals spatial terms seem overwhelmingly more important (Chapter 2). Nevertheless the path analysis reveals that environment acts principally via diet, so the baboon is not responding to the environment *per se* but to the environmentally determined dietary variation (Chapter 6). In contrast vervets appear to be more environmentally determined as shown by the path analysis (Chapter 6) and the findings of Cardini et al. (2007) which suggested rainfall underpinned the clinal trend.

7.5 HYPOTHESIS TESTING

So far this chapter has presented three hypotheses as models for the subspecific divergence in the baboon and vervet. A picture of the pre-diversification baboon and vervets have been constructed from extant characters, and the features of the two subspecific radiations have been summarised and integrated. Thus, all the information is present for testing the hypotheses. Hypothesis 1 proposed a similar trajectory of subspecific variation for vervets and baboons. This hypothesis would predict the same pattern of subspecific variation in the two taxa. For instance this hypothesis would suggest identical clinal variation, the same magnitude of phylogenetic, environmental and dietary correlation with morphology, and interrelation between these factors. However, each chapter has revealed differences (table 7.3) as well as differences in the interaction between these variables (Chapter 5). Obviously there are numerous proxies and uncertainties. For instance a lack of data may be responsible for the absence of subspecific dietary differences in vervets. However, as described in Chapter 3, were a difference to be present it would concern different food types from that of baboons. Similarly we can be confident in the different influences of past environmental variation leaving its mark on phylogenetic variation, which seems to differ between the two taxa. Thus the findings suggest that different processes are at work in structuring subspecific variation in the two taxa, falsifying hypothesis 1.

If the environment is not acting in the same way to cause the subspecific radiations of the vervet and baboons, then there are two potential explanations for this divergence, corresponding to hypotheses 2 and 3. It is possible that differences in starting condition are important. In Wright’s terms, the two taxa exist in different adaptive landscapes with radically different topologies. As such natural selection would be expected to channel subspecific divergence down two separate trajectories relating to the features of the pre-radiation vervet and baboon. Considerable correspondence between differences in starting condition and patterns of radiation would be required to prove this. However, most of the differences in the two subspecific radiations, reported so far in this work have been couched in terms of the gross differences between the two taxa. Differences in size between vervets and baboons in particular have appeared numerously as explanations for differences in the two subspecific radiations. For instance, the fact that vervets are physically unable to acquire the subterranean foods, owing to their small size (Altmann, 1998, Barrett, 2005), means that these are absent from their diet. In baboons the major dietary axis of variation is related to subterranean food eating (Chapter 3). As such the fact that vervets do not eat these foods and have a correspondingly smaller dietary repertoire and lower inter-subspecific variation can be put down to size.

Size is likely to underlie differences in the relationship between morphological and environmental variation in the two taxa. Larger animals are more buffered from environmental variation by virtue of being better able to withstanding periods of famine (Lindstedt and Boyce, 1985, Chapter 2). This doubtless has an impact on life history and general flexibility. Vervets rely very much on a seasonal peaks of food, mating in one season so as to produce young that are around at the time of peak food (Butynski, 1988). The path analysis (Chapter 6) shows a relationship between environment and morphological variation, which for vervets is high, in concordance with this environmental dependence of the species. While the environmental and morphological correlation is high for baboons the path analysis shows that baboons actually respond via diet, rather than to the environment *per se*. An inherent feature of baboons is their flexibility and nonadherence to a seasonal cycle of reproduction. When conditions are particularly good, such as windfall fruiting years or when there are swarms of edible insects, these resources can be directly invested into reproduction. There is no single window of opportunity for reproduction as there is with guenons. This flexibility thus enables baboons to greatly increase their fitness (Alberts and Altmann, 2006). For vervets there is a single mating season for good or bad years. As such vervets are adapted to the environment rather than food itself. Vervet diet is relatively inflexible, again perhaps because their small size prevents them from moving into the baboon niche, but also because they are stuck in a seasonal pattern, and being flexible in terms of food acquisition and reproduction is at a lower premium.

A scheme to attempt to make sense of these relationships between size, life history, dietary and environmental variability and environment is presented in fig. 7.3. Larger body size can be seen to cause baboons to be physically buffered from unfavourable features of the physical environment, such as food shortage on the seasonal and interannual scale. Acquiring subterranean foods further enables them to withstand environmental hardships by falling back on this superabundant but poor quality resource (fig. 7.3). This buffering enables the break with seasonal reproduction and allows the baboons to pursue a strategy of dietary generalism and flexibility, enabling them to extract more from the environment when conditions are good. Some of this variation in dietary ecology has an effect on growth and subspecific morphological variation. For vervets the limitation imposed on dietary niche width by size means the link between diet and morphology is small (Chapter

6). However, environment exerts a greater direct influence unlike with baboons, representing the findings of the path analysis (Chapter 6).

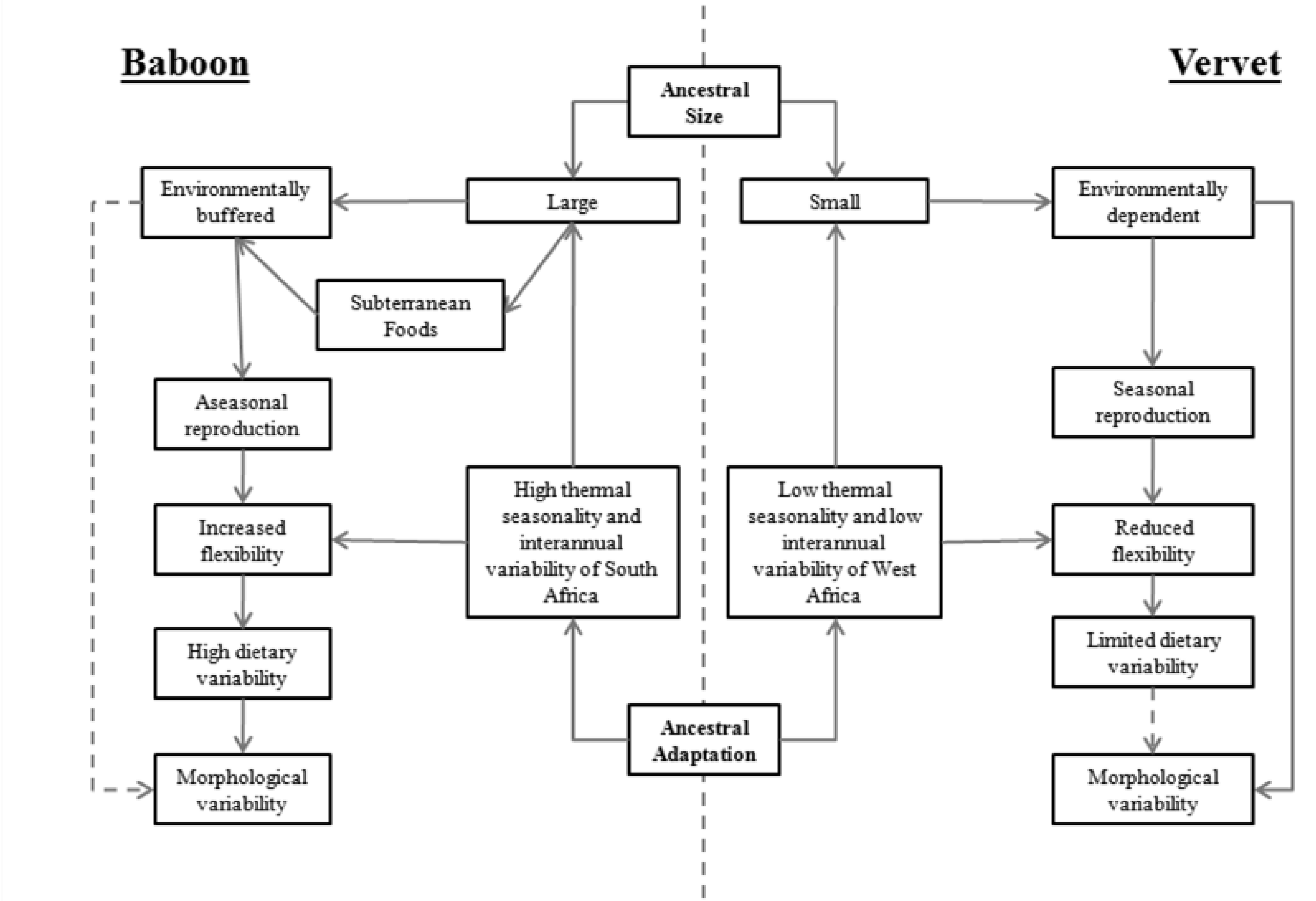


Figure 9.3. A schematic showing how intrinsic differences, in size and site of origin of the two taxa, account for differences in the subspecific radiations of the two taxa. Dashed lines denote weaker relationships than full lines.

Another aspect built into this model (fig. 7.3), though perhaps more tentatively, is differences in the site of origin of the two radiations, and its possible impact. The two taxa arose in different parts of Africa, which is likely to have some effect on how natural selection could have acted on the two subspecific radiations. Baboons evolved in southern Africa and must therefore faced quite different selection pressures, adapting them to high intra-annual, and interannual variation. Vervets on the other hand are adapted to an environment that, though exhibiting rainfall and fruiting seasonality, is low in temperature seasonality and interannual variation. As such the two have been exposed to very different selection pressures before the onset of their two subspecific radiations. Additionally subspecific range evidence suggests vervets have a shorter history in southern Africa, relative to the time baboons have had in West Africa (Chapter 5). *C. a. pygerythrus* has a very long range from East Africa to southern Africa, where one finds three subspecies of baboons. The lack of subspecific splits, suggests the vervet was not subject to the same Pleistocene environmental fluctuations that structured subspecific variation in baboons, arguing for its more recent colonisation of this habitat.

In order to differentiate between hypotheses 2 and 3, the extent of these stochastic factors must be determined. To truly disprove stochastic causes would require clear demonstration of adaptation. However, proving adaptation is difficult. The clearest way of proving selection is by measuring genetic change and demonstrating this to be elevated above that the background level of drift. Without genetic information greater care must be taken. If a trait is shown to be adaptive it might be justifiably considered the result of natural selection. However, Chapter 4 revealed no evidence to support biomechanical adaptation in the relationship between diet and morphology, and while this may be a type II error reflecting poor proxies and highly subtle differences, there is still no categorical proof of adaptation. However, the fact that the highest correlation in baboons was between dietary and morphological variation does seem highly likely to be adaptive. Baboons exhibit considerable plasticity and flexibility. That some of this morphological variation has become fixed in such a way that aligns with diet would seem to strongly imply adaptation. It resounds with the observation with field observations of baboons being excellent foragers, capable of eating an array of foods and withstanding periods of food scarcity. Vervets in contrast have constraints that keep them out of the baboon niche. This restriction from an untenable niche might be considered adaptive, though again might arise as a result of drift. On balance, therefore while correlational evidence suggests natural selection and adaptation are likely drivers of subspecific variation, unequivocal proof of adaptation and a clear causal mechanism of getting from dietary and environmental variation remains elusive.

7.7 FURTHER WORK: ADAPTATION OR DRIFT?

While it has been shown that the vervet and baboon are not similar in their pattern of subspecific radiation, the case for adaptive versus stochastic divergence as a determinant of subspecific variation is equivocal. Morphological variation is tied up with growth and is thus the result of a complex interplay between ecological factors such as resource availability, predation risk and groups size. It is probably that life history and socioecology are first to adapt to these factors, with morphology representing differential growth across certain habitats. With so much of this information missing, it is hard to establish if morphology represents an adaptive trade-off in growth. Additionally, while biomechanical adaptation has not been shown, further work incorporating stress and strain reduction theory might shed further light on the morphological-dietary axes described.

Phylogeny has been shown to be important in baboon and vervet morphological variation. Phylogeny yields information about gene flux, which, when reduced, can promote adaptation to local conditions, as well as lead to diversity without any adaptive significance. Given that both species show typological variation corresponding to subspecies, even though clinal variation and hybridisation take place, Pleistocene climate variation is likely to have resulted in some of the current morphological variation. However the extent of this is unknown. Climate modelling, and comparison with sympatric, ecologically similar species might shed light on the extent to which past reductions in gene flow (zygostructure) are responsible for structuring morphological variation.

7.8 CONCLUSION

That baboons are flexible is not a new finding. However, this works suggest that the inherent flexibility characteristic of baboons has resulted in a pattern of subspecific variation markedly different from that of vervets, which is unable to occupy the same niche space as baboons. The baboon is larger, freeing it from certain constraints of predation and nutrition that exert a considerable effect on the vervet. Additionally, and perhaps underpinning some of this flexibility, the baboon has a greater body mass, buffering it from periods of food scarcity and enabling it to more efficiently eat fibrous foods of low energetic value. Baboons exploit their environment far more efficiently than the vervet, responding to environmentally structured dietary variation. While it seems likely that these divergent patterns reflect an interaction between natural selection and the inherent differences of the two taxa, the difficulty of proving adaptation means a stochastic underpinning to these divergent trajectories cannot be ruled out.

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