The Evolution of Social Systems in Human and Non-Human Primates

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Submitted for the degree of Doctor of Philosophy
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For my Dad

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Abstract

From a Darwinian perspective, both history and environment are causal factors for change in animal social behaviour. Because behaviour leaves no fossil evidence researchers have focused on how social systems help animals and humans adapt to their current environments and have only been able to make tentative suggestions about how such systems may have evolved. However, a new theoretical framework, based on Darwin's insights, allows phylogenetic relatedness to be incorporated into comparative analyses to discover the ancestral states of social behaviour and the ultimate drivers of change in human and primate societies. This thesis uses these new methods to investigate the history and drivers of change in human and primate sociality and proposes a new model of primate social evolution. Analyses of mating systems suggest that social monogamy in humans and other primates is the result of infanticide risk brought about by life history changes. These methods were also able to reveal how changes in inheritance rules to matriliny among Bantu-speaking societies, contributed to a switch to matrilocal residence, which in turn contributed to a change from polygynous marriage to monogamy. Cultural history effects change in both descent and residence patterns, while geographical proximity also affects descent, but residence and environmental factors drive changes in marriage. This approach may provide a way for the various schools for the study of human and primate social behaviour to collaborate more closely and provide ultimate answers to the drivers of change in human society.

Contents

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Chapter 1 Introduction

1.1 History & Evolution

1.1.1 History

Darwin's *Origin of Species* (Darwin 1968 [1859]) provided the theoretical framework to explain the evolution of animal social behaviour and showed that human social behaviour was also governed by these laws of natural and sexual selection (Darwin 2004 [1871]). Early anthropologists, inspired by Darwin's insights applied evolutionary thinking to the development of culture, arguing that humans inherited their social institutions from their primate origins (Morgan 1964 [1877], Tylor 1973 [1873]). These 'cultural evolutionists' proposed that culture developed gradually; in a simple and linear way, from 'savage' beginnings to an 'ideal civilised state'. However, subsequent field studies undermined this euro-centric view, showing no clear progression from 'primitive' to 'civilised' societies, such that some researchers proposed that different societies were simply different expressions of a cultural life that fundamentally separated humans from animals (Boas 1938 [1911]). Humans were seen as separate from the animal kingdom and not governed by the same general laws (Boas 1932). Instead, customs, or cultural traits, were related to culture as a whole (Malinowski 1970 [1944]), and their importance could be judged only in that light, and not in terms of the evolutionary origins of society (Radcliffe-Brown 1950, Radcliffe-Brown 1952).

At this time, evolutionary thinking based on Darwin's view of gradual change was also facing challenge, because it could not be reconciled with the emerging field of Mendelenian genetics. It was not until the mid-1930s that the work of Fisher, Haldane and Wright, amongst others, brought about reconciliation between gradual evolution and genetics in the 'New Synthesis' (Huxley 1942). This new approach provided the basis for all subsequent evolutionary research, including the study of animal social behaviour and more recently, some approaches to human social behaviour.

1.1.2 Evolution

By making comparisons across numbers of taxa, Darwin (Darwin 1968 [1859], Darwin 2004 [1871]) was able to identify the mechanism of evolution as descent with modification by which organisms adapt to their environment. The comparative method provides the means to study trait evolution and infer instances of adaptation (Harvey and Pagel 1991, Nunn 2011). Adaptation can be seen as the evolutionary change in a trait in response to a selective pressure, which could be another trait or some aspect of the environment (Harvey and Pagel 1991). However, the comparative method cannot reveal adaptation on its own, since it can only identify correlations between traits or between a trait and the environment, but not the driver of evolutionary change. In the study of the evolution of morphology, fossils can be used to indicate ancestral and derived features, which enable the identification of causality. In the study of behaviour however, where fossils are not available, assumptions have to be made about the direction of causality, which are not always made explicit.

Furthermore, it has been argued that, while morphological traits are slow to change, behaviour is far more labile, responding only to the current environment; history is not important in its evolution (Atz 1970, Blomberg, Garland, and Ives 2003). However, more recently, tests have shown that behaviour displays similar levels of historical inertia as other traits (Rendall and Di Fiore 2007), and that living organisms carry information about both the history of a trait and its adaptive potential (Harvey and Pagel 1991). If methods are employed that use the historical information revealed by living organisms, not only can correlated evolution be established but also the drivers of adaptive change. It is these methods that I use in this thesis to reveal the evolution of primate and human social systems and their causes.

1.2 Primate Socioecology

Following the modern synthesis of evolution and genetics (Huxley 1942), early field studies of howler monkeys (Carpenter 1934) and baboons (DeVore and Washburn 1963, Kummer 1968) sought to establish a link between the social relations in primate societies and the environments in which they live. However, it was Crook and Gartlan (Crook and Gartlan 1966) that were the first to propose a broad evolutionary approach to primate sociality. Drawing on earlier studies across bird species, they suggested that environmental variables had a predictable relationship with primate social organisation, allowing them to be classified into grades. They proposed that the combination of activity level and habitat meant that nocturnal species are predominantly solitary, while diurnal species form small groups in forest habitats and large groups on the savannah, but desert species have multi-tiered societies (Crook and Gartlan 1966). However, the ecological grades they proposed were not coherent and it was not clear what selective pressures were driving them (Janson 2000). Furthermore variation between or within species could not be explained using the grade system, while guenons, for example, show a similar uni-male harem system across a wide range of different habitats (Struhsaker 1969).

Further explanations were proposed to deal with these inconsistencies, based on the nature of food distribution and habitat quality. Where the environment was poor and food was scarce, species were said to form uni-male groups, but where habitats were richer groups were thought to be able to afford to have more males, who could provide for better group defence against predators (Denham 1971). The larger the clumps of food, the lower the competition within the group and the larger the groups could be (Klein and Klein 1975). However, these explanations were seen as stemming from a group selection viewpoint and did not provide a satisfactory explanation for individual behaviour (Clutton-Brock and Harvey 1977).

Seeing primates as individual economic entities, with their behaviour driven by the distribution and availability of food, Clutton-Brock and Harvey (1977) conducted a comparative study of 100 species, to recast the Crook and Gartlan's (1966) grades into seven ecological categories. Recognising that some genera might be overrepresented, the analyses were conducted at the genera level to reduce potential bias. However, the grade approach was still not based on an underlying theory of social behaviour. Meanwhile, in the field of behavioural ecology there were theoretical developments such that the study of animal social behaviour was seen in terms of individual costs and benefits (Hamilton 1964a, Hamilton 1964b, Trivers 1972, Maynard Smith 1977). Social and mating systems were thought to be the result of individual fitness strategies, with female behaviour driven by the availability and distribution of food, while male behaviour was driven by the distribution of fertile females (Trivers 1972, Emlen and Oring 1977). Goss-Custard and colleagues (1972) were the first to apply this explicit fitness-maximisation approach to the study of primate social behaviour, suggesting that primate social organisation was the result of individual strategies for survival and mating in response to food availability and the distribution and prevalence of predation. Since primate groups could be better described as societies rather than simply aggregations, with long-term bonds between individuals, the social relationships within groups were thought to be based on the costs and benefits of individual behaviour, such a foraging efficiency (Terborgh and Janson 1986), with group size a result of competition over resources resulting in increased foraging effort and aggression.

Social relations within groups were suggested to be due to individual fitness maximising behaviour, but the question remained: why would primates form groups at all? To explain group living in primates it was first suggested that since bonded females formed the core of many primate groups, groups might be a defence against harassment from males (Wrangham 1979). Alternatively, it was argued, the nature of relations within a group is determined by the distribution of food resources in the environment (Wrangham 1980). This second model suggested that females form groups to defend resources that are clumped in space or time. Where food resources are clumped and defendable, individuals can benefit in inter-group competition for food encouraging females to stay in their natal groups to reap these benefits. In addition females may form kin-based coalitions to mitigate the cost of within-group competition. Where food resources are not defendable, because they are uniform or in small patches, females may disperse, and consequently groups are not formed around kin-based female bonds (Wrangham 1980).

While influential, this model concentrated on food distribution as the only selective pressure on individuals to form groups (van Schaik 1983, van Schaik 1989). To test this new model against earlier suggestions that focused on the role of predation (DeVore and Washburn 1963, Alexander 1974), van Schaik (1983) used the first comparative test of a specific hypothesis for sociality. He argued that predation would be supported as the reason for group living if infant survival improved in groups, whereas, if food defence was the reason then larger groups should show increased female fecundity providing reproductive benefits. The results demonstrated that there was no support for the second hypothesis, as fecundity did not increase with group size, but infant survival did increase in those groups facing a predation threat (van Schaik 1983). The benefits of resource defence do not outweigh the costs of within-group competition, it was argued, so predation risk must be another factor forcing primates to form groups (van Schaik 1989). Furthermore, female philopatry, seen as a crucial underpinning of female-bonded groups, may be affected by the costs of dispersal for young adult females, not just the benefits of kin-based bonds (Isbell and van Vuren 1996).

The costs and benefits of group living were therefore not fully accounted for by the distribution of food resources alone, leading to a reformulation of the socioecological model to take predation risk explicitly into account (Sterck, Watts, and van Schaik 1997). Moreover, the model had hitherto ignored the impact of sexual selection. Groups could also be seen as the result of female counter-strategies to the effects of male infanticide (Sterck, Watts, and van Schaik 1997). Infanticide had been documented in primate species (Hrdy 1977), but remained controversial with some (Sussman, Cheverud, and Bartlett 1995), despite a clear adaptive explanation (Hrdy, Janson, and Van Schaik 1994) and evidence from field studies (e.g. Borries *et al.* 1999). It pays a male, who is not the father of an un-weaned infant, to kill the infant if that will bring its mother back into oestrus sooner and give the male a chance to mate with her. In species where lactation is longer than gestation, post-partum oestrus is not possible and infants will be vulnerable to infanticidal males (van Schaik and Kappeler 2003). Given the high numbers of infant deaths attributable to infanticide in some species, with serious consequences for female reproductive success (Watts 1989, Sommer 1994), females will be expected to have evolved counter strategies to protect their infants (van Schaik 2000b). Females with infants may associate with a male, who may also be the father of the infant, for protection against other males (van Schaik and Dunbar 1990). Alternatively, females may adjust their mating strategy, so that none of the males in the group are certain about the infant's paternity (van Schaik 2000a). It has been suggested that females evolved conspicuous oestrous swellings in some promiscuous species, exposed to high infanticide risk, to encourage the males within the group to mate with fertile females (Hrdy 1977). Sexual swellings have been show to evolve predominantly in species with promiscuous mating (Pagel 1994b, Nunn 1999). On the other hand females may have concealed their oestrous signals to deny males information about their reproductive state and confuse paternity that way (Alexander 1979). Concealed ovulation was also shown to have evolved in promiscuous species (Sillen-Tullberg and Møller 1993). A high infanticide rate, the consequence of long relative lactation periods, can be expected to have a major impact on primate social organisation, not accounted for by the traditional model (Janson and van Schaik 2000).

The new model of primate socioecology sought to bring together the selective pressures exercised by the ecology, including food distribution and predation risk, with the effects of sexual selection, particularly in the form of infanticide (Sterck, Watts, and van Schaik 1997). While widely adopted across primatology as the explanatory framework for the social behaviour of primates, some of the predictions of the model did not match with the observations of field studies (e.g. Janson 2000, Isbell and Young 2002, Koenig 2002, Koenig and Borries 2006, Snaith and Chapman 2007). In order to improve the fit of the model, several refinements were suggested; in particular, better measures of the food supply available to individuals (Isbell and Young 2002, Koenig and Borries 2006, Snaith and Chapman 2007) and levels of predation risk primates actually perceived (Cowlishaw 1997). In addition, it was proposed that other factors should be included in the model (Thierry 2008). For example, group living allows for easy transfer of parasites, which may have an impact on social organisation especially as group size increases (Janson 2000). Group living also places constraints on individuals that may impact on their foraging, travel, social or resting time. Explicit modelling of the trade-offs between these activities, in the face of varying food availability and predation risk, have enabled better predictions to be made about group size and viability in different habitats across primate species (Dunbar 1992, Korstjens, Verhoeckx, and Dunbar 2006, Lehmann, Korstjens, and Dunbar 2007, Lehmann, Korstjens, and Dunbar 2008, Bettridge, Lehmann, and Dunbar 2010). Interspecific variation in cognition is correlated with group size (Dunbar 1995c), but cognition may also impact on social organisation as well as being influenced by it (Shultz and Dunbar 2007).

Many primatologists (Janson 2000, Snaith and Chapman 2007), see the socioecological model (Sterck, Watts, and van Schaik 1997) as a successful application of animal behavioural ecology (Krebs and Davies 1997) to the primate order, even though it has its critics (Thierry 2008). However, the basis of the model is that it seeks to explain the current function of social behaviour assuming that species are in evolutionary equilibrium (Thierry 2008, Silk 2011). From a practical point of view it is argued that since behaviour, including social behaviour, is labile, social systems will adjust according to the current environment without huge time lags (Atz 1970, Blomberg, Garland, and Ives 2003). From a conceptual point of view, explaining the current function of social behaviour may be a justifiable aspiration so long as it is clear that this is only one of the two ultimate explanations for primate social systems, the other being evolutionary history (Tinbergen 1963).

However, a number of researchers have argued that social behaviour is no more labile than morphological or physiological traits, and that the social systems of some taxa appear to show high levels of phylogenetic inertia (Struhsaker 1969, Sillen-Tullberg and Møller 1993, Di Fiore and Rendall 1994, Pagel 1994b, Rendall and Di Fiore 1995, Rendall and Di Fiore 2007). In other words, closely related species are more similar to each other, in terms of their social system, than would be expected by chance, due to a shared history, and social systems may be conserved by related species that occupy a variety of habitats (Struhsaker 1969, Di Fiore and Rendall 1994).

This has two implications. First, if species are likely to be more similar in a trait than would be expected by chance, due to a shared history, then they cannot be treated as independent data points, and this dependence must be taken into account when using comparative methods. Secondly, a full evolutionary explanation (Tinbergen 1963) for primate social systems would be expected to include the phylogenetic history of the species, how social behaviour has evolved over time, and to identify the drivers of that change (Harvey and Pagel 1991). Indeed, comparative studies that have included phylogenetic history have improved their explanatory power for the current distribution of social behaviour across primate species (Sillen-Tullberg and Møller 1993, Di Fiore and Rendall 1994, Pagel 1994b, Ossi and Jason 2006, Pagel and Meade 2006, Kamilar and Marshack 2012, Kamilar *et al.* 2012). However, while these studies have looked at aspects of social behaviour in primates and the traits that have co-evolved with them, the fundamental drivers of primate social systems themselves have not been investigated. These drivers will be investigated in this thesis.

1.3 Cultural Evolution

While humans are animals, subject to the law of descent with modification (Darwin 1968 [1859], Darwin 2004 [1871]), we are set apart from animals by our capacity for cumulative culture (Pagel 2012a), which enables us to shape the environment we inhabit, not just be shaped by it (Pagel 2012b). Following the modern synthesis (Huxley 1942), researchers assembled cross-cultural databases including the Human Relations Area Files (HRAF) (Murdock 1954), the Ethnographic Atlas (EA)

(Murdock 1967), and the Standard Cross Cultural Sample (SCCS) (Murdock and White 1969), in order to conduct comparative studies examining the impact of the environment on human cultural institutions such as polygyny (White 1988, White and Burton 1988) and inheritance (Murdock 1949). Although these studies sought to investigate the link between culture and environment, it was not until the advent of sociobiology and behavioural ecology (Wilson 1975, Dawkins 1976, Krebs and Davies 1997) that researchers started to take an explicitly Darwinian approach to human culture. Using the theoretical framework and methodological tools of evolutionary biology, studies focussed on the evolution of social systems, mating systems, inheritance and warfare (Hartung 1976, Alexander 1979, Chagnon and Irons 1979, Hartung 1982). Over the subsequent years, four schools have emerged which, while sharing an evolutionary approach to the study of human behaviour, differ in their methodology and the questions they address (Barrett, Dunbar, and Lycett 2002).

1.3.1 Evolutionary Psychology

Evolutionary Psychology (EP) takes an explicitly adaptationist approach to human social behaviour (Barkow, Cosmides, and Tooby 1992, Betzig 1997). Due to the huge cultural changes over the last 10,000 years, human cognitive processes that were selected for in the Environment of Evolutionary Adaptedness (EEA) may not be adaptive now, and therefore fitness measures of behaviours in current environments are not necessarily appropriate (Barkow, Cosmides, and Tooby 1992). Instead of studying human cultural diversity, evolutionary psychologists have focussed their investigations on human universals, such as human mate choice (Buss and Schmitt 1993, Buss 1994) and the evolution of altruistic behaviour (Curry and Dunbar 2011). However, whether and to what extent human social behaviour in the modern world is adaptive is an empirical question and open to testing (Barrett, Dunbar, and Lycett 2002).

1.3.2 Human Behavioural Ecology

Drawing explicitly on the study of animal behaviour (Krebs and Davies 1997), including primates, Human Behavioural Ecology (HBE) seeks to measure the fitness outcomes of human social behaviour. In a changing environment, humans will adapt their behaviour in order to maximise their fitness, it is argued. For example, where kin co-operate in child rearing, it is expected that maternal grandmothers, who have most confidence in their relatedness to their daughters' children, will have the most to gain in fitness terms from their survival, compared to other relatives, and will therefore contribute most. As a result, women with children are expected to remain with their mothers, other things being equal (Hawkes *et al.* 1998, Sear, Mace, and McGregor 2000, Hawkes 2003). On the other hand, where wealth is controlled by men, a woman may be expected to choose to become the second wife of a wealthy man rather than the only wife of a poor man, as predicted by the polygyny threshold model, and is therefore likely to move to her husband's residence (Borgerhoff Mulder 1990). HBE focuses strongly on the study of hunter-gatherer people (Blurton Jones *et al.* 1992, O'Connell, Hawkes, and Blurton Jones 1999, Howell 2000) on the basis that they most closely resemble the conditions of early modern humans and therefore reveal fitness consequences to behaviour, including cultural behaviour, similar to those in our evolutionary past.

1.3.3 Dual Inheritance Theory

A third approach treats culture and genes as separate and independent evolutionary agents that can nevertheless co-evolve and affect each other. Dual Inheritance Theory (Boyd and Richerson 1985) identifies additional routes for the transmission of culture, compared to the single vertical gene transmission route from parents to offspring, because culture can be borrowed or acquired horizontally between adults, such as when husbands or wives join a society from outside, or obliquely, when children learn from adults other than their parents (Henrich, Boyd, and Richerson 2008). These additional transmission routes mean that cultural evolution can be far swifter than gene evolution in the face of environmental change and then, in turn, can affect the environment for gene evolution (Richerson and Boyd 2005). Furthermore, culture can produce effects that are beneficial to the group, such as the encouragement of monogamy by rulers in some societies that reduces the number of single men, who might otherwise cause problems for the society in terms of aggression and crime (Henrich, Boyd, and Richerson 2012). A reduction in intrasexual competition can induce males to switch to paternal investment instead.

1.3.4 Cultural Phylogenetics

A more recent development, stemming largely from HBE, has been the realisation that since individual cultures cannot be treated as independent in cross-cultural comparisons (Mace and Pagel 1994), the extent of their relatedness must be taken into account. Researchers have sought to deal with 'Galton's Problem' of non-independence by drawing on developments in evolutionary biology to incorporate a phylogeny of relatedness between cultures into their analyses (Harvey and Pagel 1991). The phylogenies themselves, built most recently on linguistic information, have been able to address questions of cultural history, such as the dating of the spread of Indo-European (Gray and Atkinson 2003, Bouckaert *et al.* 2012) and Bantu-speaking cultures (Holden 2002, Holden, Meade, and Pagel 2005), and the earliest population movements across Austronesia (Gray and Jordan 2000, Gray, Drummond, and Greenhill 2009). Furthermore phylogenies have been used to address the effects of environment on cultural traits, such as political complexity and residence patterns in Austronesia (Jordan *et al.* 2009, Currie *et al.* 2010), descent patterns in Bantu societies (Holden and Mace 2003, Holden and Mace 2005), and marriage and dowry systems among Indo-European speakers (Pagel and Meade 2005, Fortunato 2011b).

This approach may have the potential to unite the three approaches to the study of cultural evolution (*i.e.* EP, HBE, DIT), since it allows for an assessment of the contribution of environmental factors as well as history to cultural change across human populations (Nunn 2011). Furthermore, where archaeological or other evidence is missing or inadequate, cultural phylogenetics raises the intriguing possibility that historical questions about cultural change can still be addressed and evolutionary drivers of cultural change identified. The approach of applying phylogenetic comparative methods to questions in animal and human behaviour will be used in this thesis.

1.4 Phylogenetic Comparative Methods

For both biological and cultural traits, it is necessary to establish that a trait has co-evolved with another trait in order to identify an instance of adaptation. The comparative method can demonstrate correlated evolution between a trait and the environment it operates in (Harvey and Pagel 1991). However, whether the units of comparison are populations, species or cultures, the trait may be shared across taxa by descent or proximity and not independent evolution (Mace and Pagel 1994). This problem was identified by Darwin (1968 [1859] p.185) for biological systems and by Galton (1889) in his comments on Tylor's (1973 [1873]) comparative cultural work.

Comparative studies have been used extensively to investigate the social behaviour of primates, for example, the effects of food competition on female relations (van Schaik 1989), the effect of day range on territoriality (Mitani and Rodman 1979), and the impact of mating systems on testes size in males (Harcourt *et al.* 1981, Harcourt, Purvis, and Liles 1995). Equally, since cultural evolution is similar to biological evolution, in that it is based on descent with modification from a single source (Cavalli-Sforza and Feldman 1981, Boyd and Richerson 1985), comparative methods have been used in the study of cultural behaviour in humans. For example, it has been used to examine the effect of inheritance patterns (Hartung 1976, Hartung 1982) and pathogen risk on marriage practices (Low 1988, Low 1990), and the link between reproduction and social organisation (Lesthaeghe 1989). However, it is not possible to assume that an association between traits is evidence for co-evolution, since patterns of historical relatedness between species or cultures mean that traits may not have evolved or been acquire independently (Mace and Pagel 1994). Instead, it is possible that the traits evolved separately in an ancestor but were then passed on together to descendent cultures or species, and now appear together in current taxa.

An early solution to this problem was to group species (Clutton-Brock and Harvey 1977) or cultures (Murdock and White 1969) into clusters based on common descent and pick representative taxa for the purposes of analysis. However, this prevents comparison between closely related cultures, which may provide the best evidence for co-evolution. Furthermore, the clusters of cultures or genera are themselves related, so the problem is just pushed further back in time. Descent with modification means that descendent taxa inherit traits from an ancestor such that those traits are described as homologous. Analogous traits, where they evolve together in unrelated species show that correlated evolution has taken place (Mace and Pagel 1994). Incorporating a phylogeny into analyses allows for the identification of independent instances of trait co-evolution when the traits are mapped onto it, since it is the number of times that a pair of traits changes together through history, rather than the number of extant taxa in which the pair of traits currently exist, that provides evidence of correlated evolution (Felsenstein 1985). Furthermore, the use of a phylogeny enables the identification of the order of trait change and therefore causality between traits (Harvey and Pagel 1991).

A phylogenetic approach is now common in evolutionary biology, but less so among primatologists (Nunn 2011). Even so, extensive phylogenies of more than 200 primate species built using genetic data, and fossils for calibration, have been freely available for some time (Purvis 1995) and are now updated regularly (Arnold, Matthews, and Nunn 2010). Early cultural analyses used trees that were based on simple classifications (Ruhlen 1987) or genetics (Cavalli-Sforza, Menozzi, and Piazza 1994) to investigate the effects of male inheritance on marriage practice (Cowlishaw and Mace 1996), the evolution of lactose tolerance among herding cultures (Holden and Mace 1997), and the evolution of marriage practice and kinship (Borgerhoff Mulder 2001), amongst others.

More recently, cultural analyses have used language phylogenies. Language evolves faster than genes do and is therefore better suited to cultural evolution, which can also be fast, and is often closely related to language change. The differences between related languages are an indication of the time since they split (Nunn 2011). By using cognates, or common meanings between languages, across a standard list of words (Swadesh 1955), homologies can be identified and phylogenies built (Atkinson *et al.* 2005). Early language phylogenies were built using parsimony methods (Felsenstein 1985, Purvis and Rambaut 1995), such as the Bantu tree, which showed that their language spread as Bantu farmers expanded from their ancestral homeland in west Africa throughout sub-Saharan Africa (Holden 2002).

However, both parsimony and maximum likelihood trees provide a single or ‘best’ tree that does not allow for any assessment of the uncertainty surrounding the tree (Huelsenbeck *et al.* 2001). A Bayesian sample of trees, on the other hand, which is the posterior probability of the phylogeny given the data and the evolutionary model used, provides a set of trees whose topologies are represented in proportion to their overall likelihood (Atkinson *et al.* 2005). This allows for the uncertainty in the phylogeny to be incorporated into subsequent analyses of trait evolution over the tree. The *10kTree* primate phylogeny used here was built using these methods, as was the phylogeny used to time the origin of the Indo-European expansion (Gray and Atkinson 2003). Other Bayesian phylogenies currently available include the Arawak (Walker and Ribeiro 2011) and Tupi (Walker *et al.* 2012) trees for those South America language families, the Semitic tree for the Near East (Kitchen *et al.* 2009), and the Bantu tree built by Holden and colleagues (Holden, Meade, and Pagel 2005) as well as the one built here.

Some researchers have objected that rapid change across some language families and reticulation, or the borrowing of cognates, may violate the assumptions of phylogenetic reconstruction (Borgerhoff Mulder 2001). While acknowledging these issues, researchers have shown that it is possible to test whether assumptions have been violated (Atkinson *et al.* 2005), and argued that even an imperfect tree is better than none (Pagel 1999a), especially one built using Bayesian methods, since that allows for the uncertainty in the phylogeny to be made explicit (Huelsenbeck *et al.* 2001).

Where fossil evidence is not available, particularly with social behaviour, phylogenies have been essential for inferring the ancestral states of traits (Pagel 1999a, Pagel 1999b, Pagel, Meade, and Barker 2004). Phylogenies have been used to infer the social behaviour of the common ancestor of chimpanzees and humans (Ghiglieri 1987, Wrangham 1987b), primate social systems (Sillen-Tullberg and Møller 1993, Di Fiore and Rendall 1994, Pagel 1994b, Nunn 1999, Shultz, Opie, and Atkinson 2011, Opie, Atkinson, and Shultz 2012) and life histories (Kappeler 1998), and human descent (Holden and Mace 2003) residence (Jordan *et al.* 2009, Fortunato and Jordan 2010) and marriage (Pagel and Meade 2005, Fortunato, Holden, and Mace 2006, Fortunato 2011b) patterns.

1.4.1 Co-evolutionary Analyses of Animals and Humans

Perhaps the most far-reaching use of phylogenetics is as part of the comparative method. By incorporating phylogenies into comparative studies it is possible to detect correlated evolution between traits, and because the ancestral and derived states of traits and the order of trait evolution can be inferred causal drivers can be identified and hypotheses tested (Harvey and Pagel 1991, Mace and Pagel 1994, Pagel 1994a, Pagel and Meade 2006). Sillen-Tullberg and Møller (1993), for example, investigated the co-evolution of concealed ovulation and mating systems across anthropoid primates. They showed that ovulation became concealed in species with polygynandrous mating rather than monogamous mating, suggesting that concealed ovulation was a mechanism to confuse paternity (Hrdy 1977) rather than to promote paternity confidence (Turke 1984). However, monogamous mating evolved in species without oestrous signals, suggesting that concealed ovulation promotes monogamy, and not the other way around.

Another analysis tested the suggestion that sexual swellings were also a mechanism for paternity confusion since they are more often associated with multi-male systems (Clutton-Brock and Harvey 1976). However, to identify causality, swellings would have to evolve after multi-male mating. By using co-evolutionary analyses, Pagel and Meade (2006) were able to show that conspicuous swelling in females evolved in species with multi-male mating and not the other way around.

In a cross-cultural study, Holden and Mace (2003) investigated the relative timing of the loss of matriliny and the adoption of cattle herding to test the proposal that ‘cattle are the enemy of matriliny, and the friend of patriliny’ (Aberle 1961 p.680). They showed that among matrilineal Bantu cultures cattle herding was adopted first, followed by the loss of matrilineal descent. In another study of Indo-European cultures, marriage system and wealth transfer were shown to co-vary with the ancestral states of monogamy and a dowry system changing to polygyny with bride price; the marriage system changed first and therefore drove the change in wealth transfer (Pagel and Meade 2005).

1.4.2 Objections

However, there have been a number of objections raised to the use of phylogenetic methods. It has been argued that there may be a number of processes, including historical, affecting the distribution of both biological and cultural traits (Borgerhoff Mulder 2001). Traits may be similar in closely spaced taxa because of the similarity in the habitat occupied and this similarity may be masked by the use of a phylogeny of historical relatedness. It is therefore important to test for other causes of autocorrelation as well as phylogenetic relatedness. Methods to incorporate similarity due to geographical proximity, as well as historical relatedness, have recently been developed (Freckleton and Jetz 2009) and will be investigated here.

While some have suggested that behavioural traits are too labile to be affected by historical relatedness (Atz 1970, Blomberg, Garland, and Ives 2003), others suggest that it is wrong to assume that history is weak compared to selection pressures exerted by the current environment (Borgerhoff Mulder 2001). Again this is an empirical question and should be tested in the traits under investigation before a decision is made on the approach to be taken (Rendall and Di Fiore 2007).

Phylogenetic methods have been used less within primatology compared to evolutionary biology (Nunn 2011). This may be because behavioural traits are assumed to be more labile, especially among primates, where social systems are thought to be flexible to current environments and unaffected by history (Di Fiore and Rendall 1994). In this thesis, measures of the phylogenetic signal will be used to determine the flexibility or otherwise of behavioural traits (Pagel 1999a), and phylogenetic methods will be used to investigate the evolutionary history of primate social systems and their evolutionary drivers.

By contrast, those investigating cultural change have embraced phylogenetic methods (e.g. Mace and Pagel 1994, Gray and Atkinson 2003) as the best way to test hypotheses about change in human history where archaeological and other evidence is missing or inadequate. This approach has the potential to settle questions about the relative effects of current environmental factors compared to cultural and historical factors in cultural change, and thereby settle long running debates within Anthropology (Mesoudi, Whiten, and Laland 2006, Ingold 2007, Mesoudi, Whiten, and Laland 2007).

1.5 Thesis Aims

As a contribution to the understanding of how human society works this thesis has two overall aims: first, to discover the evolutionary history of fundamental aspects of human and primate societies, since the evolution of the ancestral primate, and secondly, to uncover the drivers of social change for primates and humans - historical, environmental and ultimately, for humans, cultural.

Chapter One has provided a review of the approaches taken by primatologists to address the evolution of primate social systems. With a few notable exceptions (Sillen-Tullberg and Møller 1993, Di Fiore and Rendall 1994, Pagel 1994b), researchers have concentrated on the effect of current environments on primate behaviour and have been less keen than evolutionary biologists to use phylogenetic methods (Nunn 2011). However, because of the similarity between cultural and biological change, researchers have been able to use the same phylogenetic comparative methods to investigate cultural change (Nunn 2011). I have shown how researchers in cultural phylogenetics have been able to use these methods to investigate cultural change where other evidence is lacking (e.g. Gray and Atkinson 2003, Holden and Mace 2003, Jordan *et al.* 2009). Chapter Two outlines the phylogenetic methods that are common in the subsequent chapters.

For primates, including humans, two of the most important aspects of social behaviour are social organisation, the structure and size of groups, and mating systems, that is who individuals chose to mate with and in some cases rear offspring with (Kappeler and van Schaik 2002). Chapter Three investigates how and when social organisation and mating systems have evolved in primates and compares their trajectory through time. A well-established model in primatology suggests that dispersal patterns of females are the primary driver for change in primate social systems (Wrangham 1980). This hypothesis is tested across all primates and alternative causes of primate social organisation are suggested. Two published papers that were based on this chapter (Shultz, Opie, and Atkinson 2011, Opie, Atkinson, and Shultz 2012) are attached as appendices.

Despite a number of hypotheses being proposed for the evolution of monogamous mating in primates, there is no consensus about how monogamy evolved or which was the most important driver of this mating system. Some researchers have suggested that monogamy might be the result of a number of factors (Palombit 1999), or even that it might not be possible to decide between them (van Schaik and Kappeler 2003). Chapter Four investigates each of these hypotheses and tests them using phylogenetic methods. Traits are identified that are associated with each of the hypotheses and by testing between them it is possible to suggest the ultimate cause of monogamy in primates.

Since the earliest anthropological research (Morgan 1964 [1877], Tylor 1973 [1873]), kinship and marriage have been seen as some of the fundamental structures of human society. Chapter Five investigates the interplay between descent, post-marriage residence patterns and marriage practice, using the spread of Bantu speaking cultures across sub-Saharan Africa as the basis for the study.

Other factors such as geography, environment and subsistence patterns have also been suggested as important drivers of change in kinship and marriage practice across human societies. Chapter Six attempts to make an assessment of the relative impact of cultural history, and other potential drivers of change, on kinship and marriage as a contribution to the debate across anthropology about how and why human societies change.

Each of the four analysis chapters includes a discussion about the implications of the results. Chapter Seven provides a summary and conclusion to the thesis as a whole and makes an assessment of the thesis as a contribution to knowledge about the development of human society and how societies have changed.

Chapter 2 Methods & Analysis

2.1 Introduction

In order to identify an evolutionary trend, for both biological and cultural traits, it is necessary to establish that a trait has co-evolved with another trait. To establish an adaptive change of this sort, comparisons are made across taxa using the comparative method, which can demonstrate correlated evolution between phenotypic traits, or between a trait and an aspect of the environment (Harvey and Pagel 1991). These studies can show that there is an association between traits, but unless it is known that trait change is from an ancestral to a derived state, it is not clear that change in that trait is an adaptation to the other trait (Harvey and Pagel 1991). Where fossil evidence is available, inferences can be made about ancestral and derived states, but where such evidence is absent, for example with social behaviour, other methods have to be used. Incorporating a phylogeny into a comparative analysis ensures that instances of co-evolutionary change between traits are counted, rather than instances of association between traits in extant taxa, which may simply be due to shared ancestry (Mace and Pagel 1994). Furthermore, past characters can then be inferred on a tree by using the distribution of traits among contemporary populations arranged on the tips of the tree. The ancestral and derived states of the traits are then used to identify the causal drivers of trait change and adaptive hypotheses can be tested (Pagel 1999a, Pagel 1999b, Pagel, Meade, and Barker 2004, Pagel and Meade 2006).

Some researchers have suggested that behavioural traits are too labile to be affected by historical relatedness and therefore phylogenetic methods are not appropriate (Atz 1970, Blomberg, Garland, and Ives 2003), but others suggest that it is wrong to assume that history is weak compared to selection pressures exerted by current environments (Borgerhoff Mulder 2001, Rendall and Di Fiore 2007). Phylogenetic signal in data can be tested using Pagel's Lambda (Pagel 1999a), and where data shows phylogenetic inertia, such that a trait varies between extant taxa in proportion to the relatedness between those taxa, phylogenetic methods can be used (Nunn 2011).

Early methods for detecting correlated evolution between traits used parsimony, whereby ancestral states were reconstructed assuming a minimum number of changes along the branches of a phylogeny to produce the observed trait states at the tips (Maddison 1990). The statistical tests for correlated evolution then depended on this single set of inferred trait states at the ancestral nodes on the phylogeny. However, an accurate representation of the states at ancestral nodes on the tree is a probability distribution of all possible trait states, with some states more likely than others (Pagel 1994a). Pagel (1994a) introduced a method, *Discrete*, to test for correlated evolution that uses a continuous-time Markov model to estimate the transition rates between states for a pair of binary traits over a phylogeny. This method allows the traits to take all possible states at ancestral nodes, such that the results are independent of any particular node value assignment. The method then compares the fit of two different models to the data.

The fit of the independent model, which constrains the traits to evolve separately, is compared to the fit of the dependent model, where the traits are allowed to co-evolve, using a likelihood ratio (LR) statistic (Pagel 1994a), defined as

Equation 2.1

$$LR = -2 \log_e [L(I)/L(D)],$$

where L(I) and L(D) are the likelihood of the independent and dependent models respectively. The LR statistic is distributed as a χ^2 with degrees of freedom equal to the difference in the number of parameters in each model.

However, while accounting for the uncertainty in states at ancestral nodes, this method, like parsimony methods, relies on a single or ‘best’ phylogeny that does not allow for any assessment of the uncertainty surrounding the resolution of the tree (Huelsenbeck *et al.* 2001). A Bayesian tree, on the other hand, which is the posterior probability of the phylogeny given the data and the evolutionary model used, provides a set of trees whose topologies are represented in proportion to their overall likelihood (Atkinson *et al.* 2005). This allows for the uncertainty in the phylogeny to be incorporated into subsequent analyses of trait evolution over the tree.

The Bayesian statistical approach treats the evolutionary model and the parameters of the model as random variables, while the data consists of fixed observations (Ronquist 2004). A Markov chain Monte Carlo (MCMC; Metropolis *et al.* 1953) algorithm uses a rate matrix that describes the transitions between states over a very small time period. At each step the Markov chain proposes a random modification to the model parameters. If the posterior probability of the proposed model is higher than the previous model then the proposed model is accepted, if not, it is accepted with probability proportional to the ratio of its likelihood to that of the previous model (Pagel, Meade, and Barker 2004). The Markov chain ensures that the new state is a function of the current state, and wanders through state space visiting better and worse models in proportion to their posterior probability (Pagel and Meade 2005). At equilibrium, the Markov chain samples the posterior distribution of both the model of trait evolution and the parameters of the model, as well as the likelihood of the data (Pagel and Meade 2006). The primate and language phylogenies used here are both built using Bayesian methods.

The *Discrete* method for testing correlated evolution between binary traits has been updated to incorporate the use of a Bayesian phylogeny, such that the uncertainty in the data and the tree are both taken into account explicitly (Pagel and Meade 2006). Furthermore, by using a Reversible Jump (RJ) procedure in *Discrete*, an MCMC (Metropolis *et al.* 1953) sampling algorithm is made to explore the space of all possible models and can derive a Bayesian posterior distribution of model log-likelihoods, rate parameters and inferred ancestral states on a phylogeny (Pagel and Meade 2006). The MCMC integrates the transition rates of the models over a posterior probability distribution of trees, such that a comparison can be made between the independent and dependent models using a Bayes Factor (BF) (Kass and Raftery 1995). This method has been used in this thesis.

2.2 Phylogenies

2.2.1 Primate phylogeny

Purvis (1995) derived a primate phylogeny of 203 species using parsimony methods, which has since been widely used (e.g. Nunn 1999, Purvis and Webster 1999, Purvis *et al.* 2000, Reader and Laland 2002). Using improved genetic information and Bayesian methods this phylogeny has recently been updated by the *10k Tree Project* (Arnold, Matthews, and Nunn 2010). By using this large block of ultrametric trees (standardised for time) it is possible to infer the evolutionary history of traits while simultaneously taking into account the uncertainty of the phylogeny. A tree block of 10,000 primate phylogenies was downloaded from version 2 of the *10k Tree Project* (Arnold, Matthews, and Nunn 2010). This tree block provides phylogenies based on Bayesian inference using data from 6 mitochondrial (CYTB, COX1, COX2, 12S rRNA, 16S rRNA, and a gene cluster), and 3 autosomal (MC1R, CCR5, SRY) genes for 230 primate species.

For Maximum Likelihood (ML) analyses a consensus tree was produced. The consensus tree is a maximum clade credibility tree and was inferred from the complete posterior sample of trees using *TreeAnnotator* (Drummond and Rambaut 2007). This is the tree in the sample with the maximum product of the posterior clade probabilities (a measure of clade support). The nodes of the consensus tree were dated using median molecular branch lengths from the Bayesian analysis and six known fossil calibration points (Arnold, Matthews, and Nunn 2010). This tree was also used for illustrative purposes to display character traits at ancestral nodes on the primate phylogeny.

2.2.2 Language Phylogeny

Phylogenies based on molecular information (Cavalli-Sforza, Menozzi, and Piazza 1994) have been used for studies of cultural processes (e.g. Seielstad, Minch, and Cavalli-Sforza 1998). However, since intraspecific phylogenies are built on populations that are not reproductively isolated, they can be affected by gene flow. Language-based phylogenies have a number of advantages for cultural studies: their society level resolution is the same as cultural traits, languages evolve at a similar speed to cultures (Atkinson *et al.* 2005) and language information is far more widespread than genetic information (Lewis 2009).

For the purposes of the analyses undertaken here, to investigate changes between marriage states, it was important to have a language family covering cultures where polygynous marriage is permitted, as in 85% of cultures worldwide (White 1988), but unlike many modern developed cultures (Henrich, Boyd, and Richerson 2012). The Bantu phylogeny (Holden 2002) is particularly useful since, as well as polygyny being widely practiced, there are comprehensive data on marriage and kinship patterns across a large number of populations (Gray 1999).

Holden (2002) produced a Bantu phylogeny based on the linguistic data of Bastin and colleagues (1999), using maximum parsimony phylogenetic methods. The root of the tree was dated to between 5,000 and 3,000 before present (BP) using archaeological evidence for the spread of farming. This phylogeny was then used to test the view that the ancestral state of descent was matrilineal amongst Bantu speaking populations. However the results were indecisive (Holden and Mace 2005). Holden and colleagues (2005) used the same linguistic data (Bastin, Coupez, and Mann 1999) to produce a phylogeny using Bayesian methods, but this has not been used for comparative analyses.

Here, Bayesian methods (details in Chapter 5), using the same cognate set (Holden 2002) derived from linguistic data (Bastin, Coupez, and Mann 1999), was used to infer a sample of trees which will be used to deduce the ancestral state of marriage and kinship patterns for Bantu societies, test for co-evolution between these cultural traits (Chapter 5), and test for co-evolution between these cultural traits and environmental traits (Chapter 6). The Bayesian sample of 2,800 trees generated here provides the largest Bayesian Bantu phylogeny to date and allows subsequent analyses to take account of the uncertainty in the Bantu language tree. Figure 2. shows the maximum clade credibility tree derived from the Bayesian MCMC sample of 2,800 trees generated using *TreeAnnotator* (Drummond and Rambaut 2007). The node labels show the posterior probability of the existence of nodes across the Bayesian tree sample. The deepest split in the consensus tree is that between east and west Bantu, which appears in 100% of the Bayesian tree sample. Later splits within the western Bantu, between northwest and forest west, and within the eastern Bantu between the central Bantu and the east and southeast Africa have lower support, 80% and 49% respectively, across the full sample of trees. The later splits accord well with the maximum parsimony (Holden 2002) and previous Bayesian (Holden, Meade, and Pagel 2005) trees derived from the same cognate set. The difference is in the initial split between east and west Bantu, which is not supported in the other two trees.

Nevertheless, the east/west split identified here, accords well with both early lexicostatistical phylogenies (Guthrie 1967-1971, Vansina 1990, Vansina 1995) and the latest genetic study covering the area in west central Africa where the Bantu originated, and from where the initial expansion took place (Montano *et al.* 2011). It is likely that the east/west split shown by the MCMC sample has implications for the inferred ancestral states of the cultural traits tested (Holden, Meade, and Pagel 2005). Indeed, whereas a maximum parsimony tree was unable to infer the ancestral state for Bantu descent, because it was thought that descent was variable and rapidly changing (Holden and Mace 2005), ancestral state reconstructions inferred here provide clear results.

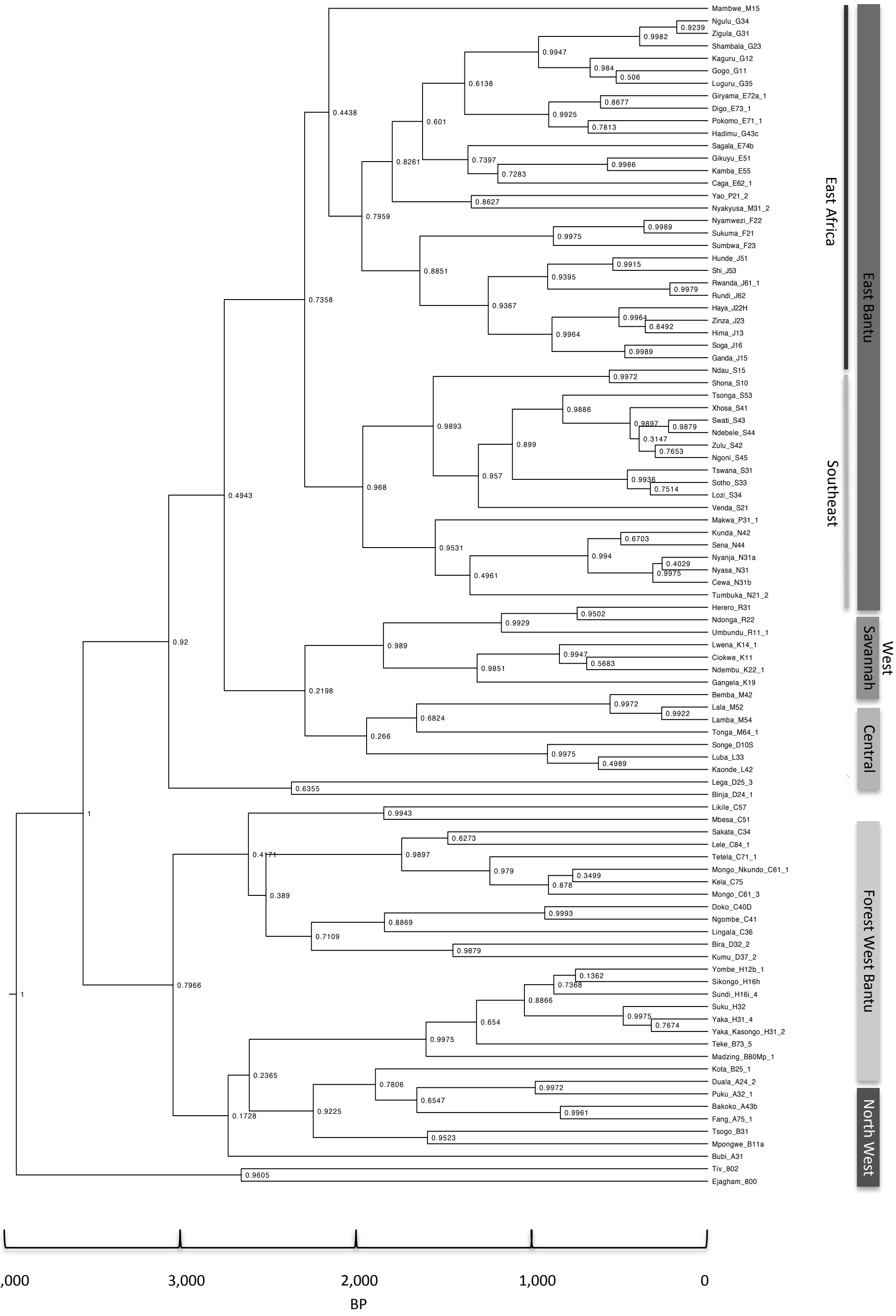

Mambwe_M15
Ngulu_G34
Zigula_G31
Shambala_G23
Kaguru_G12
Gogo_G11
Luguru_G35
Giryama_E72a_1
Digo_E73_1
Pokomo_E71_1
Hadimu_G43c
Sagala_E74b
Gikuyu_E51
Kamba_E55
Caga_E62_1
Yao_P21_2
Nyakyusa_M31_2
Nyamwezi_F22
Sukuma_F21
Sumbwa_F23
Hunde_J51
Shi_J53
Rwanda_J61_1
Rundi_J62
Haya_J22H
Zinza_J23
Hima_J13
Soga_J16
Ganda_J15
Ndau_S15
Shona_S10
Tsonga_S53
Xhosa_S41
Swati_S43
Ndebele_S44
Zulu_S42
Ngoni_S45
Tswana_S31
Sotho_S33
Lozi_S34
Venda_S21
Makwa_P31_1
Kunda_N42
Sena_N44
Nyanja_N31a
Nyasa_N31
Cewa_N31b
Tumbuka_N21_2
Herero_R31
Ndonga_R22
Umbundu_R11_1
Lwena_K14_1
Ciokwe_K11
Ndembu_K22_1
Gangela_K19
Bemba_M42
Lala_M52
Lamba_M54
Tonga_M64_1
Songe_D10S
Luba_L33
Kaonde_L42
Lega_D25_3
Binja_D24_1
Likile_C57
Mbesa_C51
Sakata_C34
Lele_C84_1
Tetela_C71_1
Mongo_Nkundo_C61_1
Kela_C75
Mongo_C61_3
Doko_C40D
Ngombe_C41
Lingala_C36
Bira_D32_2
Kumu_D37_2
Yombe_H12b_1
Sikongo_H16h
Sundi_H16i_4
Suku_H32
Yaka_H31_4
Yaka_Kasongo_H31_2
Teke_B73_5
Madzing_B80Mp_1
Kota_B25_1
Duala_A24_2
Puku_A32_1
Bakoko_A43b
Fang_A75_1
Tsogo_B31
Mpongwe_B11a
Bubi_A31
Tiv_802
Ejagham_800
0.9239
0.9982
0.9947
0.984
0.506
0.6138
0.8677
0.9925
0.7813
0.4438
0.601
0.7397
0.9986
0.8261
0.7283
0.8627
0.7959
0.9989
0.9975
0.9915
0.8851
0.9395
0.9979
0.7358
0.9367
0.9964
0.8492
0.9964
0.9989
0.9972
0.9886
0.9893
0.9897
0.9879
0.3147
0.899
0.7653
0.957
0.9936
0.968
0.7514
0.4943
0.6703
0.9531
0.994
0.4029
0.9975
0.4961
0.9502
0.9929
0.92
0.989
0.9947
0.5683
0.9851
0.2198
0.9972
0.9922
0.6824
0.266
0.9975
0.4989
0.6355
1
0.9943
0.6273
0.4171
0.9897
0.979
0.3499
0.878
0.389
0.9993
0.8869
0.7109
0.9879
0.1362
0.7368
0.7966
1
0.8866
0.9975
0.654
0.7674
0.9975
0.2365
0.7806
0.9972
0.6547
0.9225
0.1728
0.9961
0.9523
0.9605
East Africa
Southeast
East Bantu
West Savannah
Central
Forest West Bantu
North West
4,000
3,000
2,000
1,000
0
BP

Figure 2.1. Maximum clade credibility tree of the Bantu language phylogeny, with a Bantoid outgroup (Tiv and Ejagham), derived from the full MCMC sample using *TreeAnnotator* (Drummond and Rambaut 2007). Node labels show posterior probability of the node's existence in Bayesian sample of 2,800 trees. Dating of the tree is based on the mid-point of the dating interval (3,000 - 5,000 BP) suggested by archaeological evidence for the spread of farming (Holden and Mace 2005).

2.3 Statistical analyses

2.3.1 Phylogenetic Signal

Phylogenetic signal in data measures the extent to which related species are more similar in a particular trait than would be expected by chance. If the signal were low, then it would be difficult to infer the evolutionary history of that trait because phylogeny has had little or no effect on the distribution of the trait among extant species or populations. The signal was tested in all data sets by calculating Pagel's Lambda (λ) (Pagel 1994a, Pagel 1999a) using the *Ape* (Paradis, Claude, and Strimmer 2004) and *Geiger* (Harmon *et al.* 2008) packages in *R (R Development Core Team 2008)*. The test statistic is a transformation parameter that incrementally eliminates phylogenetic structure from the tree by multiplying the internal branches of the phylogeny by values ranging between 0 and 1 (Pagel 1999a). When λ is zero, the tree has a single polytomy at the base node (i.e. a tree with no structure), whereas when λ is one, the tree is left unchanged. A λ value of one for the data shows that the probability of shared inheritance of a trait between species is proportional to their relatedness, while a λ value of zero suggests evolution independent of the phylogenetic tree (Freckleton, Harvey, and Pagel 2002). The λ value of the data is compared to the value for the tree without structure (λ=0) and the original tree (λ=1) using a log likelihood ratio test (Equation

2.1), with a probability for that outcome obtained from a χ^2 distribution, with one degree of freedom.

2.3.2 Comparative Analyses

A likelihood framework together with Bayesian inference was used to model the evolution of traits along the branches of the tree. Analyses were carried out in *BayesTraits* (available from www.evolution.rdg.ac.uk) (Pagel, Meade, and Barker 2004, Pagel and Meade 2006) using an RJ MCMC procedure. Maximum likelihood analysis of both the primate and Bantu data, which gives point estimates of model parameters, indicated that the prior distributions (the prior belief about the model of evolution) could be best described by an exponential probability distribution because of the small number of changes per unit of branch length. The priors were seeded from exponential hyperpriors (a distribution from which the prior is drawn) with a mean and variance in the range of 0-10 (Pagel, Meade, and Barker 2004). The rate deviation value, which sets the amount that the rate parameters of the model change in each iteration of the Markov chain, was varied to ensure that acceptance rates were between the suggested limits of 15% and 40% (Pagel, Meade, and Barker 2004). Convergence was checked visually by evaluating changes in the log-likelihood in *Tracer* (Rambaut and Drummond 2007). Each MCMC chain was run 5 times for 5 million iterations sampled every 100, with the first 50,000 iterations discarded as the burn-in period, to ensure that convergence had been reached. The posterior probabilities for the transition models, rate parameters, log-likelihoods and states at ancestral nodes from the run with the median likelihood taken from the post-convergence portion of each run are reported.

2.3.3 Ancestral States

In order to find the posterior probability distributions of states at ancestral nodes across the phylogenies an RJ MCMC analysis was run with the additional use of the *addNode* command in *BayesTraits*, which reports the posterior probability of trait states at each internal node on the phylogenetic tree (Pagel, Meade, and Barker 2004). The ancestral state reported for each node of the tree is the combined posterior probability of each state at that node with the posterior probability that the node itself exists in the tree and is plotted on the consensus tree.

2.3.4 Model Estimation

The RJ MCMC method used simultaneously travels through the full posterior sample of trees as well as the universe of all possible models of evolution visiting those models in proportion to their posterior probability. This method provides a posterior probability sample of models of evolution as well as the rate parameters of the models (Pagel and Meade 2006, Currie *et al.* 2010). It does this by visiting the models in proportion to their likelihood and assesses which transition rates, between states, are set to zero (Z) and which are equal to other rate parameters (0, 1, 2 ..). Models visited by the Markov Chain were ranked in order of their posterior probability and the highest ranked model (the RJ-derived model) was used in later analyses (Pagel, Meade, and Barker 2004).

2.3.5 Model Comparison

The RJ-derived model can then be compared with other models derived from the predictions of hypotheses about the evolution of a trait, in order to test their validity. In these analyses the RJ procedure was switched off and an exponential prior was used set at the RJ prior mean. These unconstrained analyses are compared using a Bayes Factor (BF) (Kass and Raftery 1995). In this way it is possible to compare the performance of different models over the phylogeny and thereby test hypotheses about the evolution of a trait (Pagel, Meade, and Barker 2004).

2.3.6 Correlated Evolution

Furthermore, *Discrete*, a procedure in *BayesTraits* (Pagel, Meade, and Barker 2004, Pagel and Meade 2006), can be used to test hypotheses about correlated evolution between two binary traits. In this procedure, two models are fitted: an independent model in which the two traits evolve over the phylogeny, independently of the state of the other trait, and a dependent model in which the state of one trait affects the probability of change in the other trait. A Bayes Factor (Kass and Raftery 1995) comparison is made between the independent and the dependent models such that independent evolution can be rejected if there is support for the dependent run; support for the dependent run indicates co-evolution between the traits. For comparisons between models the Log_{10} BF was calculated, in *Tracer* (Rambaut and Drummond 2007), as twice the difference in the marginal likelihood (Pagel, Meade, and Barker 2004). The BF shows the weight of evidence to support one model over another, from 0 - 0.5 (insubstantial), to 0.5 – 1.0 (substantial), to 1.0 – 2.0 (strong), to > 2.0 (decisive) (Kass and Raftery 1995). Comparing the transition rates between states indicated the relative timing of the evolution of traits. This method allows for an evaluation of directionality such that the order of evolution can be inferred; by showing which trait evolved first it is possible to test hypotheses explicitly.

For instance, in Figure there are two routes from the ancestral state [0,0] to the derived state [1,1] for both characters, via [0,1] (transitions q_{12} and q_{24}) and via [1,0] (transitions q_{13} and q_{34}). In order to test which of the traits evolved before the other, a comparison is made between q_{13} (transition from ancestral to derived state in trait one with ancestral state of trait two) and q_{24} (transition from ancestral to derived state in trait one following a change from the ancestral to the derived state in trait two) (Pagel and Meade 2006). If transition rate q_{24} is higher than q_{13} this indicates support for change in trait two preceding change in trait one. If there is co-evolution between the two traits this indicates that the change in trait two is implicated in the evolution of trait one.

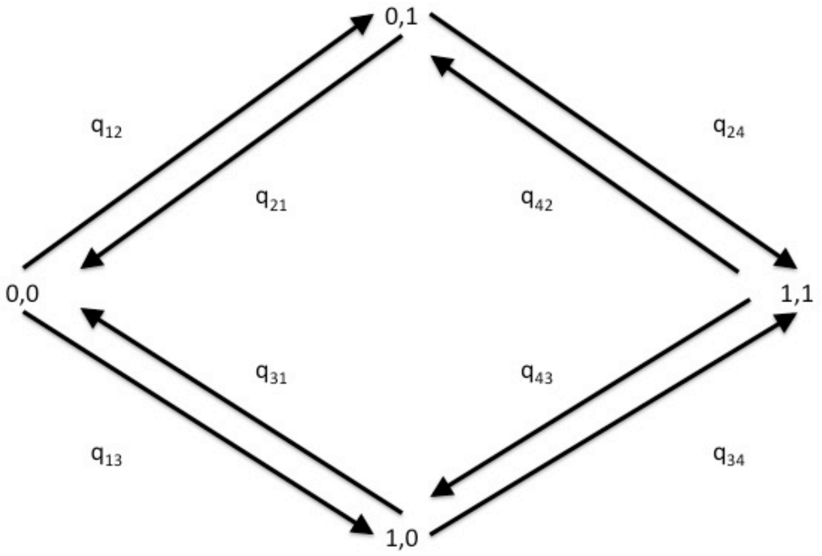


Figure 2.2. Co-evolution between two binary traits. There are two routes from the ancestral state (0,0) to the derived state (1,1), either via (0,1) a change in state one first, or (1,0) a change in state two first (it is assumed that the states do not change at the same time over a sufficiently small time period) (Pagel and Meade 2006).

2.3.7 Continuous Characters

Correlated evolution can also be tested for between a binary and a continuous trait. If a binary trait is significantly correlated with a quantitative trait, this can be interpreted such that the mean of the quantitative trait for the group coded zero on the binary trait differs from the mean of the group coded one, similar to a t-test (Pagel 1999a). Phylogenetic generalised linear model (PGLM) analyses were run using the *CAIC* package (Purvis and Rambaut 1995) in *R* (R Development Core R Development Core Team 2008), which takes phylogeny into account. CAIC can also provide values of the continuous trait at ancestral nodes, which can be plotted onto the phylogenetic tree.

2.4 Other Methods

Other analyses, specific to particular chapters are discussed in the methods sections in those chapters, along with descriptions of the data used in those analyses.

Chapter 3 Evolution of Primate Social Systems

3.1 Abstract

Phylogenetic comparative methods are a powerful way to investigate the evolutionary history of traits across taxa, which nevertheless have not been widely used to study sociality in primates. However, with a significant phylogenetic signal in any trait, social or otherwise, inferences can be made about the evolutionary history of that trait. Here Bayesian phylogenetic methods were used to investigate three crucial aspects of primate social behaviour, namely social organisation, dispersal (or philopatry), and mating systems. These methods show the most probable state for each trait at the root and ancestral nodes of the phylogenetic tree, as well as the model of trait evolution, and therefore enable fundamental assumptions in primate socioecology to be tested. All three traits display strong phylogenetic inertia in primates, suggesting that history plays an important role in the distribution of these traits among extant species. New models of primate social evolution have been developed here. Changes in social organisation are highly constrained; from a solitary root, multi-male/multi-female groups were the first to evolve, and once sociality was gained it was never lost. Dispersal patterns do not influence social organisation in primates and bi-sexual dispersal is the pattern at the root of the phylogeny and the default throughout the tree. Mating systems have a similar pattern to social organisation among diurnal primates, but not among nocturnal primates, where there were changes in mating system while solitary

living persisted. Since primates are among the most social of animal species, it is especially important that primate socioecology recognises the importance of phylogeny and takes the history of social trait evolution into account in its models.

3.2 Introduction

Hamilton's (1964a, 1964b) key insight into animal social behaviour, inclusive fitness theory, has led to a huge expansion in the study of the evolution and function of animal sociality (Krebs and Davies 1997, Janson 2000). However, subsequent research has focused almost exclusively on the function of sociality in contributing to an organism's survival and successful reproduction, telling us little of the evolutionary history of sociality, the other ultimate explanation of an individual's social behaviour (Tinbergen 1963). This omission on the part of researchers is freely acknowledged (Harvey and Nee 1997, Janson 2000), but justified because, unlike morphological traits, social traits leave no direct trace in the fossil record. Inferences have been made about ancestral social systems from fossil morphology, particularly in the area of dimorphism and the competitive regime among males, mainly in the study of hominin evolution (Plavcan 2000, Nelson and Shultz 2010), but the conclusions can be ambiguous and are sometimes highly contested (Reno *et al.* 2003, Plavcan *et al.* 2005, Reno *et al.* 2005).

An alternative approach, when direct inferences about the evolution of a trait are absent, is the phylogenetic comparative method (Harvey and Pagel 1991). By investigating the distribution of a trait among extant taxa coupled with a view of the phylogenetic relationships between those taxa it is possible to make inferences about the distribution of the trait in the past and the pathways from the ancestral distribution to the present one (Pagel 1999a). The comparative method has a long history in evolutionary biology, and recent advances in molecular analysis have led to an enormous increase in phylogenetic trees based on gene sequence data (Pagel 1999a). This, coupled with the adoption of explicit likelihood-based models of trait evolution and Bayesian inference approaches, makes it possible to infer the posterior probability of model parameters of interest, given some prior beliefs (prior probabilities) about those parameters, whilst accounting for uncertainty in the phylogeny (Huelsenbeck *et al.* 2001). While the recent advances in molecular analysis have helped to resolve the evolutionary relationships among taxa, uncertainties remain (Arnold, Matthews, and Nunn 2010). Therefore, comparative analysis of social systems using different phylogenetic trees would produce different results. Using Bayesian Markov Chain Monte Carlo (MCMC) methods allows for this uncertainty to be modelled explicitly by investigating the evolution of a trait over a large number of possible phylogenetic trees (Pagel and Meade 2006).

The availability of phylogenies and the adoption of Bayesian methods has led to a burgeoning of studies in biology, including evaluating divergence times and uncertainties in phylogenies (for a review see (Huelsenbeck *et al.* 2001), and inferring ancestral character states (Pagel, Meade, and Barker 2004) and correlated evolution between traits (Pagel and Meade 2006). In human cultural evolution there have been a number of landmark studies including into the origins of the Indo-European language family (Gray and Atkinson 2003), and matrilocality (Jordan *et al.* 2009) and political complexity (Currie *et al.* 2010) in Austronesia. Both behavioural ecology and socioecology have responded by factoring phylogenetic relatedness into comparative studies (for reviews see Harvey and Nee 1997, Chapman and Rothman 2009), but far fewer studies have explicitly sought to map the distribution of ancestral social traits and model the evolutionary pathways of those traits to the present. The most likely explanation for the reluctance among animal behaviourists to undertake studies of this type is the widespread belief that behavioural traits are much more labile over evolutionary time than morphological or physiological traits (Harvey and Nee 1997). However, while some studies (Blomberg, Garland, and Ives 2003) support this view, others challenge it (Rendall and Di Fiore 2007). Gittleman (1996) proposes that the phylogenetic inertia or signal of the particular behavioural trait under investigation should be assessed before deciding on its plasticity.

On this basis, comparative phylogenetic methods have been used to reveal the behavioural character states at ancestral nodes on phylogenetic trees (Pagel and Meade 2006), test possible models of evolution across a phylogenetic tree (Dalerum 2007), and search for correlated evolution between a social and an ecological trait (Garcia-Pena *et al.* 2009), a social and a morphological trait (Pagel and Meade 2006, Pérez-Barbería, Shultz, and Dunbar 2007) and two social behaviour traits (Cohas and Allaine 2009, Olson *et al.* 2009, Cornwallis *et al.* 2010, Shultz and Dunbar 2010).

However, while phylogenetic comparative methods have been used to investigate aspects of primate social evolution there have been no such studies of the evolution of social systems as a whole. This means that it is unknown whether primate social systems are a short-term response to ecological pressures as suggested by the socioecological model (Wrangham 1980, Sterck, Watts, and van Schaik 1997), or whether primates are phylogenetically constrained to stick with one system or with particular pathways between systems (Di Fiore and Rendall 1994). Furthermore, hypotheses about the ancestral social states and the evolutionary pathways of sociality from those ancestral states to the present distribution across taxa remain untested. Here, by using a phylogeny and a Bayesian approach it will be possible to investigate co-evolution between traits and therefore test adaptive hypotheses for the evolution of social behaviour in primates (Pagel and Meade 2006). Because the ancestral and derived states of traits can be established, as well as the relative timing of trait evolution, the drivers of change can also be determined (Harvey and Pagel 1991).

3.3 Predictions

This chapter will use a Bayesian phylogenetic approach to test a number of fundamental predictions that underpin the study of primate social behaviour. The hypotheses are:

Hypothesis 1: The socioecological model suggests that primate social systems are responses to current ecological variation (Sterck, Watts, and van Schaik 1997). If this were the case then transitions between social states would be expected to be variable across evolution in response to environmental change. This would be demonstrated by low phylogenetic inertia across social traits.

Hypothesis 2: Early primates, at the root of the primate phylogeny, are suggested to have been solitary in their social organisation (Müller and Thalmann 2000). For this hypothesis to be supported, there should be a higher likelihood of a solitary state at the primate root over all other social organisation states.

Hypothesis 3: As primates became increasingly social, and groups grew in size over evolutionary time, social complexity, in terms of social organisation, may have increased in a step-wise fashion (Dunbar 2000, Nunn 2000). Accordingly, a model of evolution such that the social organisation of primates evolved from a solitary system at the root, via small, simple groups to large, complex ones would be suggested.

Hypothesis 4: Female philopatry (or male dispersal) is proposed as the default pattern among primates as seen among cercopithecines (Sussman 1992, Alberts and Altmann 1995). Transitions between other dispersal patterns are expected to progress via male dispersal rather than following a direct route.

Hypothesis 5: Male dispersal is suggested as the ancestral state for primates (Wrangham 1987a), since it is argued most primates resemble other mammals and differ from birds in showing male-biased dispersal (Greenwood 1980). For this assumption to be supported there should be a higher likelihood of male dispersal at the primate root over female or bi-sexual dispersal patterns.

Hypothesis 6: Dispersal patterns determine primate social organisation, according to one version of the socioecological model (Wrangham 1980). Indeed, more recently, it has been argued that it is the switch from bi-sexual dispersal to sex-biased dispersal (specifically daughters staying with their mothers post puberty) that brings about sociality across animal species (Nowak, Tarnita, and Wilson 2010). In other words, the dispersal pattern is seen as the underlying determinant of social organisation. For this hypothesis to be supported, not only should these traits co-evolve, but also the transition from solitary living to sociality should be more likely with a background of sex-biased rather than bi-sexual dispersal.

Hypothesis 7: Primate societies are shaped not only by the groups that animals live in, but also by the mating strategies that they employ. While different evolutionary pressures may shape social organisation and mating systems, they are not entirely independent of each other and may influence each other's evolutionary history (Kappeler and van Schaik 2002). Mating systems and social organisation should follow similar trajectories through evolutionary history.

But these predictions, flowing from the socioecological model, remain untested using a phylogenetic approach. In this chapter, quantitative models of trait evolution and a Bayesian Markov chain Monte Carlo (MCMC) inference framework will be used to test each of these hypotheses about the way sociality evolved in primates.

3.4 Methods

To undertake a phylogenetic comparative analysis of a trait requires both a phylogenetic tree of the relationships between the taxa, and trait data for the extant species, to be mapped onto the phylogeny. This allows inferences to be made about the evolution of the trait over the phylogeny (Pagel and Meade 2006). The details of the primate phylogeny, downloaded from the *10kTree Project* (Arnold, Matthews, and Nunn 2010), and the analysis of data over that phylogeny were outlined in Chapter 2.

3.4.1 Primate Data

Data on the social organisation, dispersal, and mating system of extant primate taxa were extracted from the literature (Smuts *et al.* 1987, Dunbar 1988, Dixson 1998, Campbell *et al.* 2007). There are three fundamental types of primate social organisation: solitary, pair living and group living (Kappeler and van Schaik 2002). Here, group living is further divided into uni-male harems and multi-male/multi-female groups. The species were coded: solitary (n=39), pair living (n=56), uni-male harems (n=67), or multi-male/multi-female groups (n=123). Polymorphic species were coded as multiple states. For data on dispersal the species were coded: male dispersal (n=86), female dispersal (n=14), or bi-sexual dispersal (n=105). For the *Discrete* analysis, which requires binary traits, data were coded as solitary (0) or social (1) (including pair living) for social organisation, bi-sexual dispersal (0) or either female or male dispersal (1) for dispersal patterns. Mating systems were coded: monogamous (n=60), harem polygynous (n=60), or polygynandrous (n=111), polymorphic species were coded as multiple states.

3.4.2 Analyses

Further to the analyses discussed in Chapter 2, five different rate models for social organisation and three for dispersal were set up, in order to test the predictions from primate socioecology, and find the most likely model for the evolution of primate social organisation and dispersal (see Table 3.1, Figure 3.1 and Figure 3.2). First, for social organisation, all rates were set to be same in an ‘equal rates’ model, simulating equal likelihood for all transitions. Next, rates were allowed to vary freely without constraint to produce a ‘full’ model. Then the highest ranked model from the posterior probability distribution of the Reversible Jump procedure (RJ-derived model) was run, allowing transitions from solitary to multi-male and from multi-male to both uni-male and pair living and back from uni-male to multi-male. All other rates were set to zero. In order to test the assumption of increasing complexity in primate social systems as group size increased over evolutionary time (Crook and Gartlan 1966, Alexander 1974, Dunbar 2000, Nunn 2000) a model was run where transitions were restricted so that movements were only possible from the solitary root via pair living and then uni-male harems to multi-male social organisation, and the reverse direction; all other transition rates were set to zero. To test this ‘complexity’ model further ‘catastrophes’ were allowed for; i.e. movements back down the chain leaving out intermediate states.

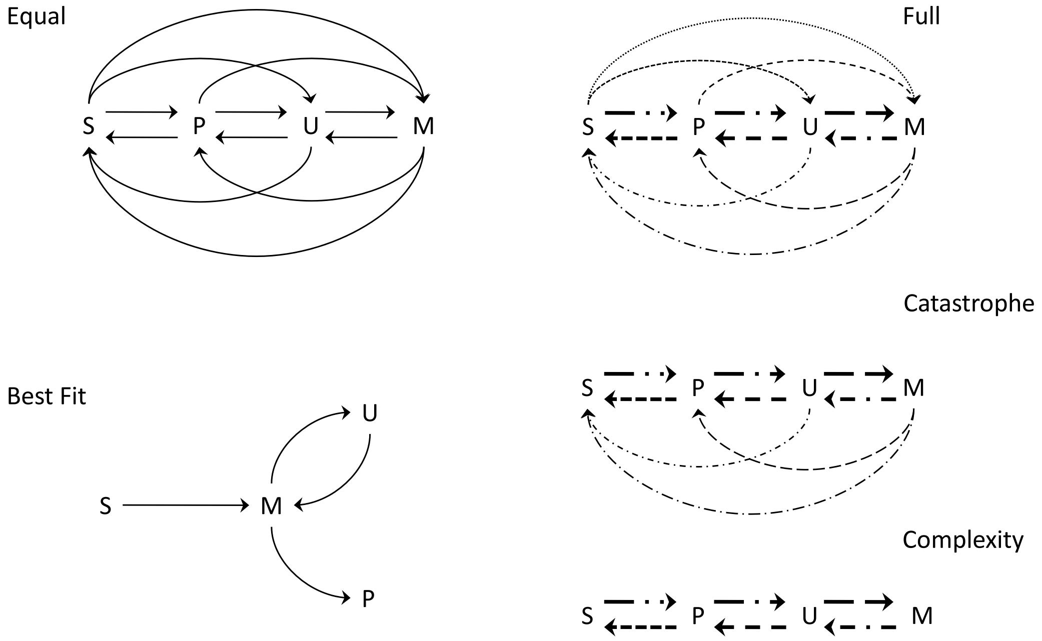


Figure 3.1 Models of Evolution for Social Organisation. Where S = Solitary, P = Pair-living, U = Uni-male, and M = Multi-male. Equal = Equal rates, Best Fit = Reverse Jump derived.

Table 3.1 Models of evolution with transition rate parameters. Rates (q_{12}, q_{13} etc.) are between state 1 and state 2, state 1 and state 3. Z denotes a zero rate, 0 denotes a non-zero rate, - denotes variable rate.

Model	**Rate parameters between character states**											
Social Organisation	q_{12}	q_{13}	q_{14}	q_{21}	q_{23}	q_{24}	q_{31}	q_{32}	q_{34}	q_{41}	q_{42}	q_{43}
Equal rates	0	0	0	0	0	0	0	0	0	0	0	0
Full	-	-	-	-	-	-	-	-	-	-	-	-
RJ-derived	Z	Z	0	Z	Z	Z	Z	Z	0	Z	0	0
Complexity	-	Z	Z	-	-	Z	Z	-	-	Z	Z	-
Complexity (+ catastrophe)	-	Z	Z	-	-	Z	-	-	-	-	-	-
Dispersal	q_{12}	q_{13}	q_{21}	q_{23}	q_{31}	q_{32}						
Full	-	-	-	-	-	-						
Male Dispersal Default	-	-	-	Z	-	Z						
RJ-derived	Z	0	0	0	0	0						
Bi-sexual dispersal default	Z	-	Z	-	-	-						

For dispersal, a 'full' model was produced where all rates were allowed to vary (Table 3.1 and Figure 3.2). Then the RJ-derived model, which has a zero rate from male dispersal to female dispersal and all other rates equal, was run. Then a 'male default' model was tested, which had zero rates between female dispersal and bi-sexual dispersal; all other rates were allowed to vary. Finally, a 'bi-sexual default' model was tested, which has zero rates between male and female dispersal; all other rates were allowed to vary.

For these analyses, the RJ procedure was switched off and an exponential prior was used, set at the RJ prior mean. To compare between models, as well as a Bayes Factor (BF), a Bayesian Information Criterion (BIC) (Posada and Buckley

2004) was used, which has the advantage that it takes account of the number of parameters in the model. This is calculated by:

$$\mathrm{BIC} = -2Lh + K\mathrm{Log}(n)$$

Equation 3.1

Where Lh is the log likelihood, K is the number of estimable parameters, and n is the sample size. However, it has been suggested that BIC may favour simple models over those with more parameters (Weakliem 1999). Therefore both comparisons were used to assess the most likely model. All other procedures, as laid out in Chapter 2, were followed.

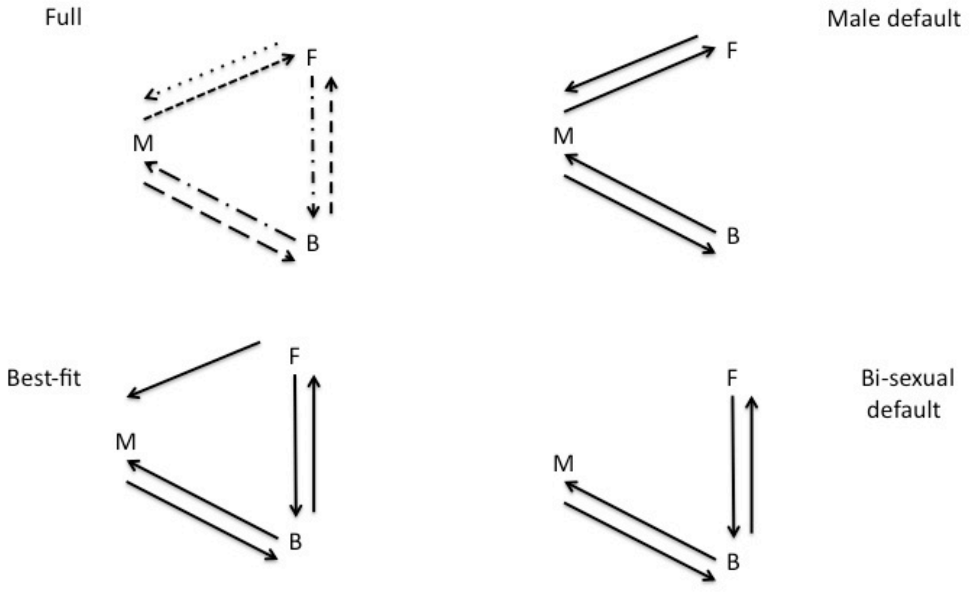


Figure 3.2 Models of Evolution for Dispersal. M = Male dispersal, F = Female dispersal, B = Bi-sexual dispersal.

3.5 Results

3.5.1 Phylogenetic Signal

The results show (Table 3.2) that all three data sets have high Lambda (λ) values, significantly different from 0 (LLR_0) and not significantly different from 1 (LLR_1). Therefore the three data sets have a strong phylogenetic signal, which means that related species are more similar in these traits than would be expected by chance. This means that inferences can be made about the evolutionary history of the three traits within primates, since phylogeny has a significant effect on the current distribution of the traits among extant taxa.

Table 3.2. Phylogenetic signal, Pagel's λ, of primate social organisation, dispersal, and mating system. N, number of species; λ_{max} lambda value from maximum likelihood analysis; LL_{max} log likelihood of λ_{max}; LL_0 log likelihood of λ_0; LL_1 log likelihood of λ_1; LLR_0 probability of log likelihood ratio of LL_0 and LL_{max}; LLR_1 probability of log likelihood ratio of LL_1 and LL_{max}.

Trait	**Pagel's Lambda (λ)**						
	N	λ_{max}	LL_{max}	LL_0	LL_1	LLR_0	LLR_1
Social Organisation	218	0.98	-150.04	-360.45	-150.88	<0.001	0.195
Dispersal	206	0.97	-74.94	-213.18	-76.06	<0.001	0.135
Mating System	214	1.00	-108.61	-224.95	-108.70	<0.001	0.679

3.5.2 Social Organisation

3.5.2.1 Root and transition rates

Using a rate deviation of 0.02 ensured the acceptance rate was within the 15% - 40% range, which gives good estimates of the rate coefficients (Pagel, Meade, and Barker 2004). The results show a mean log likelihood of -71.99 (s.e. +/- 0.02) for this analysis. The posterior probability of the state of social organisation at the root of the primate phylogeny is strongly solitary (mean probability at the root: solitary 0.9874 +/- 0.0004; pair living 0.0051 +/- 0.0002; uni-male 0.0057 +/- 0.0002; multi-male 0.0018 +/- 0.0002).

The RJ MCMC favoured a small number of parameters (1.11) suggesting that some transitions between states hardly ever occur (close to a zero rate) and some occur at a rate that does not differ greatly between transition types. The prior mean was 1.8, a figure that will be used in subsequent analyses.

The top ten models of evolution for social organisation in primates from the RJ MCMC analysis (Table 3.3) show that two models dominate the posterior distribution, accounting for 53.6% of visits of the Markov Chain between them. Furthermore, the two models differ in only one rate, namely the transition from pair living to multi-male groups. The highest ranked model (RJ-derived model) shows a zero rate for this transition, while the second model shows a positive rate. These two models suggest that the only state change from the solitary root was to multi-male groups, followed by transitions from multi-male groups to uni-male harems and back. There were also transitions from multi-male groups to pair living, but in the RJ-derived model there was no transition from pair living back to multi-male groups. The analysis also shows that there were no transitions back from any kind of sociality to solitary living in primates and there are no direct transitions between uni-male harems and pair living.

Table 3.3. Top ten evolutionary models of primate social organisation. The top ten models account for 81.7% of the posterior sample. Subscripts on the rate coefficients correspond to the transitions between the four states of social organisation such that q_{ij} is the transition rate from character state i to character state j. (Note: following the convention established by Pagel and Meade (2006), Z indicates transition rates between states in the model assigned to zero, whereas 0 and 1 indicate non-zero transition rates between states.)

Model Rank	**Rate coefficients**												**Frequency**	**Probability density**	**Cumulative density**
	q_{12}	q_{13}	q_{14}	q_{21}	q_{23}	q_{24}	q_{31}	q_{32}	q_{34}	q_{41}	q_{42}	q_{43}			
1	Z	Z	0	Z	Z	Z	Z	Z	0	Z	0	0	14726	0.295	0.295
2	Z	Z	0	Z	Z	0	Z	Z	0	Z	0	0	12029	0.241	0.536
3	Z	Z	0	Z	0	0	Z	Z	0	Z	0	0	3031	0.061	0.597
4	Z	Z	0	Z	Z	0	Z	0	0	Z	0	0	2683	0.054	0.651
5	Z	Z	0	0	Z	0	Z	Z	0	Z	0	0	2407	0.048	0.699
6	Z	Z	0	Z	Z	Z	0	Z	0	Z	0	0	1941	0.039	0.738
7	Z	Z	0	Z	Z	0	0	Z	0	Z	0	0	1675	0.033	0.771
8	Z	Z	0	Z	0	Z	Z	0	0	Z	0	0	1043	0.021	0.792
9	Z	Z	0	Z	0	0	Z	0	0	Z	0	0	816	0.016	0.808
10	Z	Z	0	Z	Z	Z	0	0	0	Z	0	0	473	0.009	0.817
50	Z	Z	0	Z	Z	0	Z	Z	1	Z	0	0	26	0.001	0.899

3.5.2.2 Equal Rates Model

An equal rates model was run, setting all transition rates to be equal (Figure 3.1). This would characterise an evolutionary model where all transitions between organisational states are equally likely. A prior on transition rate parameters was set at the RJ mean (1.8) reflecting the view (justified by Maximum Likelihood and the RJ MCMC analyses) that there were few changes along branches over time. A rate deviation of 0.009 gave an acceptance rate of 23.4%. The mean likelihood for the equal rates model is -83.94 +/- 0.01.

3.5.2.3 Full Model

As a next step the MCMC analysis was run unconstrained allowing all transition rates to vary freely (Figure 3.1). A rate deviation of 0.009 gave an acceptance rate of 21.3%. The results of this unconstrained model showed a mean likelihood of -80.48 +/- 0.03.

3.5.2.4 RJ-derived Model

For the RJ-derived model an exponential prior was set at the RJ mean (1.8) and the rate deviation was set at 0.02, giving an acceptance rate of 25.1%. The result shows a higher mean likelihood (-70.93 +/- 0.01) than the full model or the equal rates model.

3.5.2.5 Model Comparison

Table 3.4 shows a comparison between models using both Bayes Factors and BICs. A Bayes Factor comparison shows that the RJ-derived model is decisively better at explaining the data than either the equal rates model or the full model. This comparison does not support a model of equal transition rates between states. The BIC comparison ranks the three models in the same order showing that the additional parameters in the full model do not improve the fit with the data.

Table 3.4. Comparison of models of Primate Social Organisation ranked by Bayesian Information Criterion (BIC). Lh = log likelihood, n = sample size.

Model	**Lh**	**No. Estimated Parameters**	**n**	**BIC**	**Lg10 Bayes Factor (versus RJ-derived model)**
RJ-derived	-70.93	1	218	147.24	-
Equal rates	-83.94	1	218	173.26	5.69
Complexity	-92.86	6	218	218.03	10.47
Catastrophe	-85.67	9	218	219.80	7.96
Full	-80.48	12	218	225.57	6.27

3.5.2.6 Social Complexity

One important assumption of primate socioecology is that there was increasing complexity in primate social systems over evolutionary time (Crook and Gartlan 1966, Alexander 1974, Dunbar 2000, Nunn 2000). In order to test this assumption transitions were restricted so that movement was up or down the chain from the solitary root via pair living and then uni-male harems to multi-male groups (Figure 3.1). The results (Figure 3.3) show that upward movements through the chain were not consistently higher than downward movements, suggesting that the directionality of the increasing complexity view is not supported. The mean likelihood for the model was low (- 92.86 +/- 0.01). A Bayes Factor comparison shows that the RJ-derived model is decisively better at explaining the data than the complexity model (Table 3.4). Indeed, the complexity model has a decisively lower likelihood than the full model ($Log_{10}BF = 4.21$), suggesting that the complexity model is worse at explaining the data than leaving the rates to find their own level. This suggests that the complexity model as a whole is not supported.

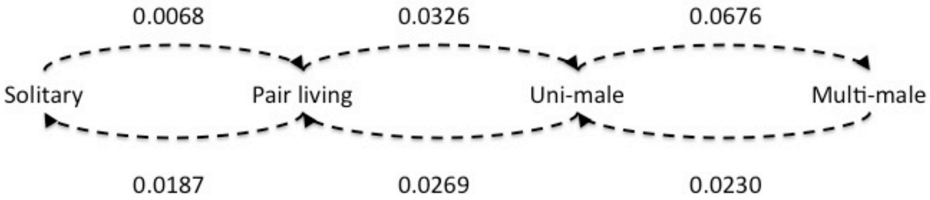
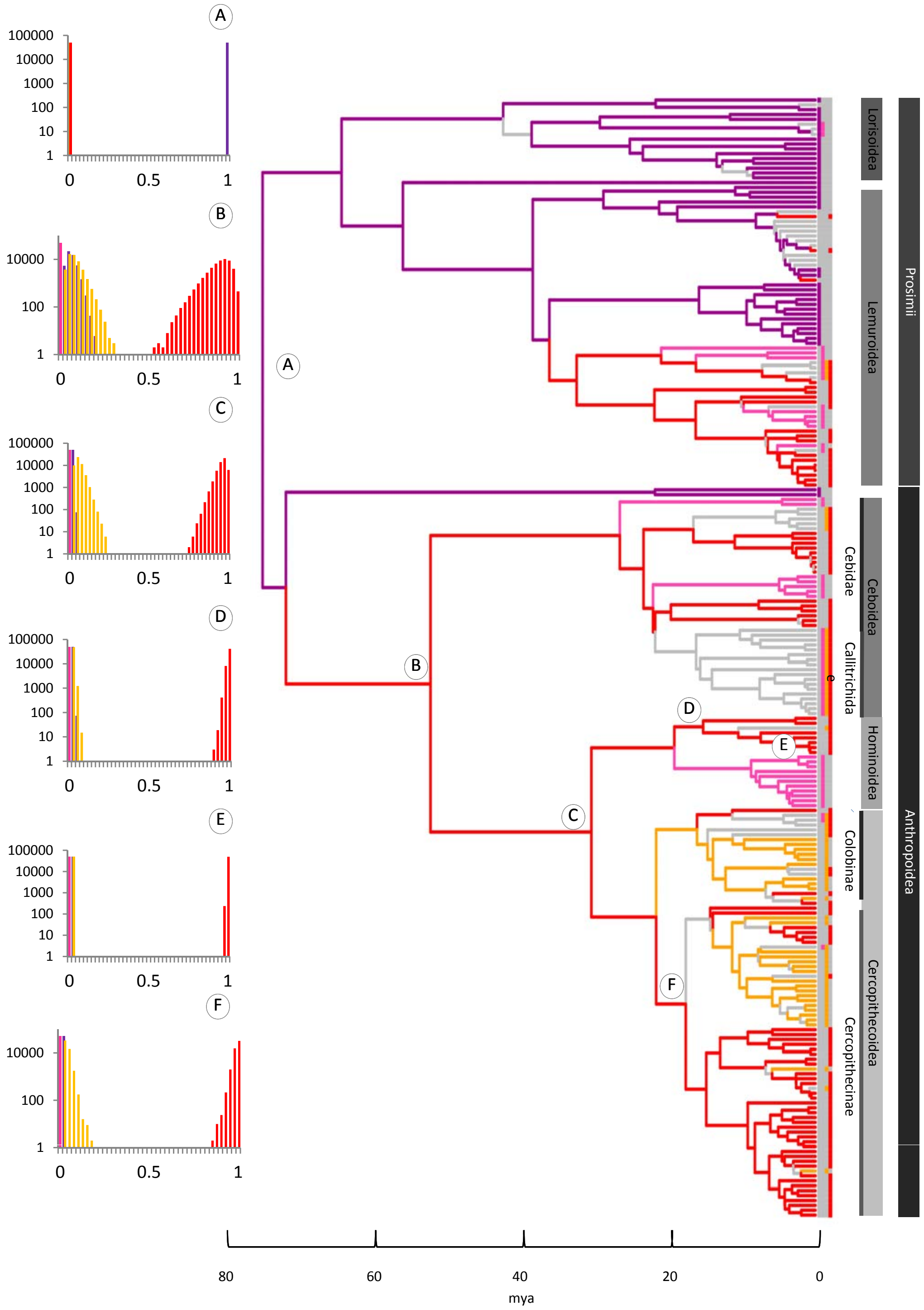


Figure 3.3 Social complexity transition rates. Rates up the chain (solitary to pair to uni-male to multi-male) are not consistently higher than the reverse direction.

Allowing for ‘catastrophes’, movements back down the chain leaving out intermediate states, meant that upward transitions through the chain became consistently more likely than downward movements, and the likelihood of the overall model increased (-85.67 +/- 0.02). A comparison with the complexity model using a Bayes factor showed that the catastrophe model was significantly better at explaining the data than the complexity model ($\text{Log}_{10}\text{BF} = 2.51$), while the BIC suggested that it was the additional parameters in the catastrophe model that improved the fit. The catastrophe model was still decisively worse than the RJ-derived model at explaining the data (Table 3.4). From these results it is clear that the RJ-derived model is decisively better at explaining the social organisation data than any other model tested.

3.5.2.7 Ancestral States

Figure 3.4 shows the state of social organisation at ancestral nodes across the primate phylogeny. A maximum-clade credibility tree was used to illustrate the ancestral states, but the data were derived from a full MCMC analysis based on the RJ-derived model. The histograms (Figure 3.4) show the posterior probability distribution of states at nodes indicated. Social organisation evolved from a solitary state at the primate root (74 mya) to multi-male/multi-female sociality at the root of the anthropoids (52 mya) and the root of the *Indriidae* and *Lemuridae* (32 mya) among prosimians. Other forms of social living evolved late in primates. Not until the root of the *Colobinae* (16 mya) did uni-male harems first appear, followed soon after in the *Cercopithecini* (14 mya). Pair living arose at a similar time at the root of the *Callitrichidae* (16 mya). All the other appearances of pair living arose much later: *Hylobatidae* (8.6 mya); *Avahi* (6.4 mya); hapalemurs (6.3 mya); *Aotus* (4.8 mya) and *Callicebus* (4.5 mya).


A
100000
10000
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10
1
0
0.5
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B
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E
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A
B
C
D
E
F
Lorisoidea
Lemuroidea
Prosimii
Cebidae
Ceboidea
Callitrichida
e
Hominoidea
Colobinae
Cercopithecoidea
Cercopithecinae
Anthropoidea
80
60
40
20
0
mya

Figure 3.4 Ancestral state reconstruction for primate social organisation using RJ-derived model of evolution. Branch and tip colours are solitary – purple, uni-male – orange, multi-male – red, and pair living – pink. Where combined probability of state and branch are less than 0.7 – grey. Histograms show posterior probability distribution of state at nodes indicated (a. primate root; b. anthropoid root; c. catarrhine root; d. great ape root; e. *Pan-Homo* split; f. Old World monkey root) (following Shultz, Opie, and Atkinson 2011).

3.5.3 Dispersal

3.5.3.1 Roots and transition rates

The results of the dispersal RJ analysis show a mean log likelihood of -67.58 (+/- 0.03). The posterior probability of dispersal at the root of the primate phylogeny is strongly bi-sexual (mean probability at the root: male dispersal 0.0066 +/- 0.0001; female dispersal 0.0071 +/- 0.0009; bi-sexual dispersal 0.9863 +/- 0.0009).

The RJ MCMC favoured a small number of parameters (1.08). By using a rate deviation of 0.015 the acceptance rate was 21.1%. The prior mean was 1.9, a figure that will be used in subsequent analyses.

Of the top ten models of evolution for dispersal patterns in primates (Table 3.5) three models account for 81.6% of visits by the Markov Chain, with the top two virtually the same proportion of the posterior distribution. All three models show a zero rate for the transition from male dispersal to female dispersal, while the second model adds a zero rate in the reverse direction and the third model includes both those zero rates as well as a zero rate for the transition from female to bi-sexual dispersal. All the other transitions in these three models are equal and non-zero. Over 80% of the models favoured by the Markov Chain have a transition rate of zero from male dispersal to female dispersal over the full phylogeny. Furthermore 53% of models show no transition in the reverse direction from female dispersal to male dispersal. These results question the view that male dispersal is the 'default' pattern among primates.

Table 3.5. Top ten evolutionary models of primate dispersal. The top ten models account for 92.4% of the posterior sample. Subscripts on the rate coefficients correspond to the transitions between the three states of dispersal such that q_{ij} is the transition rate from character state i to character state j. (Note: following the convention established by Pagel and Meade (2006), Z indicates transition rates between states in the model assigned to zero, whereas 0 and 1 indicate non-zero transition rates between states.)

Model Rank	**Rate coefficients**						**Frequency**	**Probability density**	**Cumulative density**
	q_{12}	q_{13}	q_{21}	q_{23}	q_{31}	q_{32}			
1	Z	0	0	0	0	0	14277	0.286	0.286
2	Z	0	Z	0	0	0	14224	0.284	0.57
3	Z	0	Z	Z	0	0	12318	0.246	0.816
4	0	0	Z	0	0	0	1386	0.028	0.844
5	0	0	0	0	0	0	1306	0.026	0.87
6	0	0	Z	Z	0	0	1098	0.022	0.892
7	0	0	0	Z	0	0	1064	0.021	0.913
8	0	0	Z	Z	0	Z	214	0.004	0.917
9	0	0	0	0	0	Z	176	0.004	0.921
10	Z	0	0	0	0	1	156	0.003	0.924
50	1	0	1	Z	0	1	34	0.001	0.975

3.5.3.2 Full Model

With the RJ turned off an analysis was run without constraints. A prior was set at the RJ mean (1.9). A rate deviation of 0.015 provided an acceptable acceptance rate. The results of this unconstrained model showed the same pattern of roots and transition rates but a decisively lower mean likelihood than the RJ MCMC analysis (Table 3.6).

Table 3.6. Comparison of models of Primate Dispersal Patterns ranked by Bayesian Information Criterion (BIC). Lh = log likelihood, n = sample size.

Model	**Lh**	**No. Estimated Parameters**	**n**	**BIC**	**Lg10 Bayes Factor (versus RJ-derived model)**
RJ-derived	-67.52	1	205	140.36	-
Bi-sexual Default	-68	4	205	157.29	0.65
Male Default	-74.61	4	205	170.51	3.86
Full	-70.17	6	205	172.28	2.09

3.5.3.3 RJ-derived Model

The next step was to run the RJ-derived model from the RJ MCMC analysis. An exponential prior was set at the RJ mean (1.9) and a rate deviation of 0.015 gave an acceptance rate of 23.5%. The results (Table 3.6) showed a higher mean likelihood than the Full Model. A Bayes Factor comparison with the Full Model showed decisive support for the RJ-derived model, supporting the constraints of this model.

3.5.3.4 Default Dispersal Pattern

A common view among primatologists is that female philopatry (or male dispersal) is the default pattern among primates (for example Sussman 1992, Alberts and Altmann 1995). If male dispersal were the default dispersal pattern for primates then a change from female dispersal to bi-sexual dispersal (and vice versa) would have an intermediary state of male dispersal. A model of evolution was set up with transitions directly between female dispersal and bi-sexual dispersal restricted to zero, but allowing other transition rates to vary.

The result of this analysis gave a lower mean likelihood than the RJ-derived model, an acceptance of 28.4%, and a mean likelihood of 0.910 (+/- 0.0012) for bi-sexual dispersal at the root. Comparing the ‘default’ male dispersal model to the RJ-derived dispersal model using the Bayes Factor (Table 3.6) shows decisive support for the RJ-derived model. Furthermore the male dispersal ‘default’ model shows very strong support for bi-sexual dispersal at the root of the phylogenetic tree. Even if this model of evolution were used it would not yield an ancestral state of male dispersal. These results suggest that male dispersal is a derived state in primates.

The ‘default’ male dispersal model was also compared with an alternative bi-sexual ‘default’ model. The bi-sexual ‘default’ model is characterised by no direct transitions between male dispersal and female dispersal in either direction (Figure 3.2 and Table 3.6). Comparing the two ‘default’ models shows a Bayes Factor of 3.18, further decisive support for the bi-sexual 'default' model (Table 3.6). However, the bi-sexual ‘default’ model is not as good as the RJ-derived model at explaining the trait data, but not decisively so.

Both Bayes Factors and BICs (Table 3.6) show that the RJ-derived dispersal model is substantially better than the bi-sexual default model and decisively better than the Male default and full models at explaining the data.

3.5.3.5 Ancestral States

Figure 3.5 shows the dispersal states at the ancestral nodes across the primate phylogeny. From bi-sexual dispersal at the root of the primate phylogeny it remains ubiquitous throughout the early tree. Male dispersal first appears in the prosimian family *Galagidae* at 25 mya followed by the mouse lemurs (*Microcebus*) at 21 mya. It is possible that male dispersal evolved as early as 22 mya among the *Lemuridae*, but more likely that it evolved later in Eulemur fulvus (4.8 mya) and separately in *Varecia*. In anthropoids, male dispersal appeared once at subfamily level in the *Cercopithecinae* (17 mya). Much later (7.6 mya) male dispersal also evolved in the *Cebus capucinus* group. Female dispersal has only evolved twice unequivocally: first in the *Atelinae* subfamily (11 mya) and much later in the *Pan* genus (2.9 mya).

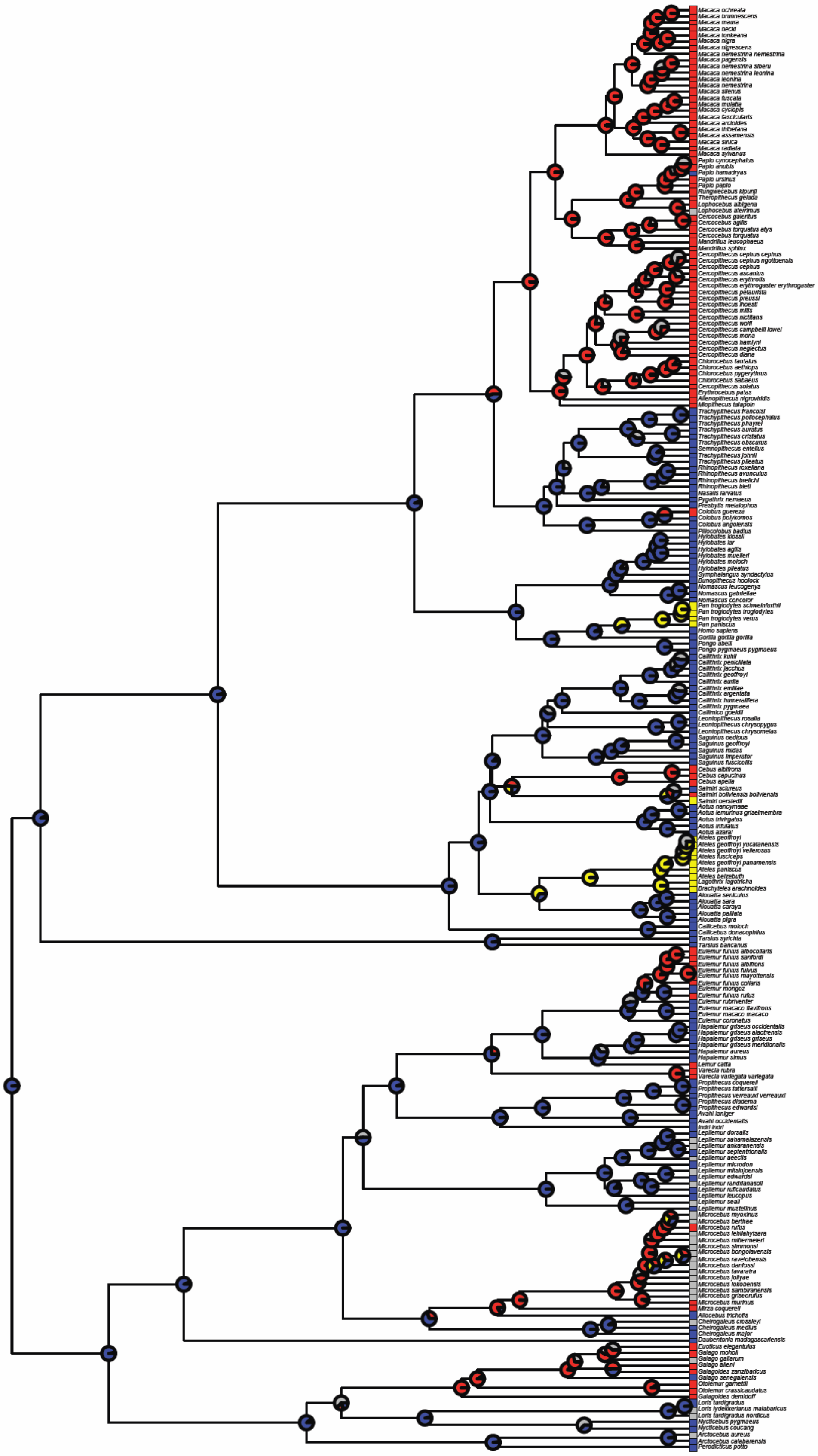
Macaca ochreata
Macaca brunnescens
Macaca maura
Macaca hecki
Macaca tonkeana
Macaca nigra
Macaca nigrescens
Macaca nemestrina nemestrina
Macaca pagensis
Macaca nemestrina siberu
Macaca nemestrina leonina
Macaca leonina
Macaca nemestrina
Macaca silenus
Macaca fuscata
Macaca mulatta
Macaca cyclopis
Macaca fascicularis
Macaca arctoides
Macaca thibetana
Macaca assamensis
Macaca sinica
Macaca radiata
Macaca sylvanus
Papio cynocephalus
Papio anubis
Papio hamadryas
Papio ursinus
Papio papio
Rungwecebus kipunji
Theropithecus gelada
Lophocebus albigena
Lophocebus aterrimus
Cercocebus galeritus
Cercocebus agilis
Cercocebus torquatus atys
Cercocebus torquatus
Mandrillus leucophaeus
Mandrillus sphinx
Cercopithecus cephus cephus
Cercopithecus cephus ngottoensis
Cercopithecus cephus
Cercopithecus ascanius
Cercopithecus erythrotis
Cercopithecus erythrogaster erythrogaster
Cercopithecus petaurista
Cercopithecus preussi
Cercopithecus lhoesti
Cercopithecus mitis
Cercopithecus nictitans
Cercopithecus wolfi
Cercopithecus campbelli lowei
Cercopithecus mona
Cercopithecus hamlyni
Cercopithecus neglectus
Cercopithecus diana
Chlorocebus tantalus
Chlorocebus aethiops
Chlorocebus pygerythrus
Chlorocebus sabaeus
Cercopithecus solatus
Erythrocebus patas
Allenopithecus nigroviridis
Miopithecus talapoin
Trachypithecus francoisi
Trachypithecus poliocephalus
Trachypithecus phayrei
Trachypithecus auratus
Trachypithecus cristatus
Trachypithecus obscurus
Semnopithecus entellus
Trachypithecus johnii
Trachypithecus pileatus
Rhinopithecus roxellana
Rhinopithecus avunculus
Rhinopithecus brelichi
Rhinopithecus bieti
Nasalis larvatus
Pygathrix nemaeus
Presbytis melalophos
Colobus guereza
Colobus polykomos
Colobus angolensis
Piliocolobus badius
Hylobates klossii
Hylobates lar
Hylobates agilis
Hylobates muelleri
Hylobates moloch
Hylobates pileatus
Symphalangus syndactylus
Bunopithecus hoolock
Nomascus leucogenys
Nomascus gabriellae
Nomascus concolor
Pan troglodytes schweinfurthii
Pan troglodytes troglodytes
Pan troglodytes verus
Pan paniscus
Homo sapiens
Gorilla gorilla gorilla
Pongo abelii
Pongo pygmaeus pygmaeus
Callithrix kuhlii
Callithrix penicillata
Callithrix jacchus
Callithrix geoffroyi
Callithrix aurita
Callithrix emiliae
Callithrix argentata
Callithrix humeralifera
Callithrix pygmaea
Callimico goeldii
Leontopithecus rosalia
Leontopithecus chrysopygus
Leontopithecus chrysomelas
Saguinus oedipus
Saguinus geoffroyi
Saguinus midas
Saguinus imperator
Saguinus fuscicollis
Cebus albifrons
Cebus capucinus
Cebus apella
Saimiri sciureus
Saimiri boliviensis boliviensis
Saimiri oerstedii
Aotus nancymaae
Aotus lemurinus griseimembra
Aotus trivirgatus
Aotus infulatus
Aotus azarai
Ateles geoffroyi
Ateles geoffroyi yucatanensis
Ateles geoffroyi vellerosus
Ateles fusciceps
Ateles geoffroyi panamensis
Ateles paniscus
Ateles belzebuth
Lagothrix lagotricha
Brachyteles arachnoides
Alouatta seniculus
Alouatta sara
Alouatta caraya
Alouatta palliata
Alouatta pigra
Callicebus moloch
Callicebus donacophilus
Tarsius syrichta
Tarsius bancanus
Eulemur fulvus albocollaris
Eulemur fulvus sanfordi
Eulemur fulvus albifrons
Eulemur fulvus fulvus
Eulemur fulvus mayottensis
Eulemur fulvus collaris
Eulemur mongoz
Eulemur fulvus rufus
Eulemur rubriventer
Eulemur macaco flavifrons
Eulemur macaco macaco
Eulemur coronatus
Hapalemur griseus occidentalis
Hapalemur griseus alaotrensis
Hapalemur griseus griseus
Hapalemur griseus meridionalis
Hapalemur aureus
Hapalemur simus
Lemur catta
Varecia rubra
Varecia variegata variegata
Propithecus coquereli
Propithecus tattersalli
Propithecus verreauxi verreauxi
Propithecus diadema
Propithecus edwardsi
Avahi laniger
Avahi occidentalis
Indri indri
Lepilemur dorsalis
Lepilemur sahamalazensis
Lepilemur ankaranensis
Lepilemur septentrionalis
Lepilemur aeeclis
Lepilemur microdon
Lepilemur mitsinjoensis
Lepilemur edwardsi
Lepilemur randrianasoli
Lepilemur ruficaudatus
Lepilemur leucopus
Lepilemur seali
Lepilemur mustelinus
Microcebus myoxinus
Microcebus berthae
Microcebus rufus
Microcebus lehilahytsara
Microcebus mittermeieri
Microcebus simmonsi
Microcebus bongolavensis
Microcebus ravelobensis
Microcebus danfossi
Microcebus tavaratra
Microcebus jollyae
Microcebus lokobensis
Microcebus sambiranensis
Microcebus griseorufus
Microcebus murinus
Mirza coquereli
Allocebus trichotis
Cheirogaleus crossleyi
Cheirogaleus medius
Cheirogaleus major
Daubentonia madagascariensis
Euoticus elegantulus
Galago moholi
Galago gallarum
Galago alleni
Galagoides zanzibaricus
Galago senegalensis
Otolemur garnettii
Otolemur crassicaudatus
Galagoides demidoff
Loris tardigradus
Loris lydekkerianus malabaricus
Loris tardigradus nordicus
Nycticebus pygmaeus
Nycticebus coucang
Arctocebus aureus
Arctocebus calabarensis
Perodicticus potto

Figure 3.5. Phylogenetic tree of Dispersal Patterns in Primates. Maximum clade credibility tree summarising the full 10k tree block. The circles at nodes on the tree represent proportional support for dispersal states (blue = bi-dispersal, red = male dispersal, yellow = female dispersal, grey = proportion of trees where node does not exist) depending on the proportion of trees with that node. Tip coding (same colours as at nodes) shows dispersal for extant species.

3.5.4 Correlated Evolution

The RJ analysis in the *Discrete* procedure in *BayesTraits* gives a mean likelihood of -82.40 for the dependent analysis and -83.50 for the independent analysis (Pagel and Meade 2006) for co-evolution between social organisation and dispersal. A Bayes Factor comparison of the likelihoods of the dependent and independent models gives substantial (but not decisive) evidence for rejecting the independent model in favour of the dependent model (Log_{10} BF 0.954). However, the RJ analysis visited the dependent model 49474 times (98.95%) against the 527 (1.05%) times for the independent model. The RJ is visiting the independent model more times than would be expected by chance (0.25%) in the dependent analysis (Pagel and Meade 2006). This suggests that the independent model cannot be rejected.

To investigate the disparity between the two results I looked more closely at the dependent analysis. In the RJ-derived model (

Figure 3.6), with 48.5% of the posterior distribution of models, the state at the root of the primate phylogeny is solitary with bi-sexual dispersal (0.9395 +/- 0.0076) and all transition rates have means of the same order except the transition from social to solitary with bi-sexual dispersal (q_{31}), which is a zero rate. Indeed across the whole posterior probability distribution the transition from social to solitary with bi-sexual dispersal (q_{31}) is in the zero bin 82% of the time while the same transition with sex-biased dispersal (q_{42}) is assigned to zero only 17% of the time. All other transitions are assigned to zero for zero or nearly zero percent of the time. Figure 3.7 shows pairs of transition rates that must be in the same rate class to show independent evolution for the two traits (Pagel and Meade 2006). All pairs are in the same rate class in the RJ-derived model, except for q_{31} and q_{42}, and the posterior distributions illustrate this (Figure 3.7). Table 3.7 shows the top ten models from the RJ MCMC analysis.

These results all suggest independent evolution except for the difference between rates q_{31} and q_{42}. This is a difference in transition rate when there is a change from social to solitary depending on the background state of dispersal. When dispersal is bi-sexual there is a zero rate and when sex-biased a non-zero rate. Since the social organisation analysis, already discussed, shows that transitions from social to solitary are rare or non-existent, the difference between these rates may be an artefact of the rarity of the event. All other rate pairs are in the same rate class as seen in the posterior distributions, the rate means and the RJ-derived model. This suggests that despite the Bayes Factor result comparing the dependent analysis to the independent analysis there is no correlation between the evolution of primate dispersal and social organisation.

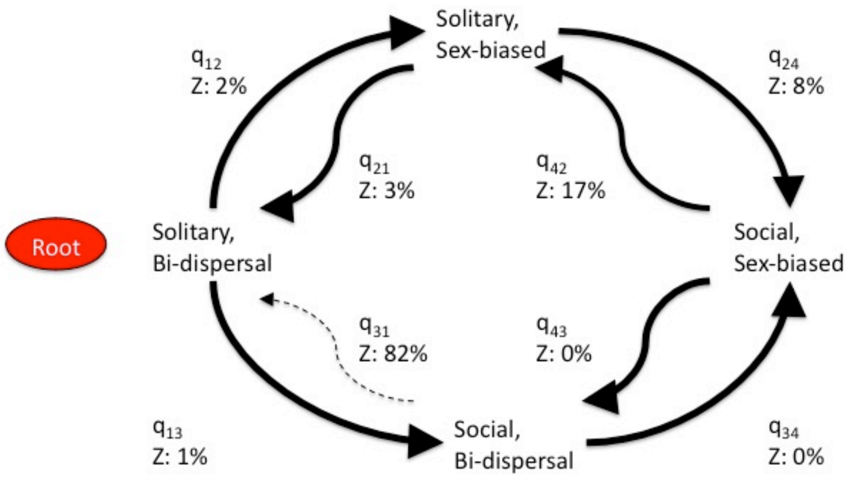

Figure 3.6. Correlated evolution between primate dispersal and social organisation. Z denotes visits assigned to zero as a proportion of posterior probability distribution. Thickness of arrows reflects proportion of time transition rate is not assigned to zero. Dashed line denotes a zero rate in the RJ-derived model.

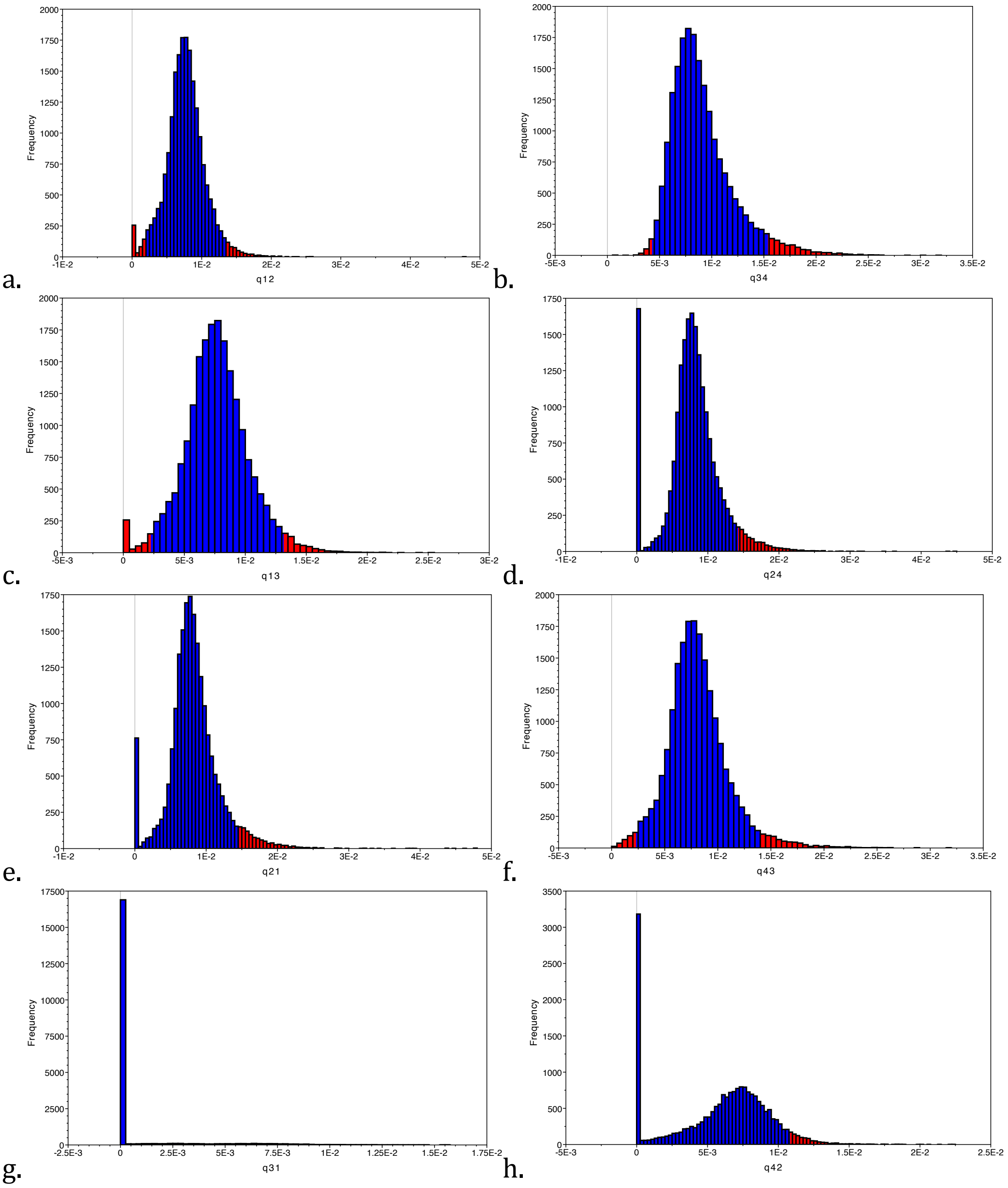

Figure 3.7. Correlated evolution between primate dispersal and social organisation. Transition rate distributions arranged in pairs (a, b; c, d; e, f; g, h) that must be in the same rate class for independent evolution to be supported.

Table 3.7. Top ten models of correlated evolution between dispersal and social organisation in primates. The top ten models account for 66.8% of the posterior sample. Subscripts on the rate coefficients correspond to the transitions between the four combinations of the two binary traits of social organisation and dispersal such that q_{12} is the transition rate from state 0,0 to state 0,1 (see Figure 1). (Note: following the convention established by Pagel and Meade (2006), Z indicates transition rates between states in the model assigned to zero, whereas 0 and 1 indicate non-zero transition rates between states.)

Model Rank	**Rate coefficients**								**Frequency**	**Probability density function**	**Cumulative density function**
	q_{12}	q_{13}	q_{21}	q_{24}	q_{31}	q_{34}	q_{42}	q_{43}			
1	0	0	0	0	Z	0	0	0	24128	0.485	0.485
2	0	0	0	Z	Z	0	0	0	3088	0.062	0.547
3	0	0	0	0	0	0	Z	0	2415	0.049	0.595
4	0	0	Z	0	Z	0	Z	0	743	0.015	0.610
5	0	0	1	1	Z	1	0	0	629	0.013	0.623
6	0	0	1	1	Z	1	0	1	502	0.010	0.633
7	1	1	0	0	Z	0	1	0	480	0.010	0.642
8	1	1	0	0	Z	0	1	1	480	0.010	0.652
9	1	0	1	1	Z	1	0	0	424	0.009	0.660
10	0	1	0	0	Z	0	1	1	401	0.008	0.668
50	1	1	1	1	Z	0	1	1	123	0.003	0.826

3.5.5 Mating Systems

The RJ analysis showed that the ancestral state at the root of the phylogeny for primate mating systems was polygynandry (polygynandry mean probability = 0.853 +/- 0.003; harem polygyny mean = 0.109 +/- 0.002; monogamy mean = 0.038 +/- 0.001).

The best fitting model from the RJ procedure (with 33% of the posterior probability distribution) revealed that from polygynandry at the root of the phylogeny there were strong transition rates into both harem polygyny and monogamy, and a non-zero but weaker rate from harem polygyny to monogamy, all other rates were zero (Figure 3.8).

Across the whole posterior probability distribution transitions out of monogamy were zero for the majority of the time, while the transition from harem polygyny to monogamy, and back to polygynandry, were zero for 18% and 41% of the time respectively (Figure 3.8). Transitions from polygynandry to the other two states were never zero.

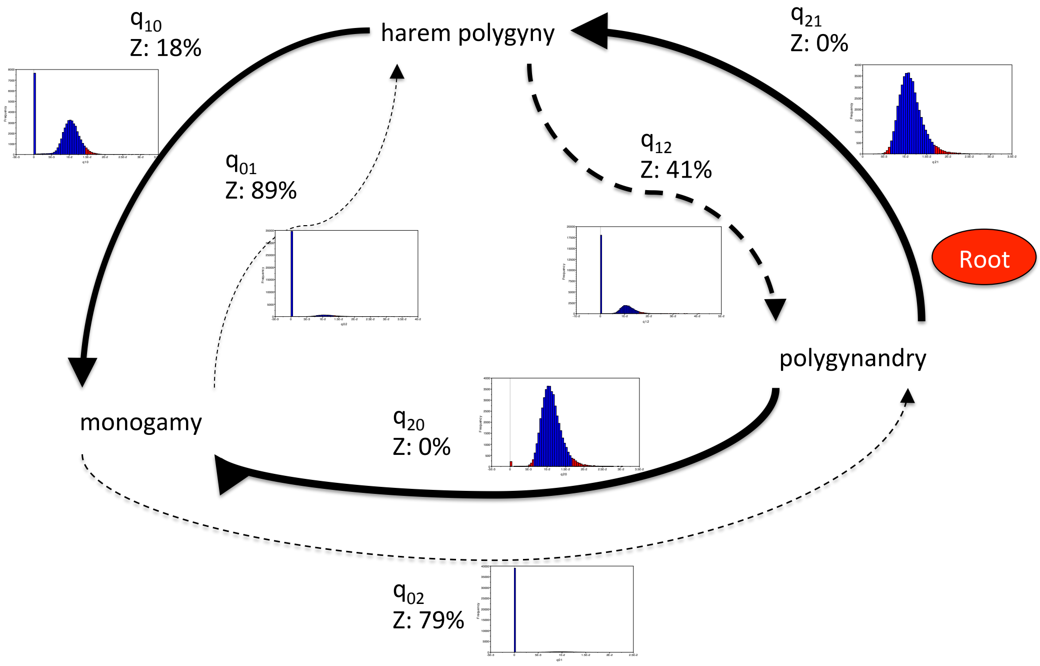

Figure 3.8 Model of evolution of primate mating systems showing posterior distribution of transition rates between states. Thickness of arrows reflects proportion of time the transition rate is not zero. Z denotes a zero transition rate as a proportion of posterior probability distribution. A dashed line denotes a zero transition rate in the RJ derived model. Graphs show posterior probability distribution of each transition rate.

Harem polygyny evolved earliest among prosimians, first at the root of the Loris sub-family *Perodicticinae* (~ 42mya) and later at the root of the Lepilemurs (~ 36mya) (Figure 3.9). Monogamy evolved in a number of Lemur families from ~ 28mya. Among anthropoids monogamy emerged first at the root of *Callicebus* (~ 26mya), followed by *Aotus* and the Callitrichids (~ 22mya) and then Gibbons (~ 19mya). Harem polygyny evolved later among anthropoids, at the root of the

Trachypithecus genus (~ 16mya), and later still at the root of the *Cercopithecus* genus (~ 11mya).

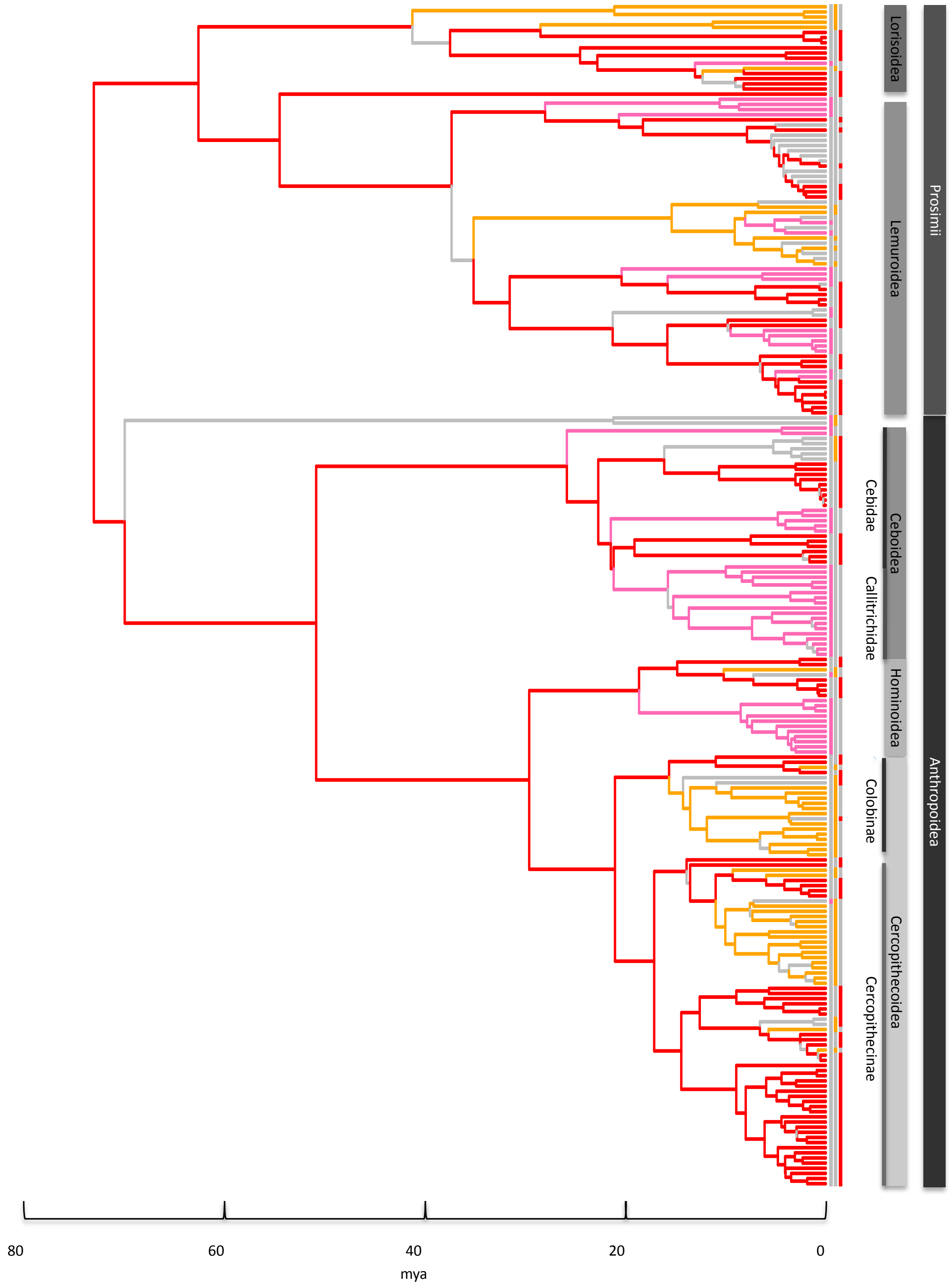
Lorisoidea
Lemuroidea
Prosimii
Cebidae
Ceboidea
Callitrichidae
Hominoidea
Colobinae
Cercopithecoidea
Cercopithecinae
Anthropoidea
80
60
40
20
0
mya

Figure 3.9 Primate phylogeny with ancestral states for mating systems derived from RJ model of evolution. The tree topology is the maximum clade credibility tree derived from the full 10k Trees Project (Arnold, Matthews, and Nunn 2010) posterior distribution with branch length drawn proportional to time. Branches and tips are coloured for polygynandry (red), harem polygyny (orange) and monogamy (pink) where the combined probability of the state and the branch is greater than or equal to 0.7. Where the combined probability is less than 0.7 the branch is grey.

3.6 Discussion

Socioecologists propose that primate social systems respond flexibly to ecological factors (Sterck, Watts, and van Schaik 1997). This is supported by studies that suggest that animal behavioural traits can be very labile (Gittleman *et al.* 1996, Blomberg, Garland, and Ives 2003). However, the results reported here show that phylogeny plays a critical role in the distribution of social organisation, dispersal and mating systems among extant primates. Far from being labile, these traits exhibit very strong phylogenetic inertia in primates. The implication of these results is that changes between social systems are constrained in primates by their phylogenetic history and may not have been able to respond to short-term ecological changes. It is not just the cercopithecines that show this phylogenetic inertia in social systems, as had been previously suggested (Di Fiore and Rendall 1994), the current study shows that this inertia occurs across all primate species (Figure 3.4).

The full model allows transition rates between trait states to vary without constraint. For social organisation this represents flexibility between social states through evolutionary time. If primate social organisation responded to changes in ecology it would be expected that this full model would have a high likelihood compared to a more constrained model. In fact the RJ-derived model, which was highly constrained (eight rates set to zero and four equal non-zero rates), was a decisively better fit to the data than the full model. This suggests that flexibility between social states is not a feature of primate evolutionary history. Rather than primate sociality responding flexibly to ecological pressures, it may be that sociality is constrained by phylogeny and primates can only survive in habitats that support their social system.

A model of evolution of social organisation implicit to socioecology is that of increasing complexity through time (Dunbar 2000, Nunn 2000). According to this view, social organisation evolved from solitary individuals at the root of the primate tree, via small groups into large complex group structures. The results presented here question this view. The complexity model was decisively worse at explaining the data than the RJ-derived model. The RJ-derived model suggests an unpredicted model of social evolution. Instead of a steady progression from small and simple to large complex structures, the social organisation of primates moved directly from solitary individuals to multi-male, multi-female groups. Only once that switch had taken place were there further moves into harems or pair living. The solitary root for primates confirms previous research (Müller and Thalmann 2000), however, the results presented in this chapter indicate for the first time that the initial transition to group living was only to multi-male/multi-female groups. This initial transition to group living has now been shown to be a response to the switch to diurnal living among primates (Shultz, Opie, and Atkinson 2011). Once sociality was established, there were no transitions back to solitary living, suggesting that the pressures for group living remain. Pair living evolved directly from multi-male multi-female groups, but not until late in primate evolution. The best fitting model shows no further transitions out of pair living once it was established, suggesting that the factors driving pair living have persisted. Harems also evolved directly from multi-male multi-female groups relatively late in primate evolution (from 16 mya), but from this social organisation, there were then transitions back to multi-male multi-female groups as well. Since there were no direct transitions from pair living, harems might be characterised as degraded multi-male groups rather than combinations of pairs (Harcourt and Greenberg 2001). Indeed, transitions between uni-male and multi-male groups provided the main flexibility between social states across primate evolution.

As well as social organisation, primate dispersal patterns also show very high phylogenetic inertia, suggesting that they were constrained over evolutionary time. Further support for this suggestion is provided by the low likelihood of the full model compared to the RJ-derived model for dispersal. A model where transition rates are allowed to vary freely is decisively poorer at explaining the data than the constrained model. The common assumption among primatologists is that male dispersal is the ancestral pattern among primates (Wrangham 1987a). This view is not supported here; instead bi-sexual dispersal is the state at the primate root and the most common state throughout the tree. Sex-biased dispersal only appeared late in primate evolution. But the transition to this dispersal pattern (male dispersal first) is by no means universal. It has also been suggested that male dispersal, common among mammals (Greenwood 1980), is the default pattern among primates (Pusey and Packer 1987, Sussman 1992, Alberts and Altmann 1995). In other words, any changes in dispersal pattern will go via male dispersal first. This suggestion was tested against the RJ-derived model and was decisively poorer at explaining the data. Instead of male dispersal as the default pattern over primate evolution, the RJ-derived model suggests a bi-sexual dispersal default. This RJ-derived model indicates that there are no direct transitions between male dispersal and female dispersal, with any changes from these states going via bi-sexual dispersal. This result supports those primatologists (Di Fiore and Rendall 1994, Strier 1994) who have long argued that it may be misleading to see the male-dispersing cercopithecines as typical primates, in terms of their social systems at least.

This bi-sexual default dispersal pattern may be the reason why there was no significant correlated evolution between social organisation and dispersal across the primate tree. The analysis here suggests that there was no co-evolution or indeed causal effect between the two traits, which is contrary to a common assumption in primate socioecology (Wrangham 1980). This result may also have wider implications; Nowak and colleagues (2010) argue that a switch to female philopatry (male dispersal) is the first crucial step to social living that can subsequently lead to eusociality in insects and co-operative living in other animals. These results suggest that, in primates at least, this was not the case. Instead, the transition from solitary to group living in primates took place with either bi-sexual or sex-biased dispersal. If there was any correlation between dispersal patterns and social organisation in primates it was that sex-biased rather than bi-sexual dispersal might be associated with a loss of sociality. However, the analysis of social organisation showed that once sociality was established in primates, it was not lost.

Like social organisation, mating systems in primates show a strong phylogenetic signal, indicating that history plays a significant role in the distribution of this trait across extant species. The model of evolution for primate mating systems is similar to that for primate social organisation, once multi-male/multi-female groups were established, with transitions to both pairs and uni-male groups. The difference with mating systems is that there was a transition from harem polygyny to monogamy; monogamy evolved from both harem polygyny and polygynandry. However, as with social organisation, once monogamy was established there were no further transitions. This may be due to the factors driving pair living that persisted or because there were changes facilitated by pair living that increased the reproductive success flowing from this social organisation (see Chapter 4). There were no direct transitions into harem polygyny from monogamy. Instead, harem polygyny evolved directly from polygynandry, and there were back transitions. An interesting question for future work is the extent to which moves between harem polygyny and polygynandry is due to ecological and physiological conditions, such as small female groups and asynchronous oestrus, enabling a single male to monopolise mating within a group of females (Dunbar 1988, Dunbar

2000). Co-evolutionary models could be used to test the factors leading to the emergence of harem polygyny.

The derived states of mating system and social organisation evolved at a similar time across diurnal primate clades such that they matched through most of primate evolutionary history, once the switch from nocturnal living had taken place. This suggests that mating systems and social organisation in diurnal primates may be influenced by the same factors. However, among those primates that remained nocturnal, solitary social organisation persisted even when mating systems changed from the ancestral state of polygynandry to the derived states of harem polygyny or monogamy.

The results presented here have wide implications for primatology. Social organisation, dispersal and mating systems display strong phylogenetic inertia in primates. This means not only that phylogenetic relationships cannot be ignored, but also that hypotheses about the evolution of social traits can be tested explicitly and accepted or rejected based on the distribution of those traits in extant taxa and their phylogenetic relationships. By using animal phylogenies and Bayesian phylogenetic methods, it is now possible to study social behaviour over evolutionary time and to test co-evolutionary hypotheses. Understanding social behaviour fully is particularly important in primatology, as primates are among the most social of animal species, and the study of their sociality is the bedrock of primatology.

Chapter 4 Evolution of Primate Monogamy

4.1 Abstract

While common in birds, social monogamy, or pair living, is rare among mammals due to internal gestation and lactation, which enables a male to leave a female after mating to seek additional mating opportunities elsewhere. However, among primates, monogamy has evolved independently in all the major clades. A number of hypotheses have been proposed for the evolution of this mating system among primates: defence against infanticide by males, the benefits of paternal care, or that through the action of females, a male is forced to guard a single female. In this chapter a Bayesian framework is used to test these hypotheses with trait data across 214 primate species. The results show that infanticide always preceded the emergence of monogamy; there was no other route into pairs across primate species. Paternal care evolved following the emergence of monogamy, not before. The prevalence of monogamy in primates compared to other mammals can therefore be explained by long lactation periods due to infant altriciality, which made them vulnerable to infanticidal males. Monogamy was a successful anti-infanticide strategy and once it had evolved it was not lost in any species.

4.2 Introduction

The prevalence of social monogamy, or pair living, among birds (90% of species) (Lack 1968) compared to mammals (less than 3% of species) (Kleiman 1977) is explained by parental investment theory, which suggests that an animal will live in a pair only when the investment required from a male for the successful rearing of offspring is more than half that of the female and so cannot be shared with another female (Bateman 1948, Trivers 1972). In many bird species, the successful rearing of offspring requires the undivided involvement of both pair members in egg incubation and the feeding of chicks, which constrains the adults to stay in a pair (Gordon 1969). In mammals, by contrast, internal gestation and lactation in females frees a male to search for other mating opportunities rather than staying with a female after mating. It is surprising therefore that among primates monogamy is more prevalent than in other mammalian orders, making up about 15% of species across all the major clades (Dunbar 1988). Five hypotheses have been proposed to explain this prevalence.

4.2.1 Paternal Care

Primates have unusually large brains relative to their body size (Byrne and Whiten 1988) and give birth to altricial young who are in need of high levels of parental care (Ross and MacLarnon 2000). The paternal care hypothesis suggests that monogamy arises where the cost of raising offspring is high, such that the female must rely on the help of others, particularly for carrying infants (Clutton-Brock and Harvey 1977, Kleiman 1977). The pair living new world primates (Callitrichids and *Aotus*) exemplify this situation; marmoset and tamarin females can increase their reproductive output by giving birth to twins, but only if males help with infant carrying and care (Kleiman 1977).

4.2.2 Dispersed Female Range

In primate species where males do not provide infant care, males might be constrained from following a ‘roving mating’ strategy due to the wide dispersal of females (Emlen and Oring 1977, Wittenberger and Tilson 1980, van Schaik and van Hooff 1983). Where predation risk is low, and food resources occur in small clumps, females spread out in the environment such that males cannot defend the territory of more than one female. Males may then resort to mate guarding since ensuring mating with one female may provide higher reproductive success than an alternative roving strategy (Kleiman 1977, van Schaik and van Hooff 1983).

4.2.3 Discrete Female Range

A refinement of the dispersed female range hypothesis has been suggested; proposing that rather than widely dispersed female ranges, it is the small but discrete ranges of solitary females that cause males to abandon a roving mating strategy and stick with a single female in a pair (Komers and Brotherton 1997). The discrete female range hypothesis proposes that monogamy is a risk-averse strategy where mate guarding provides the male with at least some mating success (Brotherton and Manser 1997, Brotherton and Komers 2003). Evidence for this hypothesis was found in a phylogenetic comparative analysis covering a number of mammalian orders, including primates (Komers and Brotherton 1997).

4.2.4 Concealed Ovulation Hypothesis

A fourth hypothesis for the evolution of pairs is based on the extended sexual receptivity of females and the loss of oestrous signal in a number of monogamous primates (Alexander 1979, Turke 1984). It is suggested that these physiological changes in females co-evolved progressively with monogamy, forcing males into extended consortships with females, as the only means of gathering information about a female's reproductive status. These consortships, it is argued, led to an increase in paternity certainty, in turn, ensuring the paternal care required for the altricial offspring of the pair. However, an alternative explanation for concealed ovulation proposed that, instead of increasing paternity certainty, oestrous signal loss resulted in paternity confusion as a way of protecting infants from infanticidal males and inducing tolerance from the males that had mated with the infant's mother (Hrdy 1981). Phylogenetic analysis of primate mating systems and oestrous signals, using parsimony methods, showed that oestrous signals were lost in polygyny, possibly for paternity confusion purposes, but before the emergence of monogamy and may therefore have influenced its evolution (Sillen-Tullberg and Møller 1993).

4.2.5 Infanticide Hypothesis

The fifth hypothesis proposes that monogamy in primates evolved as an anti-infanticide strategy, where females sought protection for their un-weaned offspring from a male, who may also be the father of the infant (van Schaik and Dunbar 1990, Dunbar 1995a, van Schaik and Kappeler 1997, Palombit 1999). Long inter-birth intervals in primates, due to long maturation lengths, make un-weaned primate infants particularly vulnerable to infanticide by males. The lack of observed infanticide in extant species has led some researchers to focus on a measure of infanticide risk, rather than infanticide rate (van Schaik 2000a, van Schaik and Janson 2000, van Schaik and Kappeler 2003). Among non-seasonal breeders, un-weaned infants are at risk from infanticide by males when the length of lactation is greater than gestation, since a male can expect to bring a lactating female back into oestrus sooner by killing her infant and then hope to mate with her (van Schaik 2000b). Monogamy may reduce infanticide risk either by shortening weaning time because of paternal care (Dunbar 1995a, Dunbar 1995b), or through the protection of a mother and her infant by a male (van Schaik and Dunbar 1990).

Despite considerable research effort over some decades, each of the hypotheses discussed has its adherents, and there is as yet no clear consensus on how monogamy evolved in primates and why it might be more prevalent among primates than other mammals. Some researchers have proposed that a combination of explanations may be plausible (Palombit 1999), while others doubt whether it is possible to test between these hypotheses effectively because it is only possible to test the current function of monogamy and not its historical origin, it is suggested (van Schaik and Kappeler 2003).

However, the use of new quantitative phylogenetic comparative methods (Felsenstein 1985, Harvey and Pagel 1991) within a Bayesian framework

(Huelsenbeck *et al.* 2001) now enable a re-evaluation of these hypotheses and can provide suggestions for the ultimate cause(s) of monogamy in primates. By using data for traits across extant primate species and the phylogenetic relationships between those species, it is possible to infer models of trait evolution and generate posterior probability distributions of the state of traits at ancestral nodes (Pagel, Meade, and Barker 2004, Pagel and Meade 2006). Here, these methods are used to detect co-evolution between pairs of traits over evolutionary history, and estimate the relative timing for the emergence of those traits to identify drivers of change.

4.3 Predictions

In order to establish which factors are associated with the evolution of monogamy in primates and whether any of the five hypotheses outlined above are supported, co-evolution between the trait in question and primate mating systems needs to be established. If, as well, the trait evolved with or before monogamy then it is likely to be the driver for the evolution of monogamy in primates. However, if the trait evolved after the emergence of pairs it could be seen as the result of monogamy and therefore involved in maintaining this mating system rather than its evolution. Predictions were generated from each hypothesis to evaluate the hypotheses for the evolution of monogamy in primates and are given in Table 4.1. These predictions were tested using Bayesian phylogenetic methods that establish both co-evolution between traits and the relative timing of the evolution of each trait (Pagel 1994a, Pagel 1997, Pagel and Meade 2006).

Table 4.1. Predictions for co-evolution between traits derived from the five hypotheses. 1. Correlated evolution between traits, 2. relative timing for the evolution of traits.

Hypothesis		**Predictions**
Paternal Care		1. Co-evolution between paternal care & mating system
		2. Paternal care coincides with or precedes monogamy
Female range size		1. Co-evolution between female range size & mating system
		2. Larger female ranges in monogamy
Discrete female ranges		1. Co-evolution between discrete female ranges & mating system
		2. Discrete female ranges precede monogamy
Oestrous signal		1. Co-evolution between oestrous signal & mating system
		2. Concealed ovulation precedes monogamy
Infanticide	*Reported*	1. Co-evolution between reported infanticide & mating system
		2. Infanticide precedes monogamy
	Risk	1. Co-evolution between infanticide risk & mating system
		2. Infanticide risk high before monogamy

4.4 Methods

4.4.1 Primate Phylogeny

A tree block of 10,000 phylogenies from version 2 of the *10k Tree Project* (Arnold, Matthews, and Nunn 2010) was downloaded and used as detailed in Chapter 2.

4.4.2 Primate Data

Data on primate traits were extracted from the literature (Smuts *et al.* 1987, Dunbar 1988, Dixson 1998, Campbell *et al.* 2007) (Table 4.2).

Table 4.2. Coding for binary traits and number by coding.

Binary trait	**Coding**				
	State (0)	N	State (1)	N	Polymorphic (01)
Mating system	Polygyny	154	Monogamy	53	7
Paternal care - narrow	No care	199	Care	31	-
Paternal care - wide	No care	182	Care	45	-
Discrete female ranges	Discrete ranges	50	Overlapping ranges	29	-
Female sociality	Solitary	87	Social	123	9
Oestrous signal	Not concealed	85	Concealed	72	-
Infanticide	No infanticide	169	Infanticide	45	-

4.4.2.1 Paternal Care

Levels of paternal care vary widely across primate species. Ross and MacLarnon (2000) used a four point scale from 1 (0 – 5% of infant time) to 4 (> 55% of infant time) for allocare, by all carers, in anthropoid primates, including feeding, carrying, playing and grooming. They suggest that category 2 (5-30% of infant time) and above represents significant allocare. This scheme has been adopted here as a narrow definition of paternal care, where males provide care for at least 5% of infant time. Original sources were checked and the Ross and MacLarnon (2000) data were used except for *Cercocebus albigena*, which was removed from the narrow definition since the primary source (Chalmers 1968) suggested variation between males and no consistent pattern of male care of 5% or more of infant time. The Ross and MacLarnon (2000) scheme was extended to cover prosimians using the available descriptions of the paternal care from the literature.

For comparison purposes a wider definition of paternal care was also used, including all instances of paternal care observed in the wild, more than mere toleration of infants by adult males (Smuts *et al.* 1987, Ross and MacLarnon 2000).

4.4.2.2 Infanticide

4.4.2.2.1 Reported Infanticide

Observations of infanticide are relatively rare in both wild and captive primates. Data for wild populations only have been used, and when the infanticide was substantiated either by direct observation or the exclusion of other possibilities.

4.4.2.2.2 Infanticide Risk

Data were collected from the literature for gestation length (G) and lactation length (L). The weaning ratio was calculated as L/G (van Schaik 2000b) where values above one suggest infanticide risk, since it would then pay a male to kill an unweaned infant in order to bring a female back into oestrus sooner. In species where females reproduce seasonally, and there is a ‘time-out’ period between the end of lactation and the subsequent conception, a weaning ratio above one would falsely suggest infanticide risk, so these data were excluded. However, those species in which females have multiple breeding events in a year, and do not have clear ‘time-out’ periods, or take more than a year to wean their infants were included (van Schaik 2000b). An alternative ‘weaning proportion’ (L/(L+G)) was also used, with a value over 50% indicating infanticide risk.

4.4.3 Analyses

The analyses carried out in this chapter are described in full in Chapter 2.

4.4.3.1 Phylogenetic Signal

The signal was tested in all data sets by calculating Pagel’s Lambda (λ) (Pagel 1994a, Pagel 1999a) using the *Ape* (Paradis, Claude, and Strimmer 2004) and *Geiger* (Harmon *et al.* 2008) packages in *R (R Development Core Team 2008)*. A λ value of one for the data shows that the probability of shared inheritance of a trait between species is proportional to their relatedness, while a λ value of zero suggests evolution independent of the phylogenetic tree (Freckleton, Harvey, and Pagel 2002).

4.4.3.2 Ancestral State & Model Estimation

An RJ MCMC analysis in *BayesTraits* was used to provide a posterior probability distribution of trait states at the root of the phylogenetic tree (Pagel, Meade, and Barker 2004). This method also provides a posterior probability sample of models of evolution as well as the rate parameters of the models (Pagel and Meade 2006, Currie *et al.* 2010). Models visited by the Markov Chain were ranked in order of their posterior probability and the highest ranked model (the RJ-derived model) was used in later analyses (Pagel, Meade, and Barker 2004).

4.4.3.3 Co-evolution

For binary traits, *Discrete* (Pagel and Meade 2006) was used to test hypotheses about correlated evolution between traits. A Bayes Factor (BF) (Kass and Raftery 1995) comparison shows whether there is support for co-evolution between traits. Comparing the transition rates between states indicates the relative timing of the evolution of traits. This allows for an evaluation of directionality such that the order of evolution can be inferred; by showing which trait evolved first it is possible to test the hypotheses explicitly. Where the comparison between transition rates does not give clear results an alternative method was used. The RJ was switched off, and two models were run, each with one of the transition rates in question set to zero. A BF comparison is made between each of these models and both the full model and the RJ-derived model (the highest ranking model in the posterior probability distribution from the RJ analysis). The zero-transition rate model that performs worse indicates that the rate that was set to zero is more important than the other transition rate in the functioning of the model, since setting it to zero disrupts the model to a greater extent.

4.4.3.4 PGLM

For the analysis of continuous variables, phylogenetic generalised linear model (pglm) analyses were run using the *CAIC* package (Purvis and Rambaut 1995) in *R* (R Development Core R Development Core Team 2008), which takes phylogeny into account.

4.5 Results

4.5.1 Phylogenetic Signal

All the traits tested, except for female range size, have high λ values, significantly different from zero, suggesting a strong phylogenetic signal (Table 4.3). Indeed four of the traits, mating system, oestrous signal, discrete female range, and the narrow definition of paternal care, have λ values that are not significantly different from one. This indicates that for all the traits, except for female range size, phylogeny has a significant effect on their current distribution among extant taxa. Inferences can therefore be made about the evolutionary history of these traits within primates.

Table 4.3. Phylogenetic signal, Pagel's λ, in the trait data sets. N, number of species; λ_{max} lambda value from maximum likelihood analysis; LL_{max} log likelihood of λ_{max}; LL_0 log likelihood of λ_0; LL_1 log likelihood of λ_1; LLR_0 probability of log likelihood ratio of LL_0 and LL_{max} (bold sign. diff. from zero); LLR_1 probability of log likelihood ratio of LL_1 and LL_{max} (bold not sign. diff. from 1).

Trait Data	**N**	**LLmax**	**λ_{max}**	**LL_0**	**LL_1**	**LLR_0**	**LLR_1**
Mating system	214	-108.61	0.99	-224.95	-108.70	**<0.001**	**0.679**
Paternal care – wide	224	-74.74	0.89	-113.73	-79.68	**<0.001**	0.002
Paternal care – narrow	224	-38.60	0.98	-91.19	-39.34	**<0.001**	**0.227**
Female range size	44	-255.84	0.00	-255.84	-2805.76	1.000	<0.001
Discrete female ranges	107	-30.13	1.00	-52.63	-30.13	**<0.001**	**1.000**
Oestrous signal	157	-92.07	0.97	-168.30	-92.77	**<0.001**	**0.237**
Infanticide	228	-107.71	0.81	-113.95	-118.77	**<0.001**	<0.001

Weaning Proportion	84	78.24	0.95	36.97	16.96	**<0.001**	<0.001

4.5.2 Mating system

The highest-ranked model in the posterior probability distribution of the reversible jump (RJ) mating system analysis in Chapter 3 (the RJ-derived model) shows that monogamy evolved either directly from a polygynandrous system or via a harem-polygynous system, but once monogamy was established there were no transitions to other mating states. Focussing here on the evolution of monogamy, a *Multistate* analysis of mating system as a binary trait shows that primate mating systems have evolved from a polygynous root (mean probability 0.974 +/- 0.001) to monogamy (mean probability 0.026 +/- 0.001) (Figure 4.1 and Table 4.4).

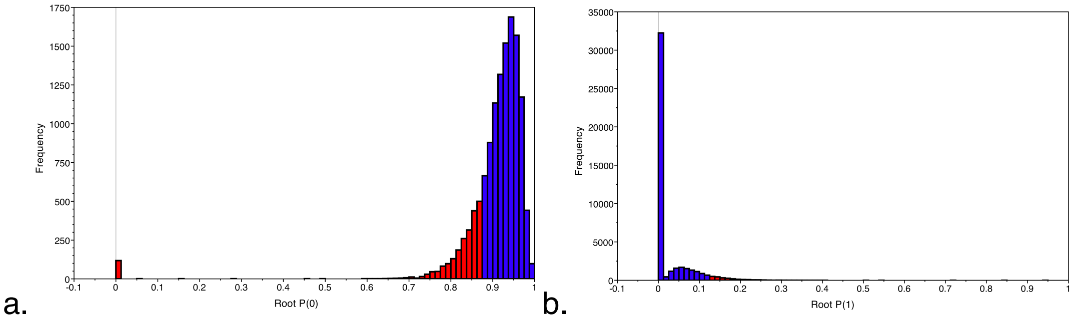

Figure 4.1. Posterior probability distribution for ancestral state from the RJ analysis of mating system as a binary trait. a. polygyny at the root, and b. monogamy at the root.

The RJ-derived model showed a positive transition from polygyny to monogamy, but a zero rate from monogamy to polygyny. Across the whole posterior probability distribution transitions from polygyny to monogamy were assigned to zero 0.2% of the time, while the reverse transitions were assigned to zero 71.4% of the time (Figure 4.2). The evolution of monogamy can be characterised as a move from the ancestral state of polygyny to the derived state of monogamy. It is possible therefore to investigate co-evolution between primate mating systems and other primate traits.

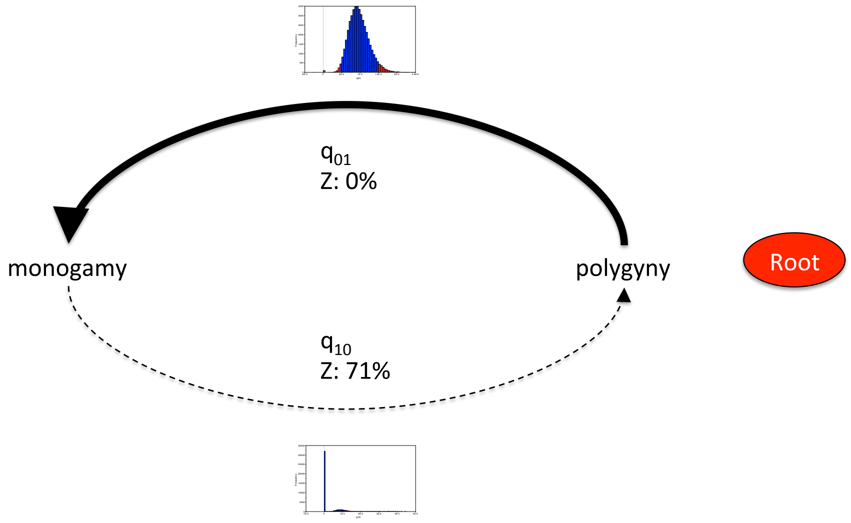

Figure 4.2. Highest-ranked model from the RJ analysis of evolution of mating systems. Z denotes visits assigned to zero as a proportion of posterior probability distribution. Thickness of arrows reflects proportion of time transition rate is not assigned to zero. Number below rate name (q_{ij}) is the mean transition rate where rate distribution has zero or very low Z. Dashed line denotes a zero rate in the RJ-derived model.

Table 4.4. Ancestral states probabilities for traits in *Multistate* and *Discrete* analyses. *(Mating system denoted first, co-evolutionary trait second).

Trait	**Probability of root in Multistate analysis**		**Probability of root in analysis of co-evolution with mating system (Polygyny (0), Monogamy (1))***			
	State (0)	State (1)	State (0,0)	State (0,1)	State (1,0)	State (1,1)
Mating system	Polygyny	Monogamy	-	-	-	-
	0.97	0.03				
Paternal care - narrow	No care	Care	0.47	0.33	0.12	0.09
	0.97	0.03				
Discrete female ranges	Discrete	Overlap	0.60	0.13	0.12	0.15
	0.64	0.36				
Female sociality	Not social	Social	0.90	0.02	0.06	0.02
	0.95	0.05				
Oestrous signal	Not concealed	Concealed	0.28	0.27	0.33	0.12
	0.40	0.60				
Infanticide	No infanticide	Infanticide	0.49	0.39	0.00	0.12
	0.50	0.50				

4.5.3 Co-evolution

4.5.3.1 Paternal Care

There is decisive support for co-evolution between paternal care and mating system (Table 4.5). The definition of paternal care makes little difference to model performance, as the highest-ranking model from the RJ analysis is the same for both definitions (Table 4.6 and Table 4.7). Indeed the top five models are the same for both definitions of paternal care, albeit in a different order, accounting for 57% of the posterior distribution for the narrow definition and 75% for the wide definition.

Table 4.5. Comparison between dependent and independent models of evolution for mating system and other traits. *(Analysis between oestrous signal and infanticide, not mating system)

Co-evolution Analysis	**Dependent model**		**Independent model**		**Log10 Bayes Factor**
	Log likelihood	S.E.	Log likelihood	S.E.	
Paternal care - narrow	- 93.82	+/- 0.05	- 101.90	+/- 0.02	3.51
Paternal care - wide	- 128.74	+/- 0.04	- 138.02	+/- 0.03	4.03
Discrete female ranges	- 56.00	+/- 0.03	- 60.94	+/- 0.02	2.14
Female sociality	- 91.42	+/- 0.04	- 103.85	+/- 0.02	5.40
Oestrous signal	- 126.20	+/- 0.03	- 129.29	+/- 0.01	1.34
Infanticide	- 154.66	+/- 0.03	- 167.17	+/- 0.02	5.43
*Oestrous signal & infanticide**	-168.87	+/- 0.04	-171.31	+/- 0.03	1.06

Table 4.6. Top ten and fiftieth model from the RJ analysis of mating system and paternal care (narrow definition) with their posterior probabilities. (Note: following the convention established by Pagel and Meade (2006), Z indicates transition rates between states in the model assigned to zero, whereas 0 and 1 indicate non-zero transition rates between states. Subscripts on the transition rates refer to the four possible states of the two binary traits. Frequency = visits to the model in the posterior sample of 50,000 observations. Approximately 60 visits are expected by chance).

Models	**Transition Rates**								**Frequency**	**Probability (%)**	**Cumulative Probability (%)**
	q_{12}	q_{13}	q_{21}	q_{24}	q_{31}	q_{34}	q_{42}	q_{43}			
1	1	1	0	1	1	1	1	Z	15942	31.9	31.9
2	1	1	0	1	1	1	1	1	4999	10.0	41.9
3	1	1	0	1	Z	1	1	1	2831	5.7	47.5
4	1	1	0	Z	1	1	1	1	2546	5.1	52.6
5	1	1	0	1	1	1	Z	Z	2083	4.2	56.8
6	0	0	1	0	0	0	0	Z	1758	3.5	60.3
7	0	0	1	1	Z	0	Z	Z	1692	3.4	63.7
8	1	1	0	Z	Z	1	1	1	1581	3.2	66.9
9	1	1	0	0	Z	1	Z	Z	1067	2.1	69
10	1	1	0	0	1	1	Z	Z	1033	2.1	71.1
50	Z	0	1	Z	0	0	0	0	30	0.1	94.2

Table 4.7. Top ten and fiftieth model from the RJ analysis of mating system and paternal care (wide definition) with their posterior probabilities. (Note: following the convention established by Pagel and Meade (2006), Z indicates transition rates between states in the model assigned to zero, whereas 0 and 1 indicate non-zero transition rates between states. Subscripts on the transition rates refer to the four possible states of the two binary traits. Frequency = visits to the model in the posterior sample of 50,000 observations. Approximately 100 visits are expected by chance).

Models	**Transition Rates**								**Frequency**	**Probability (%)**	**Cumulative Probability (%)**
	q_{12}	q_{13}	q_{21}	q_{24}	q_{31}	q_{34}	q_{42}	q_{43}			
1	1	1	0	1	1	1	1	Z	21305	42.6	42.6
2	1	1	0	1	1	1	Z	Z	6845	13.7	56.3
3	1	1	0	1	1	1	1	1	4151	8.3	64.6
4	1	1	0	Z	1	1	1	1	2974	5.9	70.5
5	1	1	0	1	Z	1	1	1	2049	4.1	74.6
6	1	1	0	Z	1	1	Z	Z	1984	4.0	78.6
7	1	1	0	Z	Z	1	1	1	1353	2.7	81.3
8	1	1	0	1	1	1	Z	1	960	1.9	83.2
9	0	0	0	0	0	0	Z	Z	916	1.8	85.1
10	0	0	1	0	0	0	0	Z	749	1.5	86.6
50	1	2	0	Z	1	2	2	Z	22	0	96.7

The RJ-derived model shows that the transition from polygyny to pair, with a background of paternal care (q_{24}), is in the same rate class as the equivalent transition without paternal care (q_{13}), so that both routes to monogamy were possible (Figure 4.3). This suggests that paternal care is not necessary for the evolution of monogamy in primates by either definition of paternal care.

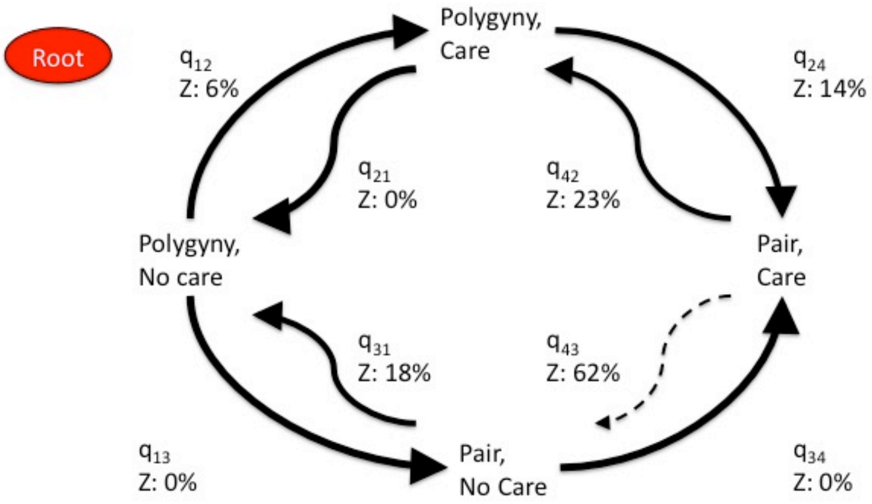

Figure 4.3. Co-evolution between mating system and paternal care (narrow definition). Z denotes visits assigned to zero as a proportion of posterior probability distribution. Thickness of arrows reflects proportion of time transition rate is not assigned to zero. Dashed line denotes a zero rate in the RJ-derived model.

Furthermore, it is possible to differentiate between transition rates by comparing the posterior probability of rates assigned to zero (Pagel and Meade 2006). Across the whole of the posterior probability distribution the transition from the ancestral state of polygyny without paternal care to the derived state of monogamy with paternal care is never assigned to zero via the intermediate state of monogamy without paternal care (q_{13} and q_{34}). On the other hand, the transition from no paternal care to paternal care within polygyny (q_{12}) was assigned to zero 6% of the time for the narrow definition of paternal care and 0% for the wide definition, and the transition from polygyny to monogamy with paternal care (q_{24}) was assigned to zero 14% of the time for the narrow definition, and 16% for the wide definition (Table 4.8 and Figure 4.3). The route from the ancestral to derived state via monogamy without paternal care (1,0) is at least as fast as the alternative route again suggesting that paternal care was not necessary for the evolution of monogamy in primates (Figure 4.4).

Table 4.8. The posterior probability of transition rate being zero for co-evolutionary analyses between mating system and other traits. *(Analysis between oestrous signal and infanticide, not mating system). Transition rates are referred to as q_{ij}, where i and j refer to the beginning and end trait states of the transition respectively (1 is the ancestral state, 4 is the derived state and 2 and 3 are the intermediate states) in the co-evolution figures.

Co-evolutionary analyses (with mating system)	**Posterior probability of a zero rate (%)**							
	q_{12}	q_{13}	q_{21}	q_{24}	q_{31}	q_{34}	q_{42}	q_{43}
Paternal care – wide	0.0	0.0	0.0	16.3	10.1	0.1	30.1	73.9
Paternal care - narrow	6.4	0.0	0.0	13.9	18.4	0.0	23.1	62.2
Discrete female ranges	26.0	0.1	52.6	36.5	79.0	4.5	3.9	2.7
Female sociality	2.1	0.1	95.4	0.2	78.1	68.0	24.0	0.0
Oestrous signal	4.6	13.4	0.0	0.5	11.3	47.1	51.0	0.9
Infanticide	0.0	100.0	0.0	0.0	100.0	100.0	4.3	0.0
*Oestrous signal & infanticide**	0.3	87.2	0.0	5.7	7.7	0.0	7.3	1.8

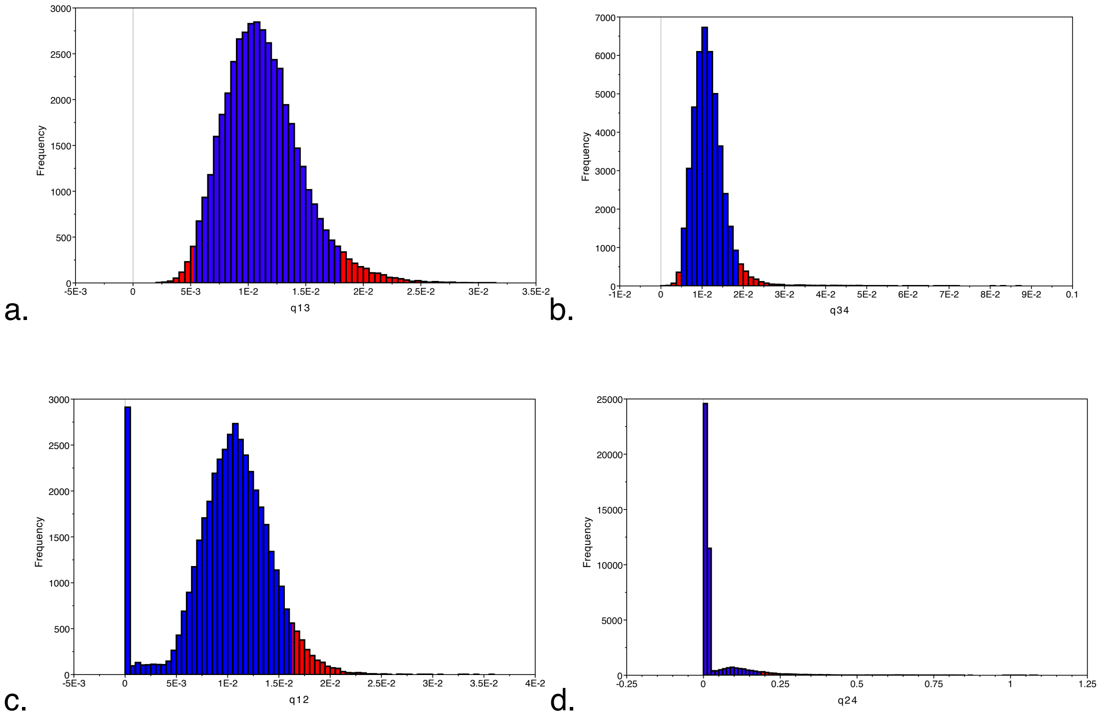

Figure 4.4. Posterior probability distribution for transition rate from a. polygyny to monogamy without paternal care (q_{13}), b. no paternal care to paternal care within monogamy (q_{34}), c. no paternal care to paternal care within polygyny (q_{12}), and d. polygyny to monogamy with paternal care (q_{24}).

To differentiate further between the routes from the ancestral to derived states, separate analyses were run restricting either the transition rate from polygyny to pair without care (q_{13}) or from polygyny to pair with care (q_{24}) to zero (leaving all other rates to vary), for the narrow definition. Restricting q_{24} (polygyny to pair with care) to zero gave a substantially higher likelihood than the full model, where all rates are allowed to vary freely, but a decisively lower likelihood than the RJ-derived model (Table 4.9). However, restricting q_{13} (polygyny to pair without care) to zero gave a decisively lower likelihood than the full model and the RJ-derived model. This suggests that the transition from polygyny to pair without care (q_{13}) is the more important rate since restricting it to zero disrupts the model to a greater extent. Although, it was possible for monogamy to evolve with a background of paternal care, monogamy was more likely to evolve without paternal care present.

Table 4.9. Comparison between models of the narrow definition of paternal care with transition rates restricted.

Analysis	**Log Likelihood**	**Bayes Factor of each model vs. Full Model**	**Bayes Factor of each model vs. RJ Model**
Full Model	-96.03	N/A	-2.83
RJ Model	-89.52	2.83	N/A
Rate q13 zero	-104.98	-3.89	-6.72
Rate q24 zero	-94.67	0.59	-2.24

Once paternal care had evolved within monogamy it was unlikely to be lost. The transition rate q_{43} (loss of paternal care within monogamy) was a zero rate in the RJ-derived model by both definitions and was assigned to zero for 74% of the posterior probability distribution, by the wide definition of care, and 62% for the narrow definition (Table 4.8 and Figure 4.3).

Paternal care (wide definition) was no more likely to evolve in monogamy than in polygyny; q_{12} (gain of paternal care in polygyny) was assigned to a zero rate for 0% of the posterior probability, as was q_{34} (gain of paternal care in pairs). Whereas in the narrow definition q_{12} was assigned to a zero rate 6% of the time, while q_{34} remained at 0%, suggesting extensive paternal care may have been more likely to evolve within monogamy than within polygyny, but the effect is small (Table 4.8).

However, an analysis of paternal care on its own showed an ancestral state of no paternal care with a posterior probability of 0.97, while the co-evolutionary analysis showed a probability for the ancestral state of no paternal care and polygyny as only 0.47, with the ancestral state of paternal care and polygyny having a probability of 0.33 (Table 4.4). Further analyses were run fossilising the ancestral state as polygyny with no paternal care to compare results. Figure 4.5 shows that the only significant difference was in the transition rate from monogamy to polygyny with paternal care (q_{42}), which was assigned to zero 33% of the time compared to 23% when the ancestral state was not fossilised. This suggests that for the results reported here the ancestral state in the co-evolutionary analyses was not a significant factor.

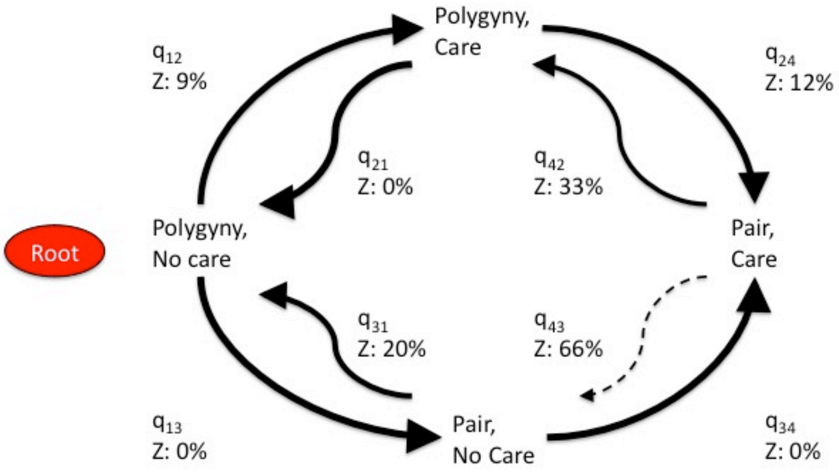

Figure 4.5. Co-evolution between mating system and paternal care (narrow definition) with ancestral state fossilised to polygyny without paternal care. Z denotes visits assigned to zero as a proportion of posterior probability distribution. Thickness of arrows reflects proportion of time transition rate is not assigned to zero. Dashed line denotes a zero rate in the RJ-derived model.

4.5.3.2 Mate Guarding

4.5.3.2.1 Female Range Size

A PGLM analysis between female range size and mating system suggests that there is no association between these two traits (Table 4.10). Since there is also no phylogenetic signal in the female range size data it is possible to conclude that female range size did not co-evolve with mating systems in primates.

Table 4.10. PGLM female range size and mating system.

Term	**Estimate**	**Std Err**	**T-value**	**P**
Intercept	42.71	30.99	1.38	0.175
Mating	-10.84	18.85	-0.58	0.568

4.5.3.2.2 Discrete Female Ranges

However, mating systems and discrete female ranges did co-evolve decisively in species with dispersed females (Table 4.5). The ancestral state was polygyny with discrete ranges (Table 4.4). The RJ-derived model suggests that the transition from polygyny to pair with range overlap (q_{24}) was a zero rate, whereas the transition from polygyny to pair with discrete ranges (q_{13}) was a non-zero rate (Figure 4.6). Indeed, across the whole posterior probability distribution the transition from polygyny to pair with range overlap (q_{24}) was zero 37% of the time, whereas the transition from polygyny to pair with discrete ranges (q_{13}) was zero 0% of the time (Figure 4.7). This suggests that the transition from polygyny to pair with discrete ranges (q_{13}) was a stronger rate than the transition from polygyny to pair with range overlap (q_{24}).

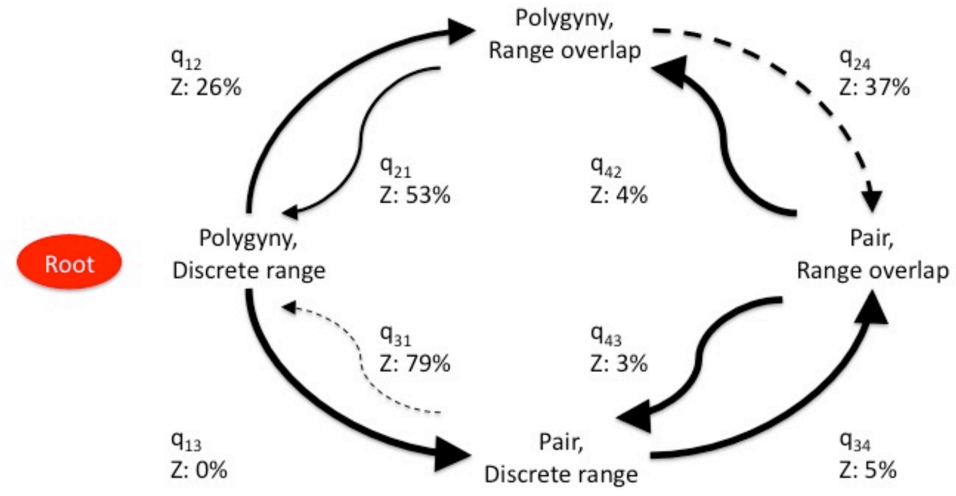

Figure 4.6. Co-evolution between mating system and discrete female ranges. Z denotes visits assigned to zero as a proportion of posterior probability distribution. Thickness of arrows reflects proportion of time transition rate is not assigned to zero. Dashed line denotes a zero rate in the RJ-derived model.

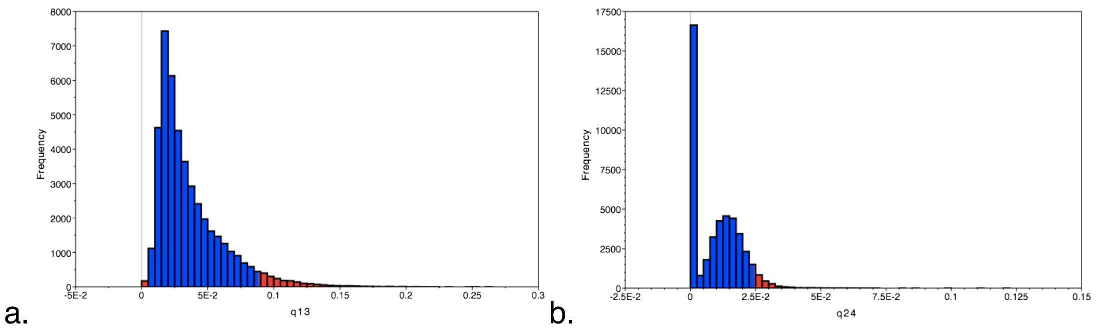

Figure 4.7. Posterior probability distribution for transition rate from polygyny to monogamy. a. with discrete ranges (q_{13}), b. with range overlap (q_{24}).

Although it was possible for monogamy to evolve where dispersed females had range overlap it was more likely to evolve in species with dispersed females that had discrete ranges. A *Multistate* analysis of discrete female ranges suggests that females had discrete ranges at the primate root (63% of the posterior probability) (Table 4.4 and Figure 4.8). However, as this is relatively low support, analyses were also carried out with the root fossilised to polygyny with discrete female ranges. These analyses showed no significant differences in model performance.

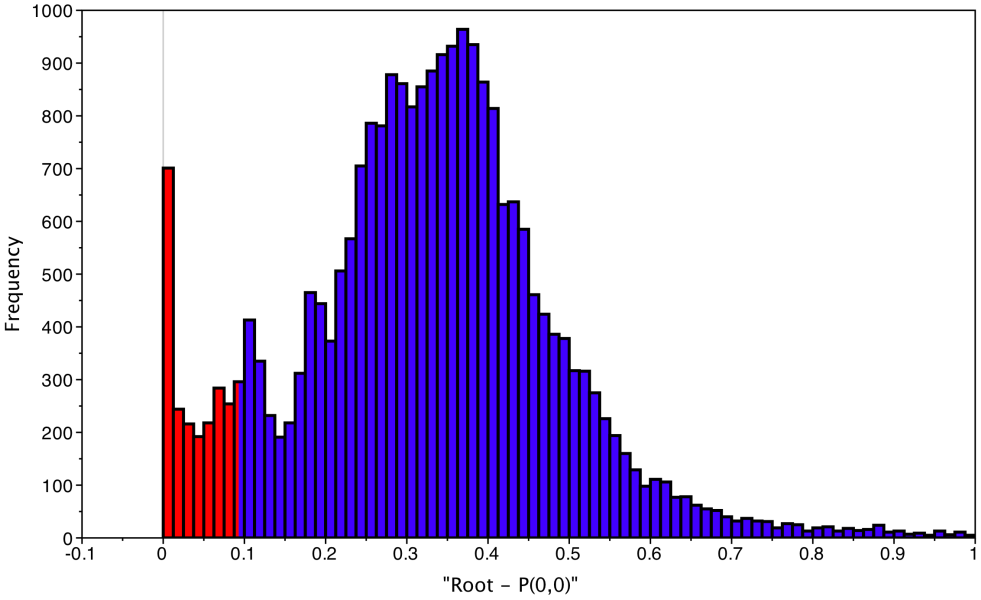

Figure 4.8. Posterior probability distribution for polygyny with discrete ranges as ancestral state.

Since monogamy evolved relatively late in primate evolution (Chapter 3), discrete ranges may not have been a sufficient condition for the emergence of monogamy.

Furthermore, an analysis of mating system and female sociality showed decisive support for co-evolution (Table 4.5). The RJ-derived model showed non-zero rates for the transition from polygyny with dispersed females, as the ancestral state, both to monogamy with dispersed females (q_{13}) and to polygyny with female sociality (q_{12}) (Figure 4.9). There were also non-zero rates from polygyny with female sociality to monogamy with female sociality (q_{24}) and from there to monogamy with dispersed females (q_{43}). In the RJ-derived model all other rates were zero. Across the whole of the posterior probability distribution the four non-zero rates in the RJ-derived model had no, or nearly no, visits assigned to zero, while rates q_{21} (gregarious to dispersed, in polygyny), q_{31} (monogamy to polygyny with dispersed females) and q_{34} (dispersed to gregarious, in monogamy) were assigned to zero more than two-thirds of time (Figure 4.9 and Table 4.8). There were therefore two routes from the ancestral state of polygyny with dispersed females to monogamy, either directly into monogamy with females remaining dispersed, or first the evolution of female sociality, followed by the evolution of pairs. The later route could well have been the one taken by anthropoids, since sociality appeared early in the evolution of this group (Chapter 3). The earlier analysis of co-evolution between mating systems and discrete female ranges showed that although discrete ranges for dispersed females might have preceded pair evolution that was not the only route for dispersed females to evolve monogamy. This analysis has shown that it was not only species with dispersed females that evolved monogamy; species with gregarious females did also.

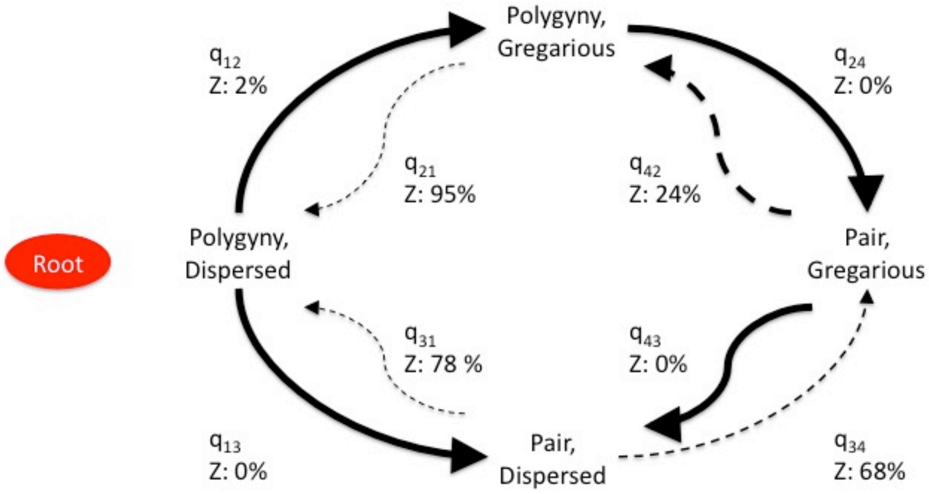

Figure 4.9. Co-evolution between mating system and female sociality. Z denotes visits assigned to zero as a proportion of posterior probability distribution. Thickness of arrows reflects proportion of time transition rate is not assigned to zero. Dashed line denotes a zero rate in the RJ-derived model.

4.5.3.2.3 Oestrous Signal

There is strong but not decisive support for co-evolution between oestrous signal and mating systems (Table 4.5). However, the root is unclear in the *Multistate* and co-evolutionary analyses, therefore only tentative conclusions can be drawn (Table 4.4). The RJ model shows two zero transition rates, the loss of oestrous signal in monogamy (q_{34}) and the loss of monogamy with concealed ovulation (q_{42}). Across the whole posterior probability distribution these rates are assigned to zero for 50% and 55% of the time respectively. It was therefore more likely for the transition from oestrous signal to concealed ovulation to take place in polygyny

(q_{12} compared to q_{34}), while changes from polygyny to monogamy took place at a higher rate with a background of concealed ovulation (q_{24} compared to q_{13}) (Figure 4.10 and Figure 4.11).

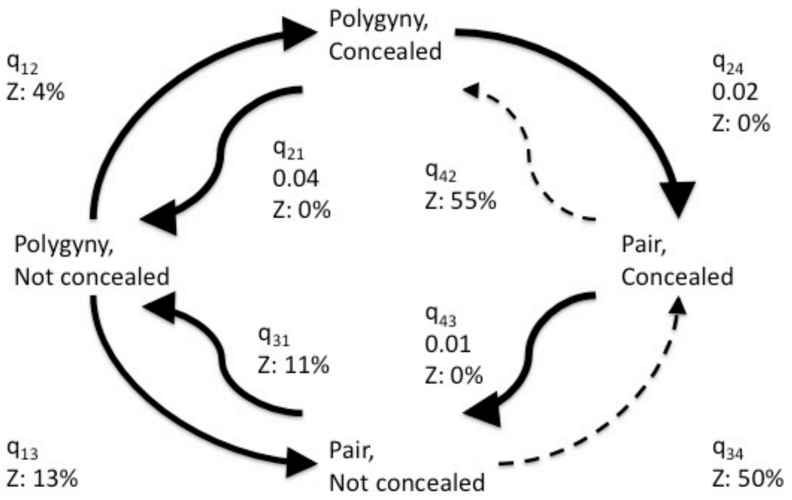

Figure 4.10. Co-evolution between mating system and oestrous signal. Z denotes visits assigned to zero as a proportion of posterior probability distribution. Thickness of arrows reflects proportion of time transition rate is not assigned to zero. Dashed line denotes a zero rate in the RJ-derived model.

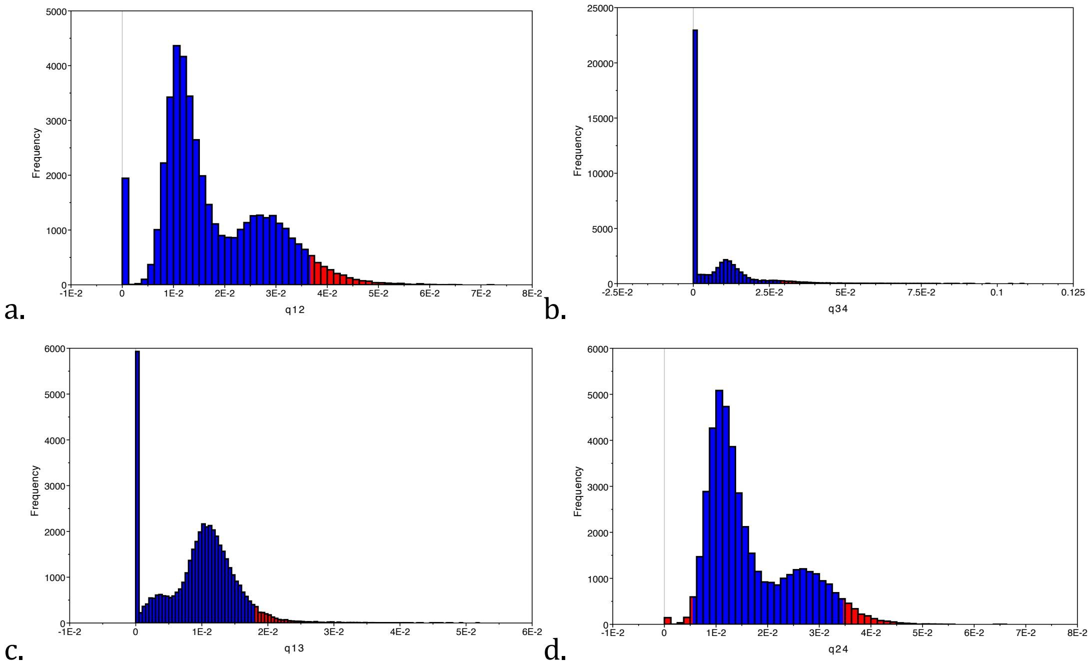

Figure 4.11. Posterior probability distribution for transition rates for mating system and oestrous signal. a. from not concealed to concealed ovulation within polygyny (q_{12}) b. from not concealed to concealed ovulation within pair (q_{34}), c. from polygyny to monogamy with non-concealed ovulation (q_{13}), and d. from polygyny to monogamy with concealed ovulation (q_{24}).

4.5.3.3 Infanticide

4.5.3.3.1 Reported Infanticide

There is decisive support for co-evolution between infanticide and monogamy (Table 4.5). The dependent analysis suggests a root of polygyny and mid-way between with and without infanticide (Table 4.4). This is confirmed by both the independent and multistate analyses showing the root as equally likely with and without infanticide (Table 4.4). Analyses were also carried out with the root fossilised to polygyny without infanticide. All analyses reported here were confirmed by the analysis with a fossilised ancestral state. The ancestral state has little effect on model performance.

There were no transitions from polygyny without infanticide to monogamy without infanticide in the RJ-derived model. Indeed, across the whole of the posterior probability distribution this rate was assigned to zero 100% of the posterior probability distribution, while the transition from polygyny to monogamy with infanticide was zero 0% of the time (Figure 4.12 and Table 4.8). This is a very strong result, suggesting that monogamy only evolved from polygyny in the presence of infanticide. Once monogamy had evolved there were high transition rates back to polygyny with infanticide, and to monogamy without infanticide, both rates more than twice as fast as the gain of monogamy with infanticide (Figure 4.13), suggesting that monogamy with infanticide was an unstable state.

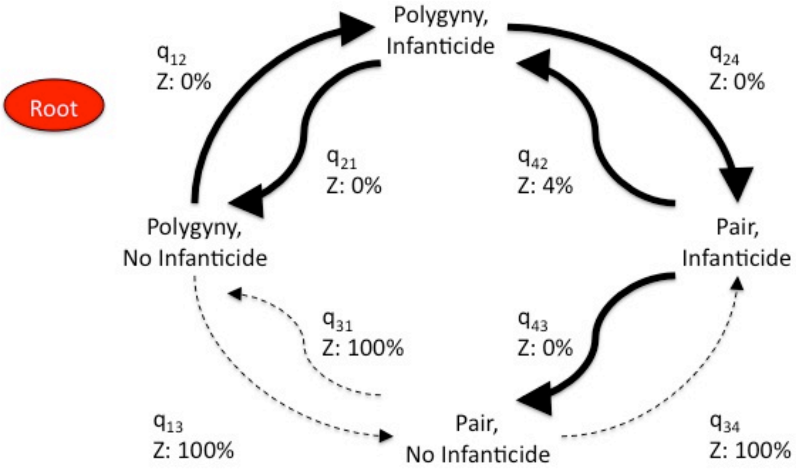

Figure 4.12. Co-evolution between mating system and reported infanticide. Z denotes visits assigned to zero as a proportion of posterior probability distribution. Thickness of arrows reflects proportion of time transition rate is not assigned to zero. Dashed line denotes a zero rate in the RJ-derived model.

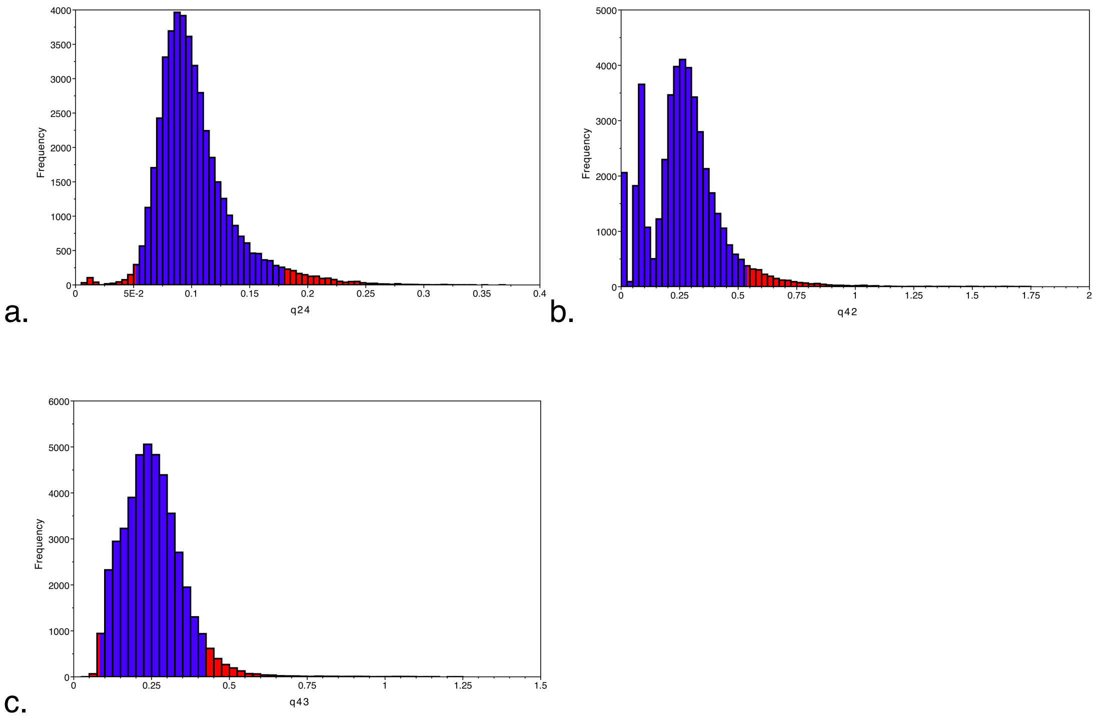

Figure 4.13. Posterior probability distribution for transition rate a. from polygyny to monogamy with infanticide (q_{24}) b. from monogamy to polygyny with infanticide (q_{42}), and c. from infanticide to no infanticide within monogamy (q_{43}).

Infanticide and oestrous signal co-evolved strongly but not decisively (Table 4.5). The RJ-derived model (with 27% of the posterior probability distribution) shows that concealed ovulation only evolved in the presence of infanticide, with a zero rate for the switch to concealed ovulation without infanticide (q_{13}) (Figure 4.14). Across the whole of the posterior probability distribution this transition rate (q_{13}) was assigned to zero 87% of the time, while the equivalent transition rate with infanticide (q_{24}) was assigned to zero 0% of the time (Figure 4.15).

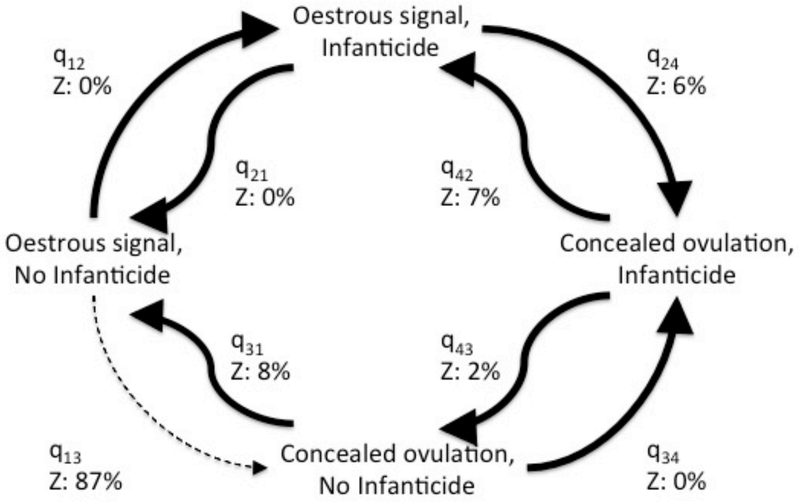

Figure 4.14. Co-evolution between oestrous signal and reported Infanticide. Z denotes visits assigned to zero as a proportion of posterior probability distribution. Thickness of arrows reflects proportion of time transition rate is not assigned to zero. Dashed line denotes a zero rate in the RJ-derived model.

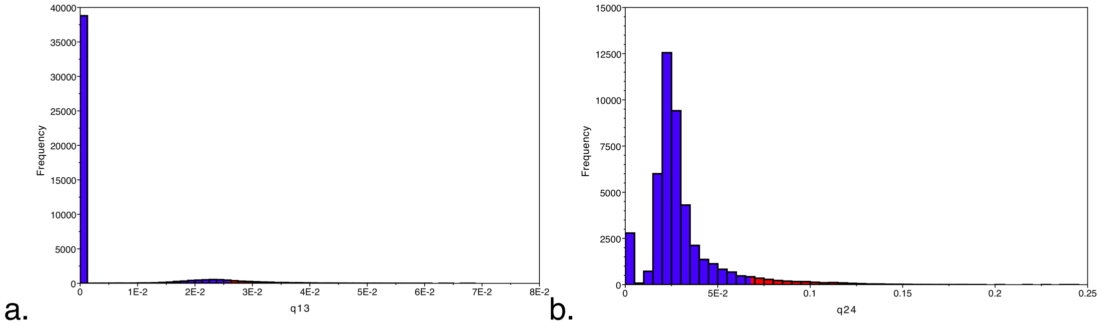

Figure 4.15. Posterior probability distribution for transition rate from oestrous signal to concealed ovulation a. without infanticide (q_{13}) b. with infanticide (q_{24}).

4.5.3.3.2 Infanticide Risk

The weaning ratio (lactation length divided by gestation length (L/G)), is the measure of infanticide risk proposed by van Schaik (2000b), who argues that values above one indicate infanticide risk in a species. However, a Kolmogorov-Smirnov test of normality shows that for the data collected this ratio is not normally distributed (V2=0.16, df=83, p<0.001). An alternative ratio was tried: lactation length divided by lactation plus gestation length (L/L+G). This weaning proportion (WP) measure would be above 50%, lactation is longer than gestation, to indicate the presence of infanticide risk in a species. A Kolmogorov-Smirnov test of normality shows that the weaning proportion data distribution is not significantly different from normal (V2=0.078, df=83, p=0.200).

A generalised linear model analysis shows significant correlation between the weaning proportion and primate mating systems (Table 4.11). However, a Phylogenetic Generalised Linear Model (PGLM), with phylogeny accounted for, shows a significant but small (T_{82} = -2.11, p = 0.038, $^{adj.}R^2$ = 0.04) difference between weaning proportion means for polygyny and monogamy (Table 4.11). Weaning proportion fell in monogamous primates, but not strongly, because of the large variance (Figure 4.16).

Table 4.11. Generalised linear model (GLM) and phylogenetic generalised linear model (PGLM) of the association between mating system and weaning proportion.

GLM				
Term	**Estimate**	**Std. Err.**	**T-value**	**P**
Intercept	0.76	0.05	15.81	<0.001
Mating	-0.15	0.04	-4.04	<0.001
PGLM				
Intercept	0.58	0.09	6.72	<0.001
Mating	-0.07	0.03	-2.11	0.038

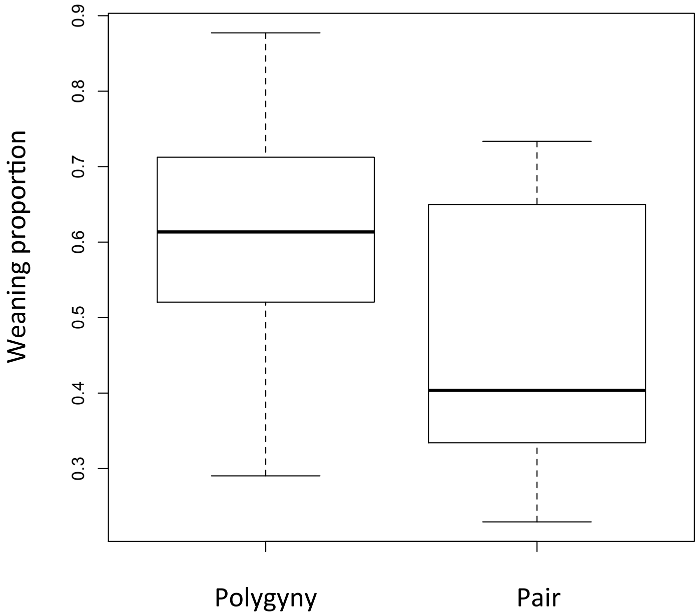

Figure 4.16. Plot of mating system and weaning proportion.

However there was a strong reduction in the weaning proportion with the emergence of monogamy in a number of taxa (A-D in Table 4.12 and Figure 4.18), while for the Indri (E) there was a marked increase. Furthermore, the ancestral primate at the root of the phylogeny had a weaning proportion of 0.53. This suggests that primates were vulnerable to infanticide throughout their evolutionary history (Figure 4.18).

Table 4.12. Comparison of weaning proportion (WP) before and after the evolution of monogamy in primate taxa taken from Figure 4.18.

Taxa	**WP before Pairs**	**WP with Pairs**	**Change**	**% change**	**Transition shown in** Figure 4.18
Ceropithecus Neglectus	0.68	0.69	0.01	1.47	
Gibbons	0.73	0.71	-0.02	-2.74	
Homo sapiens	0.81	0.73	-0.08	-9.88	A
Aotus	0.46	0.35	-0.11	-23.91	B
Callitrichids	0.45	0.36	-0.09	-20.00	C
Tarsiers	0.52	0.28	-0.24	-46.15	D
Varecia	0.48	0.47	-0.01	-2.08	
Propithecus diadema	0.52	0.51	-0.01	-1.92	
Indri indri	0.53	0.70	0.17	32.08	E

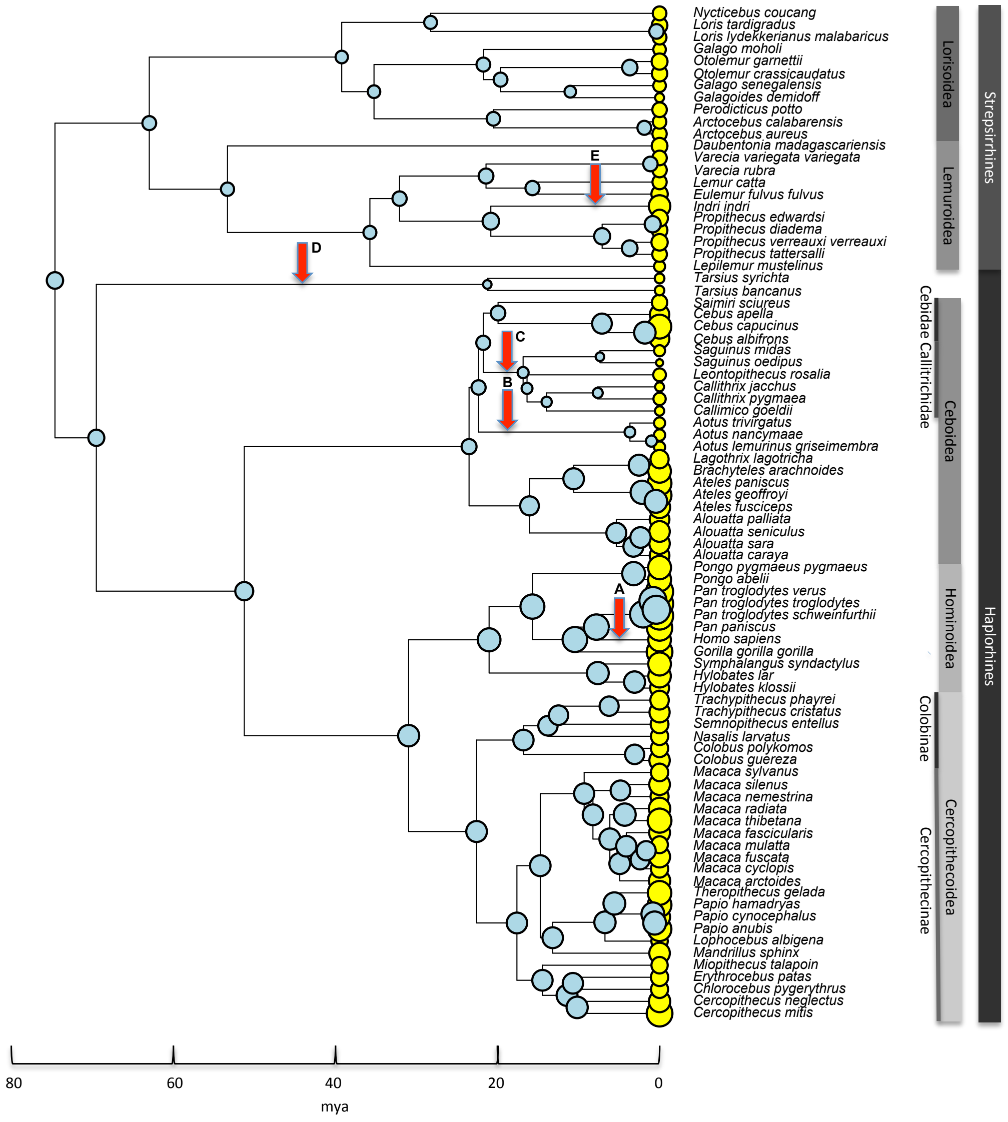

Figure 4.17. Weaning proportion at ancestral nodes of the primate phylogeny. Size of circle at nodes is proportional to value. Blue denotes ancestral node, yellow denotes extant taxa. Letters denote transitions referred to in Table 4.12.

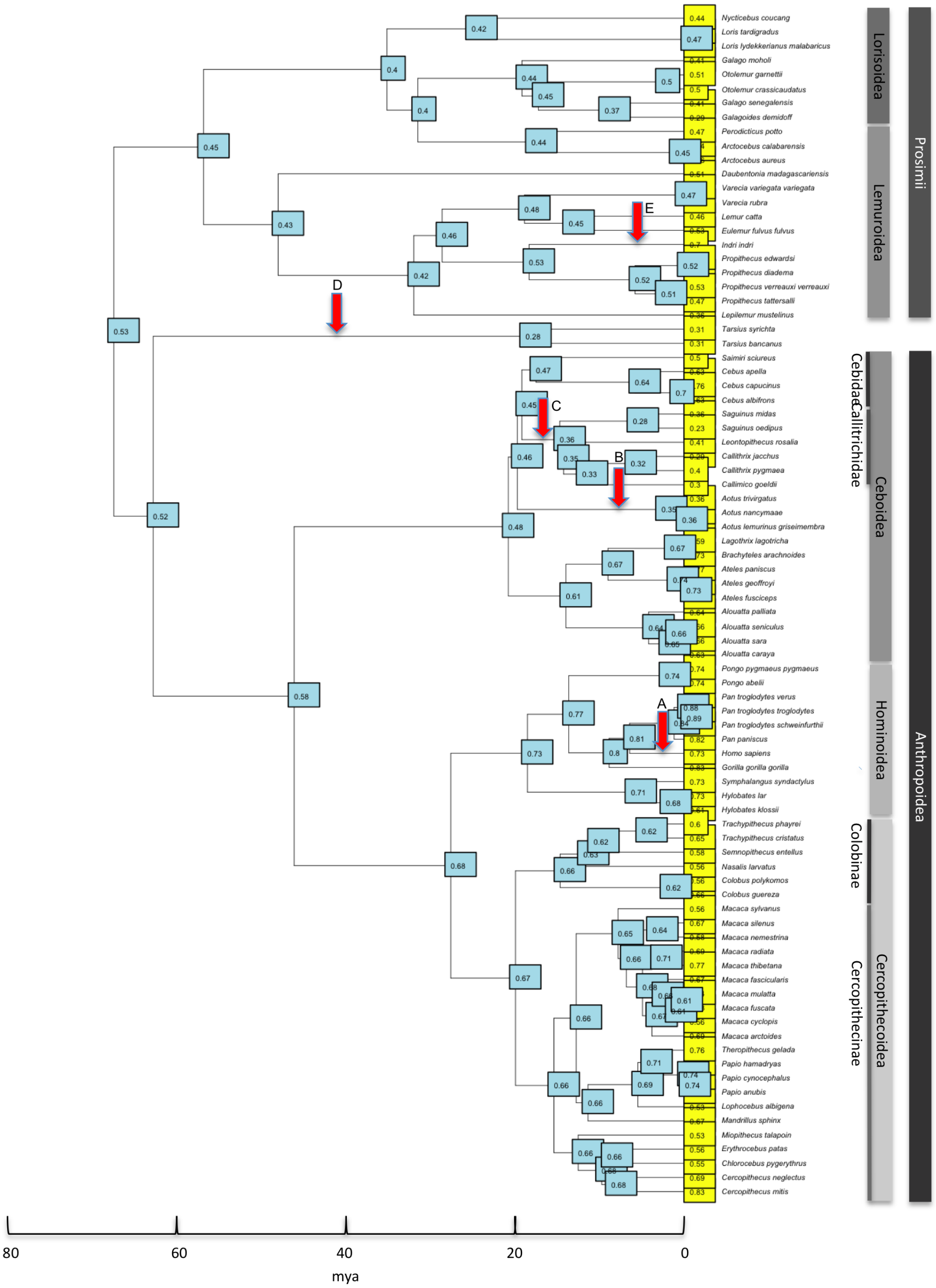

Figure 4.18. Weaning proportion values at ancestral nodes of the primate phylogeny. Blue denotes ancestral node, yellow denotes extant taxa. Letters denote transitions referred to in Table 4.12.

A PGLM of paternal care with weaning proportion shows that species without paternal care are associated with a significantly higher weaning proportion than those with paternal care (Table 4.13).

Table 4.13. PGLM of paternal care and weaning proportion.

Term	**Estimate**	**Std Err**	**T-value**	**P**
Intercept	0.30	0.09	3.45	<0.001
No Paternal Care	0.10	0.03	3.87	<0.001

4.5.4 Summary

To summarise, while paternal care and discrete ranges co-evolve with mating systems, infanticide and infanticide risk are the drivers of monogamy in primates (Table 4.14). Oestrous signal and mating system co-evolved and there was some support for causality of monogamy, but the results were unclear because the ancestral state could not be established.

Table 4.14. Hypotheses for potential drivers of social monogamy in primates. Evidence for coevolution is based on the BayesFactor for *Discrete* analysis for named traits and social monogamy. Causal support indicates evidence that the trait precedes or appears in lock-step with the evolution of social monogamy.

Hypothesis	**Evidence for co-evolution**	**Causal Support**
Paternal care	Yes	No
Larger female ranges	No	No
Discrete female ranges	Yes	No
Oestrous signal	Yes	?
Reported infanticide	Yes	Yes
Infanticide risk (weaning proportion high before monogamy)	Yes	Yes

4.6 Discussion

The quantitative phylogenetic methods used here have made it possible to test the hypotheses for the evolution of monogamy in primates and establish which of the five hypotheses can be supported. They also provide an explanation for the prevalence of monogamy among primate species compared to other mammalian orders. There was correlated evolution between paternal care and mating systems across the primate phylogeny. However, male care of infants was not necessary for the evolution of monogamy since it was possible for monogamy to evolve with or without paternal care, and more likely without. Once monogamy had evolved, extensive paternal care as seen in the Callitrichids and *Aotus*, was then more likely to follow. The input of extensive paternal care was associated with a shortening of inter-birth intervals in a number of taxa. Paternal care may have contributed to the stability of monogamy by increasing reproductive output for both pair members, but was not the cause of monogamy in the first place.

There is mixed support for ecological explanations for the evolution of monogamy in primates. While the range size of dispersed females did not co-evolve with mating systems, discrete female ranges did. This result concurs with previous research suggesting that, across a selection of mammalian taxa, females in monogamous species are less widely dispersed than those in polygynous species but have discrete ranges (Komers and Brotherton 1997, Brotherton and Komers 2003). The transition from the ancestral state of polygyny with discrete female ranges to monogamy with discrete female ranges is supported, suggesting that monogamy was more likely to evolve in primate species with discrete female ranges, in dispersed species at least. However, since there were discrete female ranges at the root of the phylogeny and monogamy emerged late in primate evolution, there must have been factors other than female ranging patterns implicated in the evolution of monogamy. Furthermore, these analyses only included species with dispersed females, while the female sociality analysis suggests that monogamy evolved in species with gregarious females as well as. Since sociality is an important feature of the primate order, explanations for the emergence of monogamy based solely on species with dispersed females may not account for the prevalence of monogamy in primates.

It has been suggested that, within large polygynous groups, monogamy evolved in species with concealed ovulation because males were forced to stay close to a female to ascertain her reproductive status thus forming consortships and ultimately pairs (Alexander 1979, Turke 1984). The results reported here show that oestrous signal co-evolved with mating systems in primates and that concealed ovulation evolved before rather than after monogamy. Furthermore, concealed ovulation only evolved in the presence of infanticide, not in species without infanticide. These results are consistent with the hypothesis that the loss of oestrous signal was a strategy used by females in polygynous species to confuse paternity and therefore to reduce the risk of infanticide (Hrdy 1981, Sillen-Tullberg and Møller 1993). However, it is also consistent with the hypothesis that the loss of oestrous signal forced males to stay with a female and form a pair (Alexander 1979, Turke 1984).

Just as the loss of oestrous signal was a response to infanticide pressure, the evolution of monogamy only takes place in species that have already evolved infanticide. This provides decisive support for the infanticide hypothesis for the evolution of monogamy in primates (van Schaik and Dunbar 1990, Dunbar 1995a, van Schaik and Kappeler 1997, Palombit 1999) whereby a female seeks the protection of a male, who may also be the father of her un-weaned infant, thus forming a pair. It is not surprising perhaps that infanticide should exert such a powerful influence on the behaviour of primates. In some well-studied primate species it has been estimated that infanticide accounts for between 34% and 64% of all infant deaths (Watts 1989, Sommer 1994).

Monogamy with infanticide was found to be an unstable combination as there were high transition rates either back to polygyny with infanticide or to monogamy without infanticide. Monogamy itself, involving the long-term association of a male and female, might reduce the incidence of infanticide because both pair members can defend the un-weaned infant. Furthermore, in species with paternal care, such as *Aotus* and Callitrichids, lactation length was shortened, presumably because females could increase the resources devoted to lactation, relieved of carrying or other infant-care duties. This could have reduced the risk of infanticide through a reduction in the time when the infant was vulnerable, as well as less benefit to a would-be infanticidal male in terms of early oestrus resumption in the mother (Lee 1999).

These results may explain why monogamy is more prevalent among primates than in other mammalian orders. Complex sociality in primates is associated with large brains in many species (Jolly 1966). Encephalised adults have altricial young who require long lactation periods compared to gestation (Charnov and Berrigan 1993, Lee 1999). This high weaning proportion may have made un-weaned infants vulnerable to male infanticide (van Schaik 2000c) for longer periods and thus increased the benefit to infanticidal males in terms of a greater reduction in the time to oestrus resumption in a female whose un-weaned infant was killed. Monogamy may have been one of the counter strategies deployed by primates to avoid the significant reproductive consequences of infanticide (van Schaik and Kappeler 2003). If monogamy in primates only evolved in the presence of infanticide, then human pair bonds may well be a response to the costs of infanticide during our evolutionary history.

The quantitative phylogenetic methods used here make it possible to outline an evolutionary scenario for the evolution of monogamy in primates. Polygyny is inferred as the ancestral mating system in primates and infanticide risk was present at the root of the primate phylogeny. In species where infanticide featured, there may have been a number of counter strategies employed. One of these strategies was for females to confuse paternity among the males with whom they had mated by dampening their oestrous signal so that males were not aware of the females' reproductive state. In some of these species, males may have developed consortships with females because of the increased costs of ascertaining the reproductive state of a female. Females in these species, and in other species also facing infanticide, opted for monogamy as a counter infanticide strategy. If infanticide risk was reduced in this way, then monogamy persisted; otherwise there would have been a return to polygynous mating. One way infanticide risk may have been reduced was by a fall in the weaning proportion due to shorter lactation periods. Paternal care may have facilitated this by allowing females to devote more resources to lactation. But even an association with a single male might have been enough to facilitate shorter weaning periods on its own, with reduced vigilance by the female allowing more time to be devoted to feeding (Dunbar and Dunbar 1974, Brotherton and Manser 1997).

Chapter 5 Evolution of Marriage & Kinship

5.1 Abstract

As mammals, human males are expected to seek to improve their reproductive success by maximising their access to fertile females. However, in many societies, males forgo the possibility of marrying a number of wives even when polygyny is not proscribed. There has been considerable debate among researchers about what factors determine marriage practice as human societies have evolved. However, few have used phylogenetic methods to reveal the mechanisms of cultural change, and answer questions about the nature of cultural evolution, so it is not clearly understood whether elements of cultural practice co-evolve or develop independently. Here, the evolution of marriage and kinship practice is investigated, using Bantu speaking populations across sub-Saharan Africa as the study group. Results suggest that while marriage practice is flexible among these farming people, inheritance, residence, and kinship terminology are highly constrained by population history. Furthermore, inheritance and residence patterns appear locked together as they evolve with the former driving changes in the latter, while marriage change is more loosely associated with both. Monogamy emerges in societies that have changed inheritance and residence patterns from the ancestral states of patriliny and patrilocality to matriliny and matrilocality, but not across all societies that undergo this transition. This suggests there may be other

factors, possibly ecological, that drive the evolution of monogamous marriage among matrilineal, matrilocal groups.

5.2 Introduction

Polygyny is widespread as a marriage system in humans and sanctioned by law or custom in 85 per cent of cultures worldwide (White 1988). As mammals with high female investment in gestation and lactation it is expected that human males should abandon a female after mating, leaving her to provide parental investment in any resulting offspring (Bateman 1948, Trivers 1972), and seek additional mating opportunities elsewhere. Chapter 4 showed that even under these circumstances, some primate species opt for monogamy as a result of the infanticide risk they face, which is particularly acute among those with long inter-birth intervals, such as humans. Indeed the suggested ancestral state for modern humans, based on a phylogenetic analysis of hunter-gatherer populations, is monogamous marriage (Walker *et al.* 2011). It is suggested that polygyny emerged where cultures switched to agriculture, particularly pastoralism, where some men had sufficient resources to attract more than one wife (White and Burton 1988, Marlowe 2000). The polygyny threshold model proposes that when there is marked resource inequality among men, females chose a polygynous marriage with a wealthy man rather than a monogamous marriage with a man without resources (Kanazawa and Still 1999). Monogamous marriage is therefore more likely to be prevalent in a society where there is little variation in male access to resources, such as among hunter-gatherer populations, while those that have adopted agriculture, where there is greater potential variation in male access to resources, polygyny can be expected (White and Burton 1988, Walker *et al.* 2011).

It is therefore somewhat surprising that some agricultural societies switch from polygyny to monogamy. It has been argued that when resources, such as land, are transferred across generations, monogamous marriage can be advantageous where the splitting of those resources among the offspring of a number of wives reduces the fitness value of the resource over time (Fortunato and Archetti 2010). It is suggested that monogamy may have emerged as the predominant marriage form across Eurasia following the adoption of intensive agriculture in the region, such that the splitting up of agricultural estates would have progressively reduced their value (Fortunato and Archetti 2010). However, reconstructions of the evolution of marriage practice across the Indo-European language family suggest that monogamous marriage may already have been present at the origin of the language tree (Pagel and Meade 2005, Fortunato 2011b), which has been dated to 8,700 BP, at the start of the initial spread of agriculture across Eurasia (Gray and Atkinson 2003), and therefore well before the advent of intensive agriculture.

Furthermore, marriage is not an isolated cultural trait but rather is part of the cultural norms of the society in which they take place (White and Burton 1988, Parkin 1997). It may be therefore, that kinship patterns, other than descent, influence the switch from polygynous to monogamous marriage practice. Indeed, residence patterns determine the nature of support for each marriage partner as well as their offspring, while prescriptions of who are eligible marriage partners, reflected in kinship terminology, determine how and between whom marriages should take place (Parkin 1997). Therefore the evolution of marriage practice should not be seen in isolation, but rather in relation to other cultural practices. According to the ethnographic literature, patrilocal residence is usually associated with polygynous marriage, while matrilocal or neo-local residence is associated with monogamous marriage (Burton *et al.* 1996). Furthermore, Murdock's (Murdock 1949) 'main sequence theory' suggests that residence patterns are a reflection of economic and social conditions, which then determine the overall social structure of society, including marriage.

Socioecological theory has traditionally stated that animal social and mating systems are flexible responses to the environment (Janson 2000). However, recent studies using Bayesian phylogenetic methods have shown that in primates (Chapters 3 & 4)(Shultz, Opie, and Atkinson 2011, Opie, Atkinson, and Shultz 2012) and birds (Cornwallis *et al.* 2010) social and mating systems are highly constrained by history. Studies using phylogenetic methods have also suggested that marriage and kinship may be influenced by history (Pagel and Meade 2005, Jordan *et al.* 2009, Fortunato and Jordan 2010, Fortunato 2011a). This raises the intriguing possibility that, even where historical records or archaeological evidence are absent, changes in marriage practice and the associated changes in kinship patterns can be tracked through time and their influence on each other revealed using Bayesian phylogenetic methods.

For the vast majority of human history we have lived as hunter-gatherers in small groups dependent on wild food sources. Only in the last 10,000 years have a number of human populations developed food production, which has led to the expansion of agricultural techniques, cultures, and in some cases their populations too (Diamond and Bellwood 2003). The spread of farming throughout the world has led to fundamental changes in all aspects of life including marriage and kinship. Bayesian phylogenetic methods can be used to reveal the history of marriage and kinship and the interaction between them as farming spread worldwide (Pagel and Meade 2005). For this purpose it is necessary to identify a number of related human populations where the relationships are known in the form of a phylogenetic tree. The Bantu speaking people of sub-Saharan Africa provide a particularly useful group in this regard. They represent one of the major farming expansions where the advantage of food production allowed them to displace and expand into the lands of previous hunter-gatherer populations (Diamond and Bellwood 2003). Also, a language phylogeny of the relationships between the societies (Holden 2002, Holden, Meade, and Pagel 2005) and comprehensive data on marriage and kinship patterns across a large number of cultures (Murdock 1967, Gray 1999) are available for Bantu populations. Indeed, there have been a number of studies that have used a Bantu phylogeny to investigate various aspects of cultural evolution (for example Holden and Mace 2003, Holden and Mace 2005, Atkinson *et al.* 2008, Walker and Hamilton 2011). The history of marriage and kinship among Bantu-speaking people may be able to provide insights into the fundamental processes that drive the evolution of marriage and kinship in humans during the Holocene, and the reason for the emergence of monogamous marriage within agricultural societies.

Bantu speaking people originated in the Benue valley in Eastern Nigeria about 5,000 BP (Greenberg 1963). Their Neolithic economy was based on yam cultivation and hunting, only later acquiring cereals and iron. It is argued that there was a split in the Bantu languages between eastern and western Bantu as they expanded out of their homeland into the equatorial rainforest and southward beginning a millennium later (Vansina 1990). This may have coincided with regional climate change that led to an expansion of savannah habitat (Bayon *et al.* 2012). It is also suggested that before their expansion they may have kept cattle, which they subsequently lost to tsetse fly-borne trypanosomes, only to reacquire them from their Nilo-Saharan and Afro-Asiatic speaking neighbours in East Africa a millennium later (Ehret 2002).

Proto-Bantu society had, it is suggested, a bilateral descent and bi-local residence system (Table 5.1) that was adaptive as they expanded (Vansina 1990, Vansina 1995), around 4,000 BP into the Cameroonian rainforest and from there onto the savannah (3-4,000 BP) and the Western Rift valley (3,000 BP) (Ehret 1998). In particular, it is argued that hunting, which required co-operation and mobility, would be best served by males having a choice about their residence rather than being constrained by unilocality (Vansina 1990, Vansina 1995). Only in the eighteenth or nineteenth century, due to wealth and disorder faced by some Bantu-speaking people, did unilineal descent and residence patterns begin to emerge, it is suggested (Vansina 1990).

This account of Bantu kinship is vigorously contested by Marck and colleagues who propose instead a unilineal descent and unilocal residence system for the ancestral Bantu people (Hage and Marck 2011, Marck and Bostoen 2011). They argue that male absence, due to a reliance on hunting, would suggest that the early Bantu speakers were in fact matrilocal and matrilineal (also see Hill *et al.* 2011). This fits more neatly with the suggestion that matriliny is consistent with a people that face an external threat that would be experienced as populations expand and colonise new territory, displacing existing inhabitants (Divale 1974, Divale 1984). These are also the factors faced by other matrilineal peoples such as: the Iroquois (Morgan 1964 [1877]) in North America with a short growing season, hunting and warfare, the Lapita people of Micronesia (Hage and Marck 2002, Hage and Marck 2003) as they colonised the Pacific islands, and the Yao, a Bantu trading people with prolonged male absence (Mitchell 1956). Furthermore, Marck and colleagues (Hage and Marck 2011, Marck and Bostoen 2011) argue that the Bantu would have originally had Iroquois kinship terminology, since the great majority of unilineal societies have this terminology (Murdock 1967), prescribing which classificatory ‘cousins’ were potential marriage partners. There is therefore no agreement among researchers about the ancestral state of kinship traits among Bantu societies.

The evolutionary history of marriage systems among Bantu speaking populations has not been inferred, although it is suggested that the ancestral state for marriage in the Niger-Kordofanian language tree, of which Bantu is a part, would have been polygynous (Cowlishaw and Mace 1996). However, the base of the language tree is estimated to 10,000 years BP, 5,000 years earlier than the ancestral population of the Bantu (Cowlishaw and Mace 1996). It is therefore unclear what the ancestral marriage state for Bantu speaking people may have been.

Here Bayesian phylogenetic methods will be used to infer the extent of historical constraint on the evolution of marriage and kinship patterns as well as the ancestral states for these Bantu cultural practices. These methods will allow for inferences to be made of the models of evolution of marriage and kinship as Bantu populations spread throughout sub-Saharan Africa. Also co-evolution between these cultural traits will be tested for, and the traits that may drive the evolution of other traits identified. In this way it will be possible to assess the extent to which marriage practice is constrained by history and whether the evolution of marriage form can be explained by changes in kinship practice.

5.3 Methods

5.3.1 Phylogenetic Trees

A Bantu tree sample was built for subsequent analyses using a publicly available cognate set (words with shared meanings in different languages assumed to have a common origin) (Holden 2002, Holden, Meade, and Pagel 2005, Atkinson *et al.* 2008) derived from linguistic data (Bastin, Coupez, and Mann 1999) for 93 Bantu and two Bantoid languages (Tiv and Ejagham). The two Bantoid languages were used as an out-group to root the tree (Holden 2002, Holden, Meade, and Pagel 2005). The linguistic data comprised 92 items of basic vocabulary derived from previously coded cognates covering all 95 languages (Bastin, Coupez, and Mann 1999); 1,649 cognates in total (Holden, Meade, and Pagel 2005). *Beast* (Drummond and Rambaut 2007) was used to sample 14 million trees from the posterior distribution of a Bayesian analysis, using a Markov chain Monte Carlo (MCMC) method, of the Bantu cognate set. Following Gray, Drummond and Greenhill (2009), a covarion model of cognate replacement was used, which allows characters to switch between fast and slow rates on different branches of the tree. A Yule prior on branch lengths was used as a model of language speciation, similar to that used for biological species, with a constant rate of speciation assumed. An uncorrelated log normal relaxed clock was used to allow rate heterogeneity across branches in the tree (Drummond and Rambaut 2007). From the output, one tree in every 5,000 was selected to avoid auto-correlation within the sample. The final sample consisted of 2,800 trees. For a comparison of this phylogeny with other Bantu phylogenies see Chapter 2. A maximum clade credibility tree was derived from the final sample, for illustrative purposes, using *TreeAnnotator* (Drummond and Rambaut 2007) and displayed using *FigTree* (Drummond and Rambaut 2007).

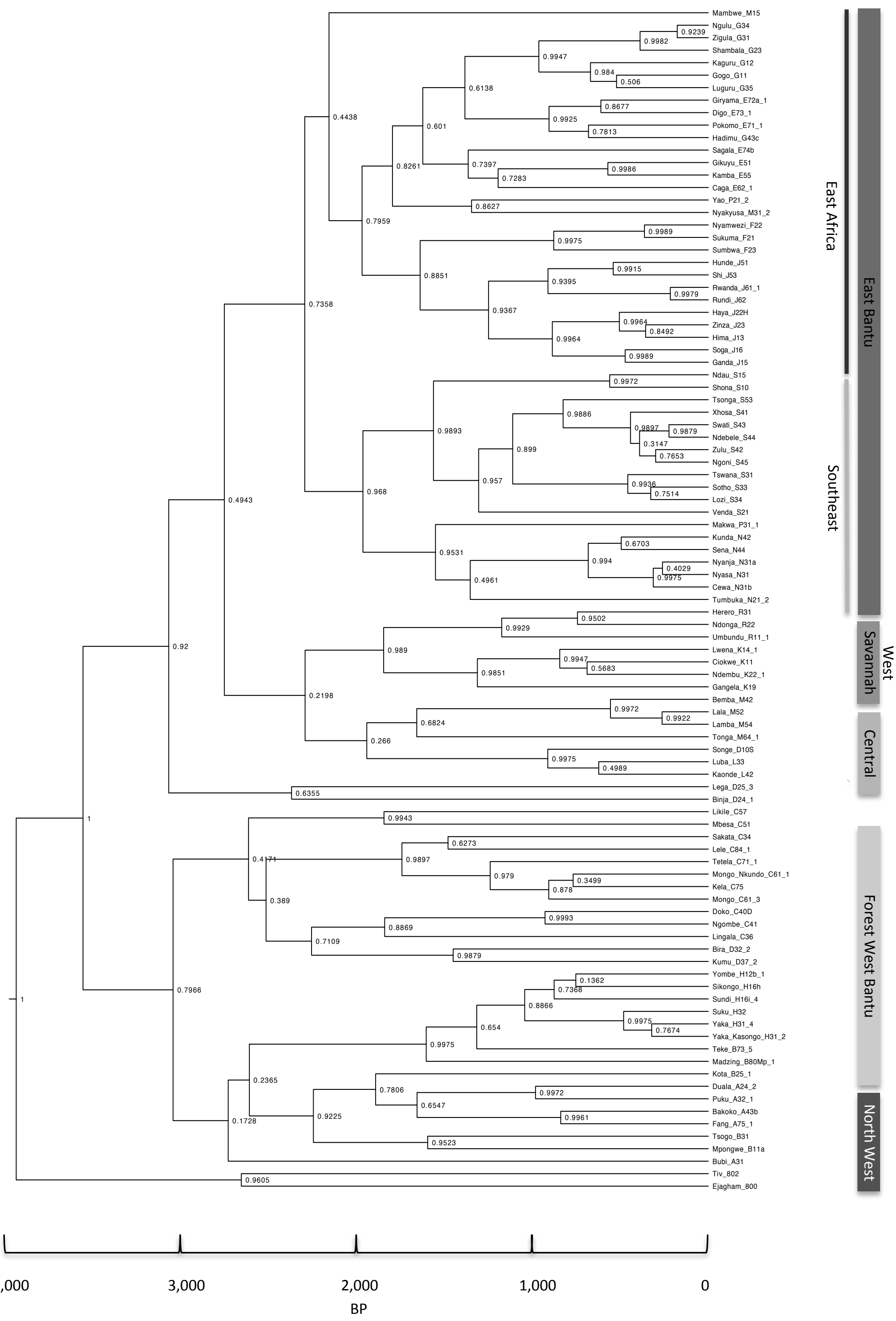
Mambwe_M15
Ngulu_G34
0.9239
Zigula_G31
0.9982
Shambala_G23
0.9947
Kaguru_G12
0.984
Gogo_G11
0.506
Luguru_G35
0.6138
Giryama_E72a_1
0.8677
Digo_E73_1
0.4438
0.9925
Pokomo_E71_1
0.601
0.7813
Hadimu_G43c
Sagala_E74b
Gikuyu_E51
0.7397
0.8261
0.9986
Kamba_E55
0.7283
Caga_E62_1
Yao_P21_2
0.8627
Nyakyusa_M31_2
0.7959
Nyamwezi_F22
0.9989
Sukuma_F21
0.9975
Sumbwa_F23
Hunde_J51
0.9915
0.8851
Shi_J53
0.9395
Rwanda_J61_1
0.9979
Rundi_J62
0.7358
0.9367
Haya_J22H
0.9964
Zinza_J23
0.8492
Hima_J13
0.9964
Soga_J16
0.9989
Ganda_J15
Ndau_S15
0.9972
Shona_S10
Tsonga_S53
0.9886
Xhosa_S41
Swati_S43
0.9897
0.9879
Ndebele_S44
0.9893
0.3147
Zulu_S42
0.7653
Ngoni_S45
0.899
Tswana_S31
0.957
0.9936
Sotho_S33
0.7514
Lozi_S34
0.968
0.4943
Venda_S21
Makwa_P31_1
Kunda_N42
0.6703
Sena_N44
0.9531
0.994
Nyanja_N31a
0.4029
Nyasa_N31
0.9975
Cewa_N31b
0.4961
Tumbuka_N21_2
Herero_R31
0.9502
Ndonga_R22
0.9929
Umbundu_R11_1
Lwena_K14_1
0.989
0.92
0.9947
Ciokwe_K11
0.5683
Ndembu_K22_1
0.9851
Gangela_K19
0.2198
Bemba_M42
0.9972
Lala_M52
0.9922
Lamba_M54
0.6824
Tonga_M64_1
0.266
Songe_D10S
0.9975
Luba_L33
0.4989
Kaonde_L42
Lega_D25_3
0.6355
Binja_D24_1
Likile_C57
0.9943
1
Mbesa_C51
Sakata_C34
0.6273
Lele_C84_1
0.4171
0.9897
Tetela_C71_1
0.979
Mongo_Nkundo_C61_1
0.3499
Kela_C75
0.878
Mongo_C61_3
0.389
Doko_C40D
0.9993
Ngombe_C41
0.8869
Lingala_C36
0.7109
Bira_D32_2
0.9879
Kumu_D37_2
Yombe_H12b_1
0.1362
Sikongo_H16h
0.7368
0.7966
1
Sundi_H16i_4
0.8866
Suku_H32
0.9975
Yaka_H31_4
0.654
0.7674
Yaka_Kasongo_H31_2
Teke_B73_5
0.9975
Madzing_B80Mp_1
Kota_B25_1
0.2365
0.7806
Duala_A24_2
0.9972
Puku_A32_1
0.6547
Bakoko_A43b
0.9225
0.1728
0.9961
Fang_A75_1
Tsogo_B31
0.9523
Mpongwe_B11a
Bubi_A31
Tiv_802
0.9605
Ejagham_800
East Africa
Southeast
East Bantu
West
Savannah
Central
Forest West Bantu
North West
4,000
3,000
2,000
1,000
0
BP

Figure 5.1. Maximum clade credibility tree of the Bantu language phylogeny, with a Bantoid outgroup (Tiv and Ejagham), derived from the full MCMC sample using *TreeAnnotator* (Drummond and Rambaut 2007). Node labels show posterior probability of the node's existence in Bayesian sample of 2,800 trees. Dating of the tree is based on the mid-point of the dating interval (3,000 - 5,000 BP) suggested by archaeological evidence for the spread of farming (Holden and Mace 2003).

5.3.2 Ethnographic Data

Ethnographic data was derived from the Ethnographic Atlas (Murdock 1967, Gray 1999) and matched to the language data by name and geographic location (Jordan *et al.* 2009).

Table 5.1. Kinship Terminology (Murdock 1949, Parkin 1997)

Term		**Definition**
Descent	Patriliny	Descent traced through the male line
	Matriliny	Descent traced through the female line
	Unilineal	Descent traced through either male or female line
	Bilateral	Descent traced equally through the both male and female line
	Duo lateral	Descent traced through the male or female line, situation dependent
	Quasi-lineages	Filiation based, not descent
	Ambilineal	Choice over descent
	Mixed descent	No clear descent pattern
Post-marital Residence	Patrilocal	Couple reside with husband's kin
	Matrilocal	Couple reside with wife's kin
	Neolocal	Couple reside in new area, not with kin
	Bilocal	Couple reside with either kin
Kinship Terms	Iroquois	Genealogical relationship: traced through same sex siblings classed as a blood relations, traced though opposite sex siblings classed as in-law relations
	Crow	Like Iroquois, but relatives on the mother's side descriptive terms, relatives on the father's side classificatory terms
	Omaha	Like Iroquois, but relatives on the mother's side classificatory terms, relatives on the father's side descriptive terms
	Hawaiian	Classificatory terms; only distinguishes between sex and generation, siblings and cousins not distinguished
	Sudanese	Descriptive terms; no two types of relatives share the same term

5.3.2.1 Descent

Variable 43 of the Ethnographic Atlas (Murdock 1967, Gray 1999), *descent: major type*, was used for descent patterns. Among Bantu speaking populations six states feature: 1. patrilineal; 2. duolateral; 3. matrilineal; 4. quasi-lineages; 5. ambilineal; 6. Mixed (Table 5.1). For ancestral state analyses three states were used: patrilineal, matrilineal and bi-lateral (including states 2, 4, 5 and 6 above) (following Holden and Mace 2003) to allow for a comparison with the results of Holden and Mace (Holden and Mace 2003, Holden and Mace 2005). Two binary variables were used in the co-evolution analyses: patrilineal versus matrilineal or bi-lateral, and matrilineal versus patrilineal or bi-lateral to test for the effects of coding.

5.3.2.2 Residence

Variable 11 of the Ethnographic Atlas (Murdock 1967, Gray 1999), *transfer of residence at marriage: after first years*, was used for residence patterns (following Jordan *et al.* 2009, Fortunato and Jordan 2010). This variable excludes a short stay after marriage by the husband in the wife's group to perform bride service, capturing the permanent move of one or both marriage partners to a new location. Among Bantu speaking populations three states feature: 1. wife to husband's group (patrilocal); 2. couple to either group or neolocal; 3. husband to wife's group (matrilocal) (following Jordan *et al.* 2009, Fortunato and Jordan 2010). Two binary variables were used in the co-evolution analyses: patrilocal versus matrilocal or bi/neo-local, and matrilocal versus patrilocal or bi/neo-local to test for the effects of coding.

5.3.2.3 Marriage

Variable 9 of the Ethnographic Atlas (Murdock 1967, Gray 1999), *marriage composition*, has seven trait states, but only three feature among Bantu speaking peoples: 1. independent nuclear, occasional polygyny; 2. polygyny – preferentially sororal (sisters), co-wives in separate dwellings; 3. polygyny – non-sororal, co-wives in separate dwellings. State one is here called predominant monogamy, although it could also be referred to as limited polygyny. For the co-evolutionary analyses a binary variable was used: polygyny (both sororal and non-sororal) versus monogamy (independent nuclear, occasional polygyny) (following Pagel and Meade 2005).

5.3.2.4 Kinship Terminology

Variable 27 of the Ethnographic Atlas (Murdock 1967, Gray 1999), *kin terms for cousins*, was used for kinship terminology. Among Bantu speaking populations five states feature: 1. Crow, 2. Hawaiian, 3. Iroquois, 4. Omaha, 5. Sudanese (Table 5.1). Since Omaha and Crow are variants of Iroquois (Parkin 1997, Allen) a binary trait of Iroquois-like (Iroquois, Omaha and Crow) versus non-Iroquois (Hawaiian and Sudanese) was used in the co-evolutionary analyses.

5.3.3 Analyses

Phylogenetic signal, root probabilities, ancestral states, evolutionary models and co-evolutionary results were derived using procedures detailed in Chapter 2.

5.4 Results

5.4.1 Phylogenetic Signal

Among Bantu speaking populations marriage has a low phylogenetic signal, with a λ value not significantly different from zero (Table 5.2), while the other three traits (descent, residence and kinship terminology) have λ values not significantly different from one. The low signal in marriage is probably due to the overwhelming presence of one state, non-sororal polygyny (Figure 5.4); monogamy is spread across five clades (the eastern Bantu of East Africa, central, west Savannah, west Bantu and northwest). It may be that a continuous variable of extent of polygyny would have a stronger phylogenetic signal, but is not currently available.

Table 5.2. Phylogenetic Signal in Trait Data on the Bantu Language Tree. N, number of populations; λ_{max} lambda value from maximum likelihood analysis; LL_{max} log likelihood of λ_{max}; LL_0 log likelihood of λ_0; LL_1 log likelihood of λ_1; LLR_0 probability of log likelihood ratio of LL_0 and LL_{max}; LLR_1 probability of log likelihood ratio of LL_1 and LL_{max}.

Trait Data	**N**	**LLmax**	**λ_{max}**	**LL_0**	**LLR_0**	**LL_1**	**LLR_1**
Marriage	93	-59.25	0.079	-59.27	0.854	-66.68	<0.001
Residence	92	-66.58	1.000	-83.56	<0.001	-66.58	1.000
Descent	94	-88.02	0.949	-101.25	<0.001	-88.25	0.500
Kinship Terminology	65	-76.95	0.850	-81.05	0.004	-78.06	0.136

5.4.2 Ancestral States

Bayesian analysis infers the ancestral state of the traits at the root of the Bantu phylogeny (Table 5.3). For descent there is a high probability of patriliny at the root, while for residence the root is patrilocality. Marriage is very strongly indicated to have non-sororal polygyny at the root, while for kinship terminology there is a high probability of Iroquois.

Table 5.3. Mean probability of ancestral state for marriage and kinship traits at the root of the Bantu phylogeny.

Trait	**Log Likelihood**	**Ancestral State**	**Mean probability**	**S.E.**
Descent	-87.33	Patriliny	0.897	0.0016
Residence	-64.54	Patrilocality	0.989	0.0001
Marriage	-66.09	Polygyny	0.995	0.0004
Kin Terminology	-71.60	Iroquois	0.874	0.0014

From a descent pattern of patriliny at the root of the Bantu phylogeny, matriliny evolved in four clades predominantly: the Eastern Bantu of Southeast and East Africa, the central Bantu, the west Savannah Bantu, and the equatorial West Bantu (Figure 5.2). Matriliny most likely appeared first in the population that gave rise to the forest west Bantu about 2,900 years ago and at about 2,500 in the population that gave rise to the central and west savannah Bantu. Cognatic descent most likely appeared first within the Southeast Bantu about 1,250 years ago followed by other Eastern Bantu populations.

Residence patterns followed a similar pattern to descent among the Bantu. The earliest appearance of matrilocality was most likely among the central Bantu about 2,000 years BP (before present), with no unequivocal appearance for bi/neo-locality until the present (Figure 5.3).

Marriage composition, predominantly non-sororal polygyny at the root of the phylogeny gave way to monogamy late in the Bantu expansion (~ 800 BP) and only within clades that had already adopted matriliny and matrilocality (predominantly the east Bantu of East Africa and the central and Savannah Bantu) (Figure 5.4). This suggests that there is a switch in descent and/or residence patterns before changes take place in marriage composition. This possible link between descent, residence and marriage is explored further in the 5.4.4 Co-evolution section below. Sororal polygyny appears in the same clade as cognatic descent suggesting that there may be a link between them.

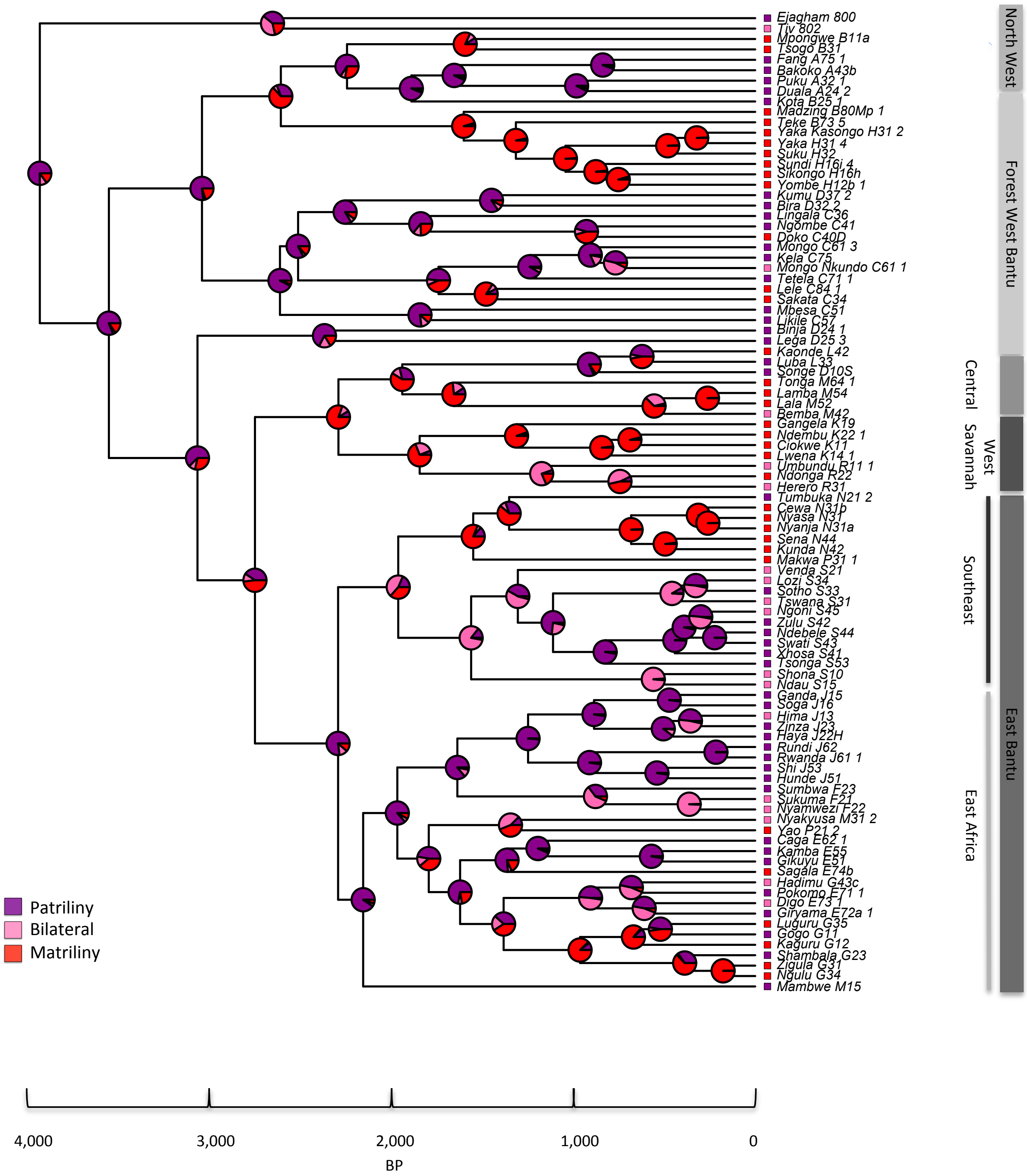

Figure 5.2. Plot of descent state at ancestral nodes of the Bantu phylogeny using Bayesian analysis. Purple – patriliny, pink - cognatic, red – matriliny. Pies show probability of descent state at ancestral nodes. Squares show descent state at tips.

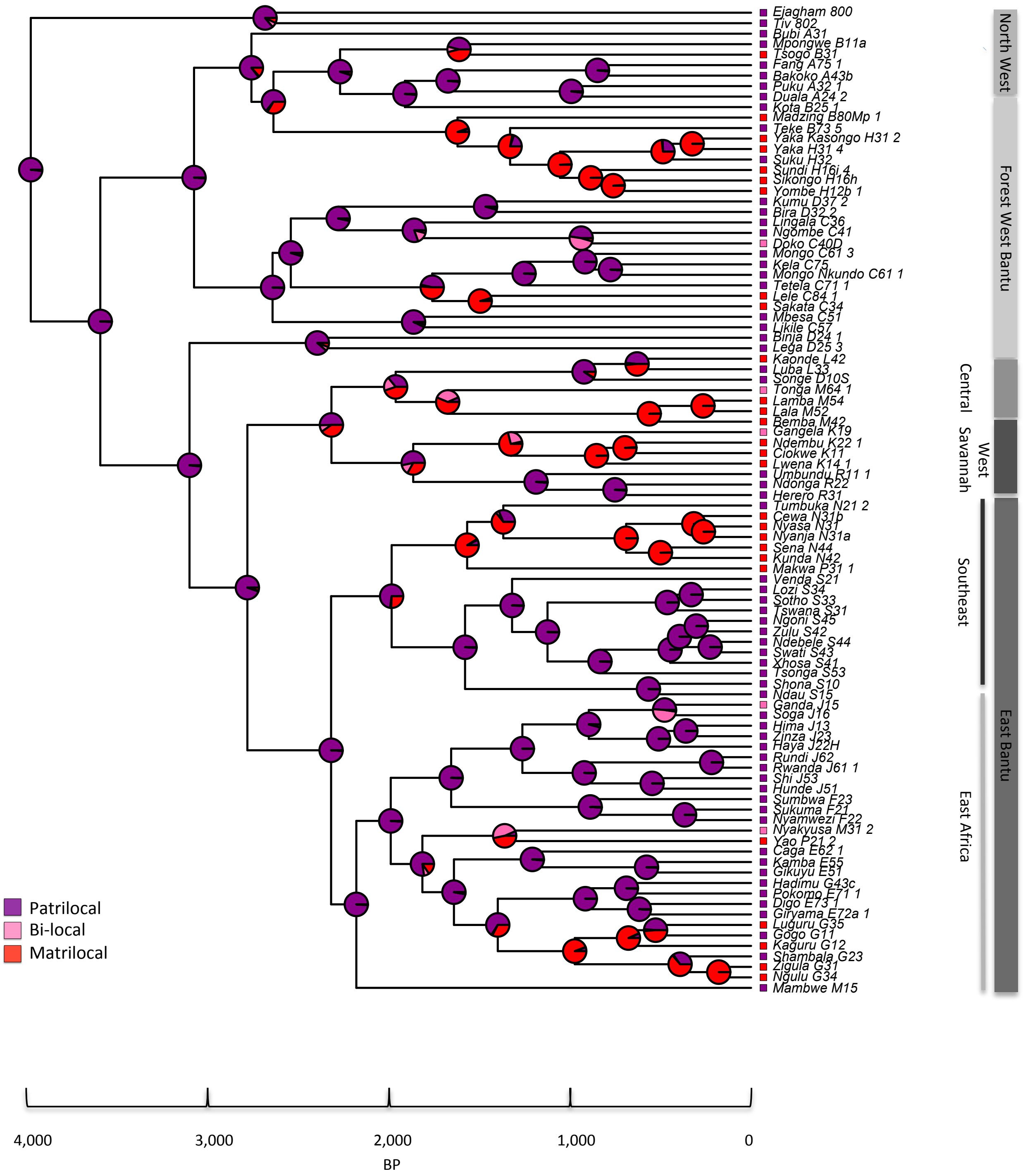

Figure 5.3. Plot of residence state at ancestral nodes of the Bantu phylogeny using Bayesian analysis. Purple – patrilocal, pink - bi-local, red – matrilocal. Pies show probability of residence state at ancestral nodes. Squares show residence state at tips.

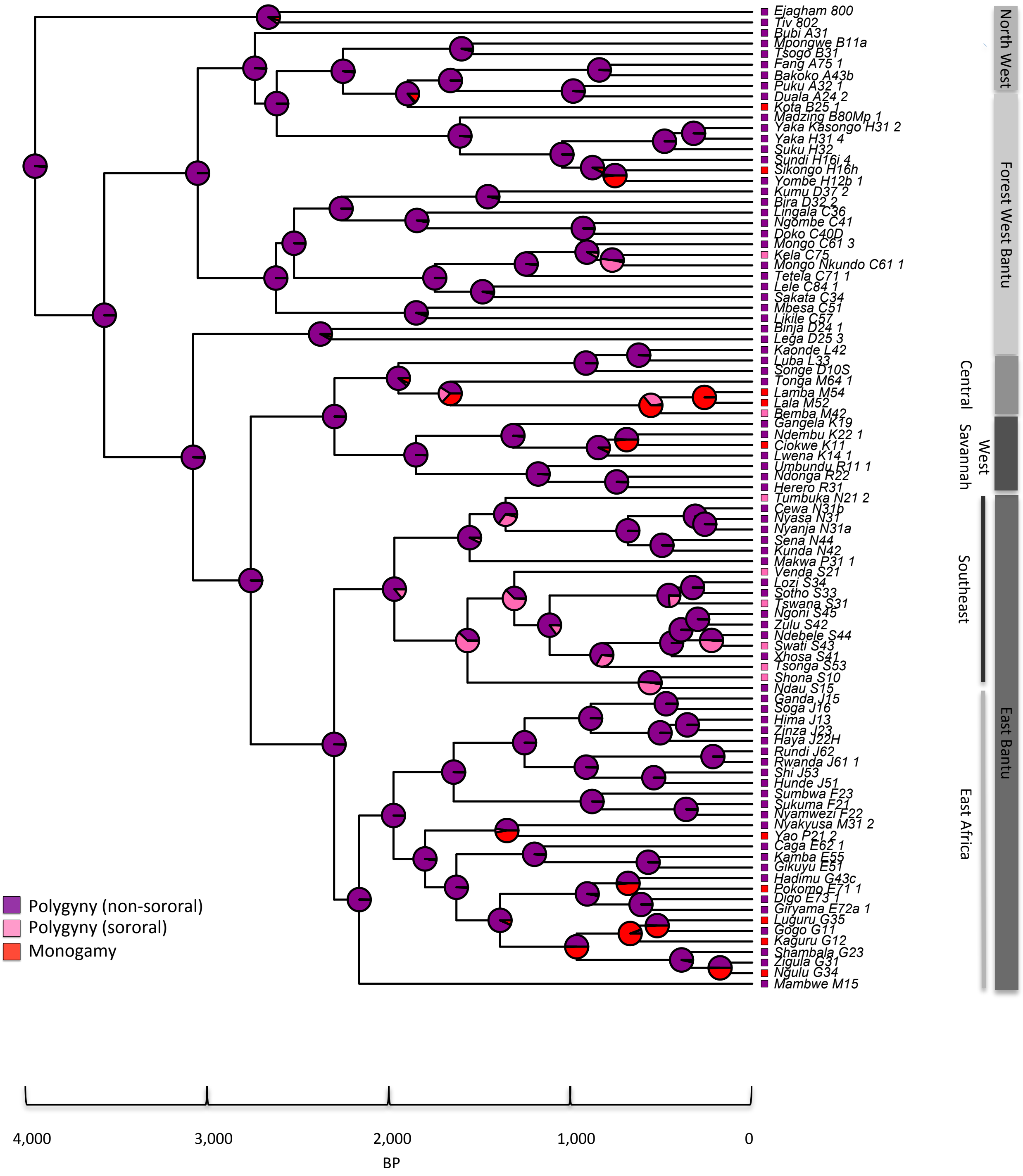

Figure 5.4. Plot of marriage state at ancestral nodes of the Bantu phylogeny using Bayesian analysis. Purple – polygyny (non-sororal), pink - polygyny (sororal), red – nuclear with occasional polygyny. Pies show probability of states at ancestral nodes. Squares show marriage state at tips.

5.4.3 Evolutionary Models

The RJ-derived model of descent (the highest-ranked model in the posterior probability of the RJ MCMC analysis) shows that from patriliny at the root of the phylogeny there are strong transition rates into both a bi-lateral (cognatic) and a matrilineal pattern (Figure 5.5). There are weaker rates out of bi-lateral descent to the other two states. The transition rates out of matriliny are weaker still with a zero rate back to patriliny in RJ-derived model.

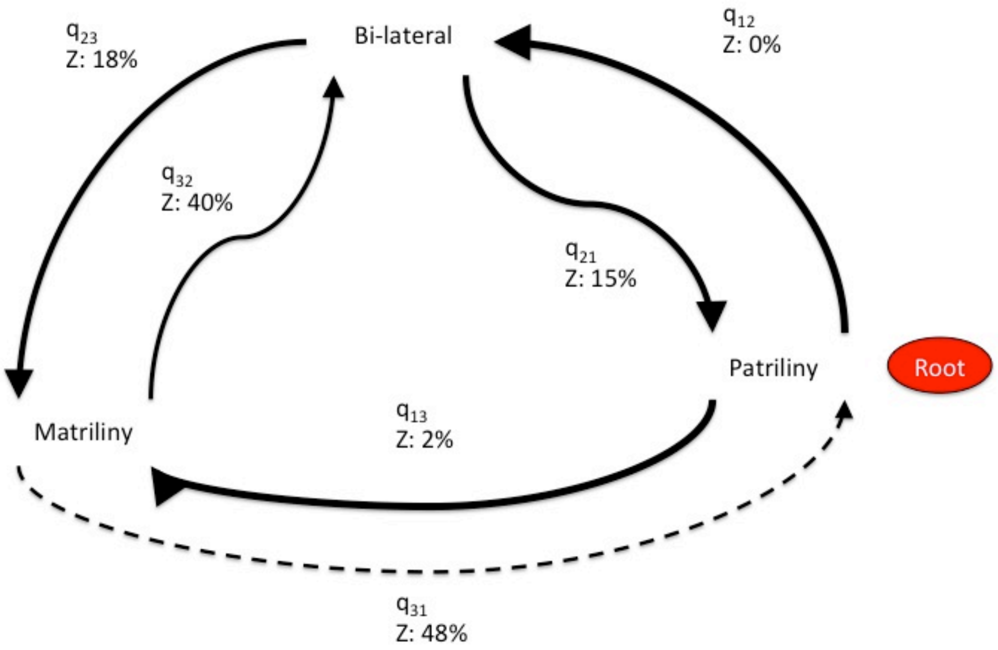

Figure 5.5. Model of evolution for descent among Bantu populations. Z denotes visits assigned to zero as a proportion of posterior probability distribution. Thickness of arrows reflects proportion of time transition rate is not assigned to zero. Dashed line denotes a zero rate in the RJ-derived model.

For residence, the RJ-derived model suggests there are strong rates out of the ancestral state of patrilocality to both other states and back to patrilocality from matrilocality (Figure 5.6). The rates out of neo/bi-locality are weaker, while the transition from matrilocality to neo/bi-locality is a zero rate in the RJ-derived model.

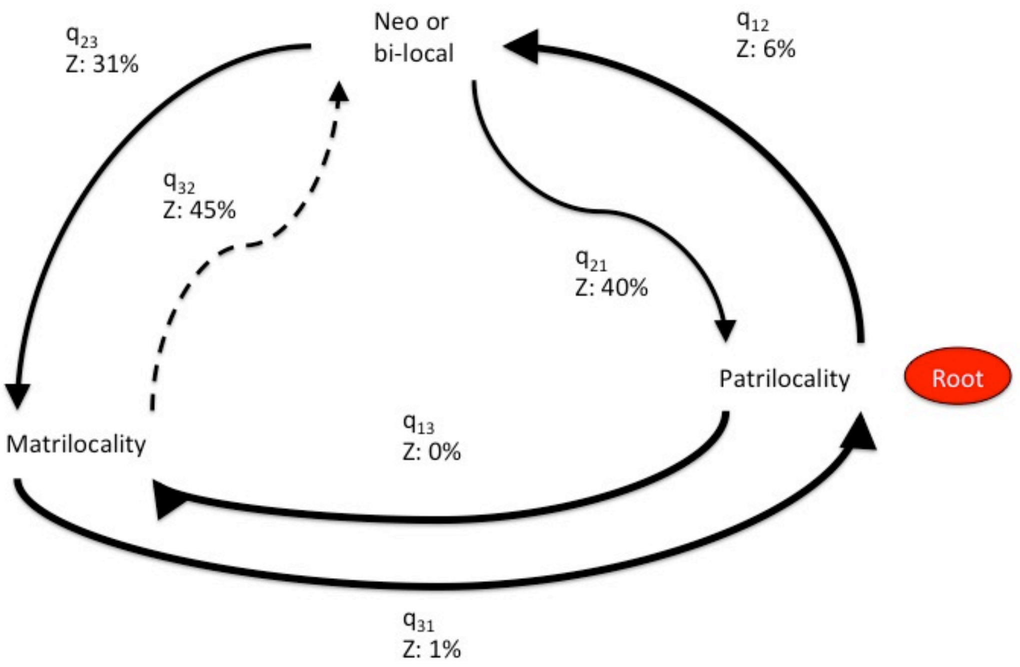

Figure 5.6. Model of evolution for residence among Bantu populations. Z denotes visits assigned to zero as a proportion of posterior probability distribution. Thickness of arrows reflects proportion of time transition rate is not assigned to zero. Dashed line denotes a zero rate in the RJ-derived model.

For marriage composition, the RJ-derived model suggests there are strong rates out of non-sororal polygyny, the ancestral state, to the other two states (Figure 5.7). All the transition rates from monogamy and sororal polygyny to the other states are substantially weaker.

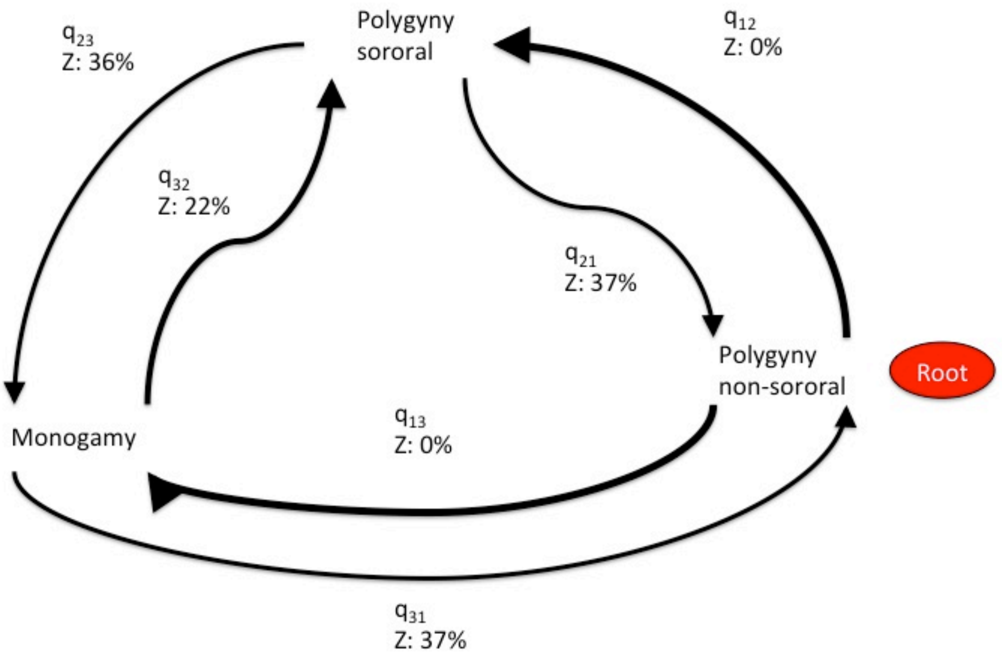

Figure 5.7. Model of evolution for marriage among Bantu populations. Z denotes visits assigned to zero as a proportion of posterior probability distribution. Thickness of arrows reflects proportion of time transition rate is not assigned to zero.

5.4.4 Co-evolution

The similarity between the ancestral state plots for descent and residence suggest that there might be co-evolution between these two traits (Figure 5.2 and Figure 5.3). In addition Figure 5.4 appears to show that monogamy only evolved in clades that have already evolved matriliny and matrilocality. To test these observations quantitatively co-evolution was tested for between the marriage and the kinship traits (Table 5.4). There was decisive co-evolution between descent and residence patterns; the dependent model was more likely than the independent model by a Bayes Factor well above two. Furthermore marriage co-evolved strongly with both descent and residence patterns, with the dependent model more likely than the independent model by a Bayes Factor of more than one. Residence also co-evolved strongly with kinship terminology, but descent and marriage did not co-evolve with kinship terminology. All other combinations showed less than strong evidence for co-evolution. Analyses were run with descent and residence binary traits in both states (see 5.3.2 Ethnographic Data above). Since there was no appreciable difference between analyses the results reported here use descent (patriliny versus matriliny or bilateral) and residence (patrilocal versus matrilocal or bi/neo-local) binary traits, unless otherwise stated.

Table 5.4. Comparison of dependent and independent models shows co-evolution between traits.

Co-evolution	**Dependent model**		**Independent model**		**Log10 Bayes Factor**
	Log likelihood	S.E.	Log likelihood	S.E.	
Descent - Residence	- 98.29	+/- 0.05	- 110.03	+/- 0.03	5.10
Marriage - Descent	- 97.47	+/- 0.05	- 101.87	+/- 0.03	1.91
Marriage - Residence	- 84.12	+/- 0.05	- 87.46	+/- 0.03	1.45
Residence - Kinship Terminology	- 75.74	+/- 0.03	- 78.18	+/- 0.03	1.06
Marriage - Kinship Terminology	- 64.59	+/- 0.02	- 64.24	+/- 0.02	- 0.15

Descent - Kinship Terminology	- 90.43	+/- 0.03	- 89.93	+/- 0.02	- 0.22

5.4.4.1 Descent and Residence

Transitions from the ancestral state of patriliny and patrilocality to the derived state of matri/bi-lateral descent and matri/neo-local residence are stronger for the route in which descent changes first (transitions q_{13} and q_{34}) compared to the route where residence changes first (q_{12} and q_{24}). Descent and residence co-evolved decisively and descent patterns changed first, so this result suggests that changes in descent caused changes in residence across Bantu evolution.

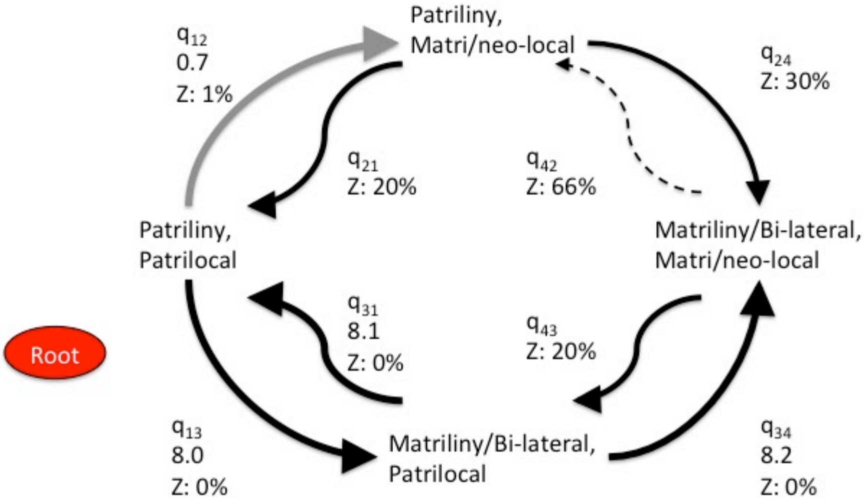

Figure 5.8. Co-evolution between descent and residence among Bantu cultures. Z denotes visits assigned to zero as a proportion of posterior probability distribution. Thickness of arrows reflects proportion of time transition rate is not assigned to zero. Dashed line denotes a zero rate in the RJ-

derived model. Grey arrow denotes different rate in the RJ-derived model. Number below rate name (q_{ij}) is the mean transition rate where rate distribution approximates normal.

5.4.4.2 Marriage and Descent

Transitions from the ancestral state of polygyny and patriliny to the derived state of monogamy and matri/bi-lateral descent are stronger for the route in which descent changes first (transitions q_{12} and q_{24}) compared to the route where marriage composition changes first (q_{13} and q_{34}). There is strong co-evolution between descent and marriage composition, so this result suggests that the changes in descent pattern drive the changes in marriage composition across the Bantu phylogeny.

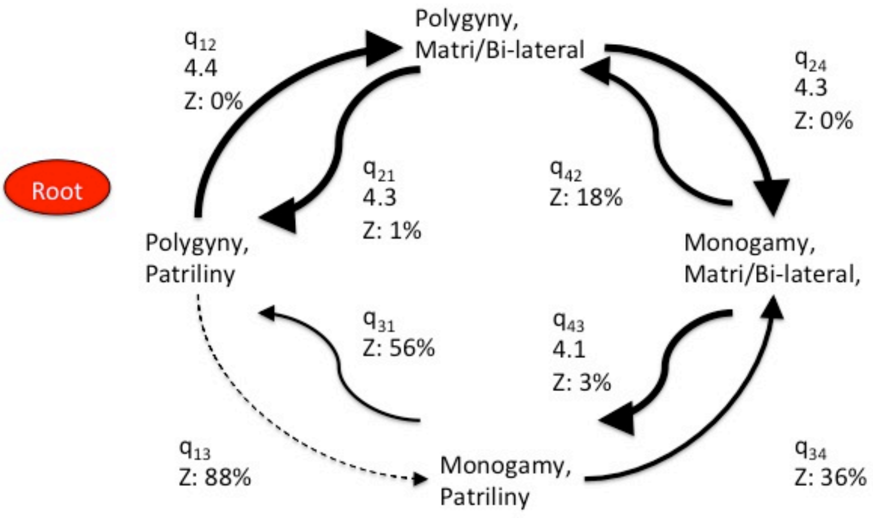

Figure 5.9. Co-evolution between marriage composition and descent among Bantu cultures. Z denotes visits assigned to zero as a proportion of posterior probability distribution. Thickness of arrows reflects proportion of time transition rate is not assigned to zero. Dashed line denotes a zero rate in the RJ-derived model. Number below rate name (q_{ij}) is the mean transition rate where rate distribution approximates normal.

5.4.4.3 Marriage and Residence

Transitions from the ancestral state of polygyny and patrilocality to the derived state of monogamy and matri/neo-locality are stronger for the route in which residence changes first (transitions q_{12} and q_{24}) compared to the route where marriage composition changes first (q_{13} and q_{34}). This suggests that as with descent, residence patterns may drive changes in marriage composition. Since descent and residence have strongly correlated evolution it may be that both traits have an effect on marriage patterns. However, changes in descent precede changes in residence so that changes in the descent pattern may be driving the whole system.

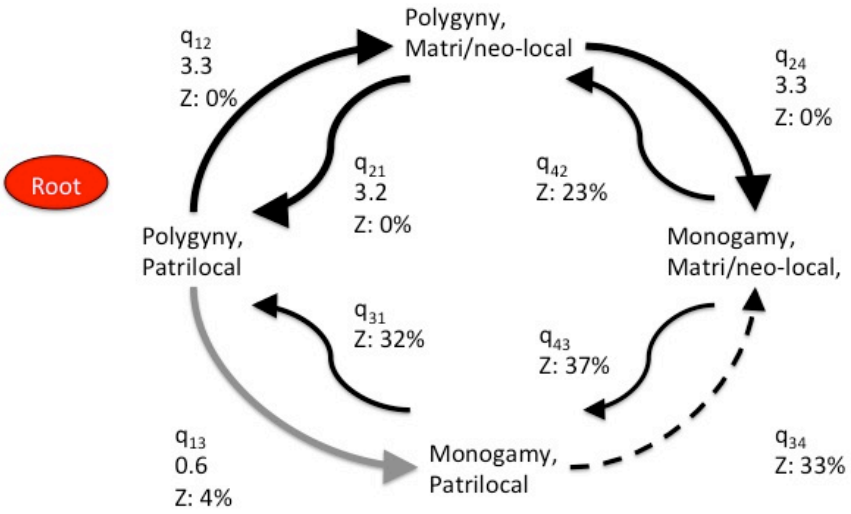

Figure 5.10. Co-evolution between marriage composition and residence among Bantu cultures. Z denotes visits assigned to zero as a proportion of posterior probability distribution. Thickness of arrows reflects proportion of time transition rate is not assigned to zero. Dashed line denotes a zero rate in the RJ-derived model. Grey line denotes a different rate in the RJ-derived model. Number below rate name (q_{ij}) is the mean transition rate where rate distribution approximates normal.

5.4.4.4 Residence and Kinship Terminology

Transitions from the ancestral state of patrilocality and Iroquois-like terminology to patrilocal and non-Iroquois (q_{12}) and to matri/neo-local while remaining Iroquois-like (q_{13}) were strong (Figure 5.11). This result suggests that kinship terminology only changes from the ancestral state of Iroquois-like to non-Iroquois in patrilocality, not in matri/neo-locality.

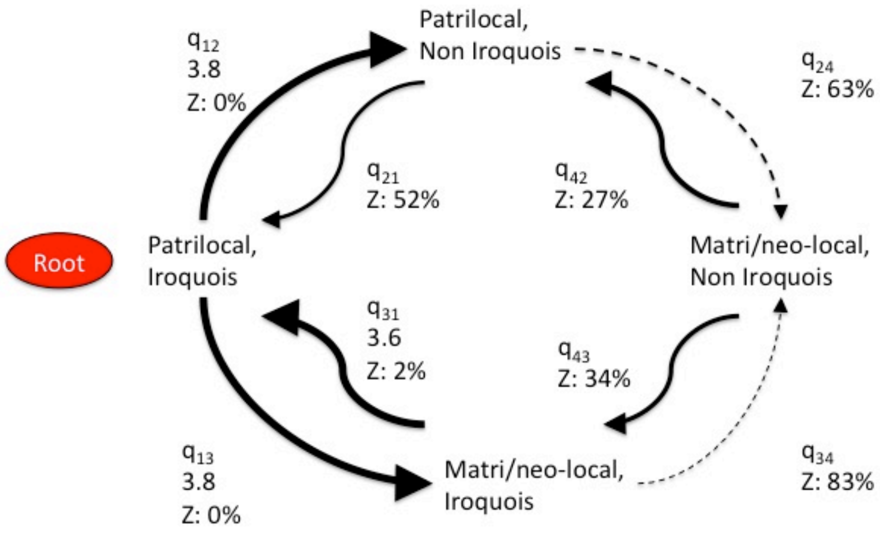

Figure 5.11. Co-evolution between residence and kinship terminology among Bantu cultures. Z denotes visits assigned to zero as a proportion of posterior probability distribution. Thickness of arrows reflects proportion of time transition rate is not assigned to zero. Number below rate name (q_{ij}) is the mean transition rate where rate distribution approximates normal.

5.5 Discussion

Bayesian methods were used to infer the ancestral states and models of evolution of marriage and kinship traits among Bantu-speaking populations, as well as correlated evolution between those traits. The Bayesian tree sample inferred here accords well with phylogenies derived from the same Bantu language cognate set (Holden 2002, Holden, Meade, and Pagel 2005) in all respects except for the initial split between East and West Bantu, which has 100% support in this tree, but is not supported in either of the other two trees. There is support for this early split during the Bantu expansion from lexicostatistical phylogenies (Guthrie 1967-1971, Vansina 1990, Vansina 1995) and also from a recent genetic study covering the area in west central Africa where the Bantu originated and from where the initial expansion took place (Montano *et al.* 2011). However as well as the previous trees for the same cognate set (Holden 2002, Holden, Meade, and Pagel 2005), the early split is not supported in a recent study using both linguistic and genetic data (de Filippo *et al.* 2012). The validity of the early split has implications for both ancestral state reconstructions as well as correlated evolution between traits across the tree. Further work will need to be done to resolve the nature of the early expansion of Bantu speaking people, and the results derived here may need revision in the light of that work.

The results reported here show that marriage practice was flexible with regard to history among the Bantu-speaking peoples of sub-Saharan Africa. In other words, closely related populations were not more likely to have a similar marriage system than would be expected by chance. This is surprising since, while marriage is flexible, the kinship system that surrounds marriage, including descent, residence and kinship terminology, which determine inheritance patterns, post-martial location and suitability of marriage partners respectively, were highly constrained by history throughout the Bantu expansion.

The reason for the low phylogenetic signal in marriage composition may be explained by the overwhelming presence of polygyny from the root and across most of the Bantu tree (Figure 5.4), with monogamous marriage prevalent in only ten, not closely related, extant populations. This raises the intriguing question of what prompted the development of monogamy among Bantu populations. The reconstruction of polygynous marriage at the root of the Bantu phylogeny is in line with earlier work suggesting that the root of the Niger-Kordofanian language phylum, of which Bantu is a part, also had polygynous marriage at its root (Cowlishaw and Mace 1996). Polygynous marriage has been associated with variable resource holding among men, as in farming communities, where those with sufficient resources can pay for and keep more than one wife (White and Burton 1988). Ancestral Bantu speakers were incipient farmers with their agriculture based on yam cultivation (Greenberg 1963) and possibly cattle (Ehret 2002). Another language phylum, Indo-European, whose root was also among incipient farmers, instead had monogamous marriage at its root (Fortunato 2011b). However, this reconstruction of the ancestral state of Indo-European marriage may be unreliable since polygynous marriage became proscribed across many populations as Christianity spread, which may distort the result for the ancestral state. Furthermore, there may be gradations in the extent of polygyny within polygynous cultures that are not picked up in the binary trait provided by the Ethnographic Atlas (EA) (Murdock 1967, Gray 1999). It could be that there are reductions in the extent of polygyny in a society that predate a full switch to monogamy that the analyses presented here do not show.

However, the EA data used here demonstrate that Bantu populations with predominant monogamy are relatively rare, only appear late in the Bantu expansion and are not more likely among closely related populations. Furthermore, monogamy appears in populations that have already adopted matriliny and matrilocality. This result is different from that found for Indo-Europeans, where monogamy is associated with patriliny and patrilocality (Fortunato, Holden, and Mace 2006, Fortunato and Archetti 2010, Fortunato 2011b), but accords with the world-wide pattern of a link between monogamy and matrilocal or neo-local residence (Burton *et al.* 1996). Furthermore, the results reported here confirm that there is strong co-evolution between marriage and both descent and residence. The co-evolution between marriage and residence appears to be a contrary result to the primate analysis, which found no co-evolution between social organisation and dispersal pattern (Chapter 3). This suggests that primate dispersal may have a different underlying mechanism to human residence patterns. Indeed, results here show that there was decisive co-evolution between descent and residence and that descent patterns changed before residence patterns, suggesting that descent drives residence changes. From a patrilocal state at the root of the Bantu phylogeny, confirming the results of genetic studies on sub-Saharan farmers (Seielstad, Minch, and Cavalli-Sforza 1998, Hammer *et al.* 2001), matrilocal residence emerged in cultures that adopted matrilineal descent. Residence in humans may simply be the resulting post-marriage living arrangements that flow from the particular descent, or inheritance, pattern of the society. This result questions the ‘main sequence theory’, which proposes that it is changes in residence that drive changes in the whole social structure of a society (Murdock 1949).

Inheritance patterns co-evolve with marriage practice, supporting the conclusions of earlier phylogenetic-based research across a number of language phyla (Cowlishaw and Mace 1996). However, that study suggested that transitions to predominant monogamy were equally associated with both matriliny and patriliny. Here, the results suggest that monogamy emerged only after inheritance had changed from patriliny to matriliny. For marriage, then there appears to be a two-stage process. First, in some Bantu societies, inheritance changed from the ancestral state of patriliny to the derived state of matriliny, followed by a change in residence patterns from patrilocal to matrilocal. Then, in some of the matrilineal and matrilocal populations, marriage switched from polygyny to monogamy. The initial change in inheritance may itself be driven by ecological changes. In earlier phylogenetic analyses it was shown that the adoption of cattle holding by matrilineal Bantu societies changed inheritance patterns to patriliny (Mace and

Holden 1999, Holden and Mace 2003). However, those analyses, using parsimony techniques, were unable to suggest the ancestral state of Bantu descent. Here, Bayesian methods have allowed for an inference of the ancestral state for descent as patriliny and to show that in the best-supported evolutionary model there were no back transitions to patriliny once the move to matriliny had taken place. If cattle were a feature of early Bantu society that was lost as populations expanded into the tsetse fly belt, this may have encouraged a switch to matriliny.

Furthermore, the results reported here show that once matriliny and matrilocality had been adopted by some Bantu societies, there was a second move from polygyny to monogamy among some of those populations. This second change may also have been driven by ecological factors, such as women's subsistence contribution or land scarcity. In other research it has been suggested that the degree of polygyny is positively correlated with women's contribution to subsistence (Low 1988), while monogamy emerges where land is scarce (Fortunato and Archetti 2010). Low levels of women's subsistence contribution and land scarcity, as suggested explanations for the adoption of monogamous marriage, will be investigated in Chapter 6.

From the earliest anthropological research, kinship terminology has been seen as an important determinant of whom marriage is sanctioned between within a society (for example Morgan 1964 [1877]). It is surprising therefore that the results reported here suggest that there is no correlated evolution between kinship terminology and marriage practice, or between kin terms and descent patterns, while there is between kin terms and residence pattern. Kinship terminology appears to be a reflection of the residence pattern rather than an indication of preferred marriage partners or linked to inheritance.

This gives further support to the suggestion that it is descent patterns that drive the marriage and kinship system with both residence and marriage changes following those in descent. Marriage, among the Bantu at least, is not subject to historical constraint. However, predominant monogamy only arises following a shift from the ancestral state of patriliny to the derived state of matriliny, but by no means among all matrilineal societies. If these results are applicable to other farming expansions across the globe they may provide a model for the changes that take place in marriage and kinship practice that have produced the current worldwide distribution.

The results reported here therefore suggest that from an ancestral monogamous and matrilocal state among hunter-gatherers (Destro-Bisol *et al.* 2004, Walker *et al.* 2011), polygyny, patriliny and patrilocality evolved among incipient farmers, perhaps more likely among pastoralists (Holden and Mace 2003). Then, if patriliny is associated with pastoralism (Holden and Mace 2003), the loss of cattle, due to tsetse fly infestation or some other cause, may have reduced the pressure for inheritance through the male line and enabled the emergence of matrilineal inheritance patterns instead, which in turn may have driven residence patterns to change to matrilocal. Matrilineal inheritance, through the female line, may have reduced the inequality of wealth among men such that, in some of these populations, monogamous marriage emerged as the predominant form. Further changes such as a reduction in the levels of female subsistence contribution (Low 1988), or a scarcity of agricultural land for some populations (Fortunato and Archetti 2010), may have been the reason for some matrilineal and matrilocal societies to adopt monogamous marriage. These possibilities will be investigated in Chapter 6.

Chapter 6 Marriage, Kinship, Ecology & Phylogeny

6.1 Abstract

Marriage and kinship co-evolved in Bantu societies as they expanded across sub-Saharan Africa, but it is not known whether descent or residence was the main driver for the emergence of monogamous marriage and if other cultural and ecological factors were also involved. Here, new methods from biology that weigh the contribution of factors in trait evolution are used to investigate the drivers of change in marriage and kinship practices across Bantu cultures. The results suggest that descent rules were driven by both phylogenetic and geographic proximity, indicating that history and cross-cultural influence may have been important. Residence patterns were driven by changes in descent rules, and also by cultural history, but not by proximity. Marriage practice was driven by residence patterns, but not by either history or proximity, although monogamy is associated with high temperature areas. These results suggest that for descent and residence cultural history is an important factor in trait change, but once matrilocality had evolved among the Bantu, monogamous marriage was influenced by factors independent of history and geography. The approach used here can determine the relative impact of history, proximity and environment on cultural change, and could be useful in other areas of cultural phylogenetics.

6.2 Introduction

Human Behavioural Ecology (HBE) seeks to measure the fitness outcomes of social behaviour. Drawing explicitly on the behavioural ecology approach of animal studies (Krebs and Davies 1997), it is proposed that in a changing environment humans will adapt their behaviour in order to maximise their fitness (Borgerhoff Mulder 1990), with HBE studies used to identify the drivers of adaptive behavioural change (Betzig 1997). Researchers, following an explicitly evolutionary approach, assembled and used cross-cultural databases such as HRAF (Murdock 1954), the Ethnographic Atlas (Murdock 1967), and the Standard Cross Cultural Sample (SCCS) (Murdock and White 1969) to study the impact of economic and social factors on human cultural institutions (Murdock 1949).

These comparative studies have been used to suggest that marriage patterns are associated with: cultural factors, such as inheritance and post-marital residence patterns, social factors, such as the size and complexity of societies, and ecological factors including environmental productivity, seasonality, and pathogen stress. Polygynous marriage, it has been argued, is associated with male-biased inheritance (Hartung 1976, Hartung 1982, Hartung 1997) because it pays men to pass wealth to their sons who can then use that wealth as bride price enabling them to secure more that one wife, increasing a father’s reproductive success. It is further argued that patrilocal residence patterns ensure that a man’s wives are mate-guarded by his kin such that he can retain multiple wives without suffering the costly burden, in reproductive terms, of raising other men's offspring (Low 2003, Low 2007).

A reduction in polygynous marriage is associated with an increase in the size of societies (Low 2003, Low 2007). Political leaders, faced with increasing numbers of men excluded from any possibility of acquiring a wife, as populations increase, may seek to reduce a potential source of instability in society by imposing monogamous marriage, thereby reducing the variation in male reproductive success. Harsh environments are also associated with monogamous marriage in the same way that monogamous mating is ecologically imposed in some bird species (Alexander *et al.* 1979). Males may be forced to abandon mating effort and switch to parental investment to ensure the survival of their offspring and therefore remain in a pair. The features of harsh environments associated with monogamous marriage in humans are low population density, low sociality and limited variation in the resources available to individuals within a group (Low 1990). While no association between marriage state and climate variables such as temperature and rainfall or the variation in either has been found, lower seasonality in rainfall is associated with a prevalence for monogamous marriage (Low 2003, Low 2007). Conversely, pathogen stress has been associated with increased rates of polygyny, particularly non-sororal polygyny (Low 1988, Low 1990). Indeed, it is argued that in areas of high pathogen stress monogamy is absent (Low 2003). It is not clear though, whether pathogen stress is a feature of high human density, environmental factors such as climate, or the causal factor itself.

However, these studies have been criticised because they take no account of the relatedness between societies, thereby increasing the chance of inflating correlations between traits (Mace and Pagel 1994). As well as phylogenetic relatedness, it may be that neighbouring cultures are more similar than would be expected by chance due to a shared environment or because a trait is passed between cultures. Disentangling these effects is important when testing hypotheses for change in cultural traits. Phylogenetic methods, widely used in evolutionary biology, have recently been incorporated into comparative studies of cultural traits to account for the relatedness between societies (Nunn 2011). These studies have largely confirmed the associations previously found, but for the first time have also been able to suggest causality. For example, Cowlishaw and Mace (1996) showed that across eight language families, polygyny was associated with male biased inheritance (patriliny), and changes in inheritance drove changes in marriage, such that a reduction in male biased inheritance led to a switch from polygynous to monogamous marriage. These results have also been shown to hold across Bantu societies (Chapter 5).

Furthermore, male wealth, in terms of cattle ownership, has been suggested as the driver of changes in descent from matriliny to patriliny (Holden and Mace 2003, Holden and Mace 2005). This confirmed the view that the adoption of pastoralism, especially in the form of cattle herding, led to the loss of matrilineal descent; ‘cattle are the enemy of matriliny, and the friend of patriliny’ (Aberle 1961 p. 680). Holden and Mace (2003, 2005) suggested that where there is a resource that benefits sons more than daughters, that resource is likely to be passed down the male line. In the case of cattle herding, cows can be used as a bride price payment to the parents of a prospective wife. In some pastoralist societies wealthy men can use cattle to secure more than one wife, leading some patrilineal societies to adopt polygynous marriage.

Subsistence patterns have also been suggested as a driver of post-marital residence, which, in turn, drives changes in the whole social structure (Murdock 1949). Across Austronesian societies, long male absence due to a reliance on deep-sea fishing subsistence practices are thought to lead to matrilocal residence, as wives choose to stay with their own relatives post-marriage (Fortunato and Jordan 2010).

These cultural phylogenetic studies, including those undertaken here (Chapter 5), have been useful in testing hypotheses for the drivers of change in marriage and kinship practices. However, co-evolutionary studies of this nature are restricted to analyses between two traits. While these Bayesian phylogenetic methods are powerful in detecting the timing of trait evolution and therefore proposing causality between cultural traits, in Chapter 5 it was not possible to distinguish between descent and residence as the driver of marriage change across Bantu societies. In addition, it has not been possible to include the effects of spatial proximity or ecological factors in the analysis that might also have impacted on the shift to monogamous marriage among the Bantu, or to weigh the relative impact of cultural, geographic and ecological factors on marriage and kinship practice.

However, new methods have recently been developed in evolutionary biology, that enable the inclusion of both a phylogeny and a geographical matrix into a general linear model approach (Freckleton and Jetz 2009). This allows for historical and spatial, as well as ecological effects on cultural traits to be studied. These methods have been used to assess the impact of phylogeny and geography on primate traits (Kamilar *et al.* 2012). Here these methods are used to assess the relative impact of cultural history, spatial proximity and ecology on the evolution of marriage, descent and residence as Bantu cultures expanded throughout sub-Saharan Africa. It has been established (Chapter 5) that these three cultural traits co-evolve and that for descent and residence the historical relatedness of Bantu populations is important. However, it is not clear whether descent or residence is more important in the switch to monogamous marriage and what other factors, such as the environment or geographical proximity, may have influenced change in marriage, descent and residence during the Bantu expansion.

6.3 Methods

6.3.1 Phylogeny

The Bantu phylogeny derived in Chapter 5 will be used here to investigate the drivers of change in descent, residence and marriage practices among Bantu societies.

6.3.2 Ecological Data

Data were collected on a range of ecological traits in order to test the proposed hypotheses for cultural change. Annual average temperature and rainfall, as well as biome data were used to test the impact of the environment, while human, cattle and goat density data were used to test the impact of population and farming practices. Tsetse fly have previously been found to impact both cattle and human populations in sub-Saharan Africa (Wint and Rogers 2000, Ehret 2002), and are thought to affect the distribution of cultural traits.

The geographic distribution of each Bantu language, as recorded in the Ethnologue (2009) and based on digitised language maps (Global Mapping International http://www.gmi.org), was used to extract language ranges. These language ranges were imported into *ArcGIS* (2011) to produce a vector layer of the language polygons. A grid (at 0.01 degree intervals) was laid over the Bantu language polygons and a centroid value extracted for each cell of the grid for the raster data layers detailed below. A weighted mean of the centroid values from each data set was estimated for each language polygon. These data were then used in the analyses described below.

6.3.2.1 Livestock

Livestock data for the number of cattle and goats per square kilometre were derived from satellite presence predictions of variables that have established statistical relationships with livestock data (Wint and Robinson 2007); a mean value of each livestock type for each language polygon was extracted using *ArcGIS* (2011).

6.3.2.2 Human Population

Human population estimates were extracted from the Gridded Population of the World, version 3 (Center for International Earth Science Information Network (CIESIN) and Centro Internacional de Agricultura Tropical (CIAT) 2005). These data are population densities in 2005, adjusted to match UN totals, in persons per square kilometer. Mean values were extracted for each language polygon.

6.3.2.3 Climate

Data for rainfall and temperature for Africa were taken from *WorldClim* (http://www.worldclim.org) (Hijmans *et al.* 2005). *WorldClim* provides climate data with a spatial resolution of 1 square kilometre, are interpolations of observed data from weather stations and representative of 1950 - 2000.

6.3.2.4 Biome

The predominant habitat for each language polygon was taken from Terrestrial Ecosystems of the World (WWF 2012). Habitat states: 1 (n = 53, tropical and subtropical moist broadleaf forest), 2 (n = 3, tropical and subtropical dry broadleaf forest), 7 (n = 34, tropical and subtropical grassland, savannah and shrub-land), and 10 (n = 1, montane grassland and shrub-land) occurred within Bantu populations.

6.3.2.5 Tsetse Fly

The tsetse fly is the primary vector of human and animal sleeping sickness (trypanosomiasis) (Ford 1963). Data on presence probability of tsetse fly based on satellite derived measures of vegetation cover, ground surface temperature, middle infra-red reflectance (a temperature measure less susceptible to atmospheric interference), vapour pressure deficit, and cold cloud duration (a measure of surface rainfall) (Wint and Rogers 2000) were used. The three major species groups of tsetse fly *Glossina fusca*, *G. palpalis* and *G. morsitans* are associated with forest, riverine and savannah areas respectively across sub-Saharan Africa (Wint and Rogers 2000). For PGLM analyses the tsetse fly density values were used. For the *Discrete* co-evolutionary analyses binary traits were produced for each tsetse fly group of presence or absence depending on whether the probability of presence was above or below 0.2. Below 0.2 is the lowest category reported by Wint and Rogers (2000) and is also suggested by the presence probability histogram of each tsetse fly group.

6.3.3 Ethnographic Atlas Data

Cultural data were taken from the Ethnographic Atlas, a database of cultural data covering 1,167 cultures worldwide compiled from the ethnographic literature (Murdock 1967, Gray 1999).

6.3.3.1 Descent

Variable 43 of the Ethnographic Atlas (Murdock 1967, Gray 1999), *descent: major type*, was used for descent patterns. Among Bantu speaking populations six states feature: 1. patrilineal, 2. duolateral, 3. matrilineal, 4. quasi-lineages, 5. ambilineal, and 6. mixed. For ancestral state reconstructions three states were used: patrilineal, matrilineal and bi-lateral (including states 2, 4, 5 and 6 above). Two binary variables were used in the co-evolution analyses: descent (patriliny) - patrilineal versus matrilineal or bi-lateral, and descent (matriliny) - matrilineal versus patrilineal or bi-lateral (following Holden and Mace 2003) to allow for a comparison with the results of Holden and Mace (2003, 2005).

6.3.3.2 Residence

Variable 11 of the Ethnographic Atlas (Murdock 1967, Gray 1999), *transfer of residence at marriage: after first years*, was used for residence patterns (following Jordan *et al.* 2009, Fortunato and Jordan 2010). This variable excludes a short stay after marriage by the husband in the wife's group to perform bride service, capturing the permanent move of one or both marriage partners to a new location. Among Bantu speaking populations three states feature: 1. wife to husband's group (patrilocal), 2. couple to either group or neolocal, 3. husband to wife's group (matrilocal). A binary variable was used in the co-evolution analyses: patrilocal versus matrilocal or bi/neolocal (following Jordan *et al.* 2009, Fortunato and Jordan 2010).

6.3.3.3 Marriage

Variable 9 of the Ethnographic Atlas (Murdock 1967, Gray 1999), *marriage composition*, has seven trait states, although only three feature among Bantu speaking peoples: 1. independent nuclear, occasional polygyny, 2. polygyny – preferentially sororal (sisters), co-wives in separate dwellings, 3. polygyny – non-sororal, co-wives in separate dwellings. State one is here referred to as monogamy. A binary variable was used: polygyny (both sororal and non-sororal) versus monogamy (independent nuclear, occasional polygyny) (following Pagel and Meade 2005).

6.3.3.4 Animal Husbandry

For the analysis of cattle herding variable 40, *predominant type of animal husbandry*, from the Ethnographic Atlas (Murdock 1967, Gray 1999) was used, where states: 1 (n = 8, absence or near absence of large domestic animals), 3 (n = 40, sheep and/or goats without larger domestic animals), and 7 (n = 39, Bovine animals) occur within Bantu populations. A binary trait ‘cattle herding’ was derived from the animal husbandry trait where state 0 is cattle herding (n = 39) and state 1 is no cattle herding (n = 48).

6.3.3.5 Subsistence Economy

For the analysis of type of farming, variable 42, *subsistence economy*, from the Ethnographic Atlas (Murdock 1967, Gray 1999) was used, where states: 2 (n = 3, fishing contributes most), 4 (n = 1, pastoralism contributes most), 6 (n = 65, extensive agriculture contributes most), 7 (n = 17, intensive agriculture contributes most), 8 (n = 1, two or more sources contribute equally), and 9 (n = 7, agriculture contributes most, type unknown) occur within Bantu populations.

6.3.3.6 Crop Type

For the analysis of crop type variable 29, *major crop type*, from the Ethnographic Atlas (Murdock 1967, Gray 1999) was used, where states: 1 (n = 1, none or none specified), 4 (n = 17, tree fruits), 5 (n = 25, roots or tubers), 6 (n = 45, cereal grains) occur within Bantu populations. A binary trait 'grain crop' was derived from the crop type trait where state 0 is non-grain (n = 43) and state 1 is grain (n = 45).

Figure 6.1. Bantu populations plotted on Google Earth based on latitude and longitude (variables 104 and 106, respectively, of the Ethnographic Atlas (Murdock 1967, Gray 1999)). Language name: yellow = monogamous marriage, black = polygynous marriage, white = not known. Location marker: blue = patriliny; red = matriliny/bilateral, white = not known; round = patrilocal, square = matrilocal, round without black dot = not known.

6.3.4 Analyses

Phylogenetic signal, root probabilities, ancestral states, evolutionary and co-evolutionary models, for discrete characters, were derived using procedures detailed in Chapter 2.

6.3.4.1 Co-evolution Including Continuous Characters

In order to test the hypotheses and infer the drivers of change for descent, residence and marriage among Bantu populations a model building approach was used. Where it is not known whether the full set of relevant independent variables have been selected, stepwise multiple regression can select a ‘best’ model that fits the data no better than other candidate models (Whittingham *et al.* 2006). Therefore, an information theoretic model selection approach, based on Akaike’s Information Criterion (AIC), was used, which selects the model that best fits the data among all candidate models regardless of the significance of the variables included in that model (Johnson and Omland 2004). Since there are a very large number of alternative models possible, the model selection approach ensures that a manageable number of variables are selected that best fit the data.

6.3.4.1.1 Model Building

The *stepAIC* procedure (Venables and Ripley 2002) in *R* (R Development Core R Development Core Team 2008) was used to perform stepwise model selection on the binary and continuous traits to find the best predictive model for each of the cultural traits by successively removing traits based on their AIC, an estimate of the expected Kullback-Leibler information lost by using the model (Johnson and Omland 2004). AIC combines a measure of lack of model fit, negative log likelihood, and a penalty for the number of model parameters, such that the model with the lowest AIC has the best relative fit (Whittingham *et al.* 2006). Currently the *stepAIC* procedure is not compatible with a phylogenetic approach; therefore a general linear model (glm) approach with a binomial distribution was used to perform the model selection.

6.3.4.1.2 PGLM

Once best-fit regression models were identified for each of the cultural traits, phylogenetic generalised linear model (pglm) analyses were run using the *CAIC* package (Purvis and Rambaut 1995) in *R* (R Development Core R Development Core Team 2008), which takes phylogeny into account. As well as the significance of the model (F statistic) the pglm reports the log likelihood for the model, the Aikaike Information Criterion (AIC) and the Lambda (λ) measure of phylogenetic signal. For binary dependent variables and a mixture of binary and continuous independent variables a binomial regression model would be optimal, however, implementation of this model is still under development (Nunn 2011). In the absence of this implementation a Gaussian model was used. The AIC value was used to compare the performance of the model with phylogeny included to that of the model without phylogeny included.

6.3.4.1.3 Phylogeny and Space

The third step was to run a pglm that also takes geography into account using the *SpatialFit* procedure (Freckleton and Jetz 2009) in *R* (R Development Core R Development Core Team 2008). This procedure enables both phylogenetic relatedness and spatial proximity to be accounted for in the model. As well as phylogenetic inertia in traits it may be that neighbouring cultures are more similar than would be expected by chance, due to sharing similar environments, or because a trait is transferred horizontally between neighbouring cultures. A variance-covariance matrix was produced from the latitude and longitude data for the Bantu populations from variables 104 and 106, respectively, of the Ethnographic Atlas (Murdock 1967, Gray 1999). This enabled the analysis to take account of autocorrelation in both the phylogenetic and geographic distribution of Bantu speaking cultures. The *SpatialFit* procedure estimates the λ value for the model as a measure of the impact of phylogeny as well Phi (ϕ), a measure of the impact of the geographic distribution of populations, and the impact of factors independent (ϒ) of both.

6.4 Results

6.4.1 Phylogenetic Signal

There is a strong phylogenetic signal in all the traits, with a λ value significantly different from of zero, except for marriage (Table 6.1). Indeed, animal husbandry, crop type, descent, and residence have a λ value not significantly different from one. This suggests that all the traits, apart from marriage, are more similar in closely related societies than would be expected by chance.

Table 6.1. Phylogenetic signal in discrete trait data on the Bantu language phylogeny. N, number of populations; λ_{max} lambda value from maximum likelihood analysis; LL_{max} log likelihood of λ_{max}; LL_0 log likelihood of λ_0; LL_1 log likelihood of λ_1; LLR_0 probability of log likelihood ratio of LL_0 and LL_{max}; LLR_1 probability of log likelihood ratio of LL_1 and LL_{max}.

Trait Data	**N**	**LLmax**	**λ_{max}**	**LL_0**	**LLR_0**	**LL_1**	**LLR_1**
Animal Husbandry	87	- 64.76	0.824	- 93.23	< 0.001	- 66.56	0.058
Crop Type	86	- 84.86	0.763	- 108.92	< 0.001	- 86.77	0.051
Subsistence Economy	94	- 96.46	0.736	- 106.55	< 0.001	- 98.45	0.046
Descent (from Chapter 5)	94	- 88.02	0.949	- 101.25	< 0.001	- 88.25	0.500
Residence (from Chapter 5)	92	- 66.58	1.000	- 83.56	<0.001	- 66.58	1.000
Marriage (from Chapter 5)	93	- 59.25	0.079	- 59.269	0.854	- 66.68	< 0.001

6.4.2 Ancestral State

The RJ MCMC analyses show a strong posterior probability that the ancestral state of the subsistence economy trait at the root of the phylogeny was pastoralism, but this trait does not differentiate between pastoralism based on sheep/goats or on cattle (Table 6.2).

The analyses for the animal husbandry trait show a strong posterior probability that cattle herding was the ancestral state, rather than sheep/goats (Table 6.2). Figure 6.2 shows that cattle herding was lost among the Bantu populations that moved south into the rainforest, but was retained among the populations that moved east.

Table 6.2. Mean probability of ancestral state for kinship and ecological traits at the root of the Bantu phylogeny from Bayesian RJ MCMC analyses.

Trait	**Log Likelihood**	**Ancestral State**	**Mean probability**	**S.E.**
Descent	- 87.33	Patriliny	0.90	0.002
Subsistence Economy	- 38.06	Pastoralism	0.79	0.022
Animal Husbandry	- 63.27	Cattle	0.75	0.007
Cattle Farming	- 38.92	Cattle	0.98	0.002
Crop Type	- 79.72	Roots/tubers	0.82	0.002

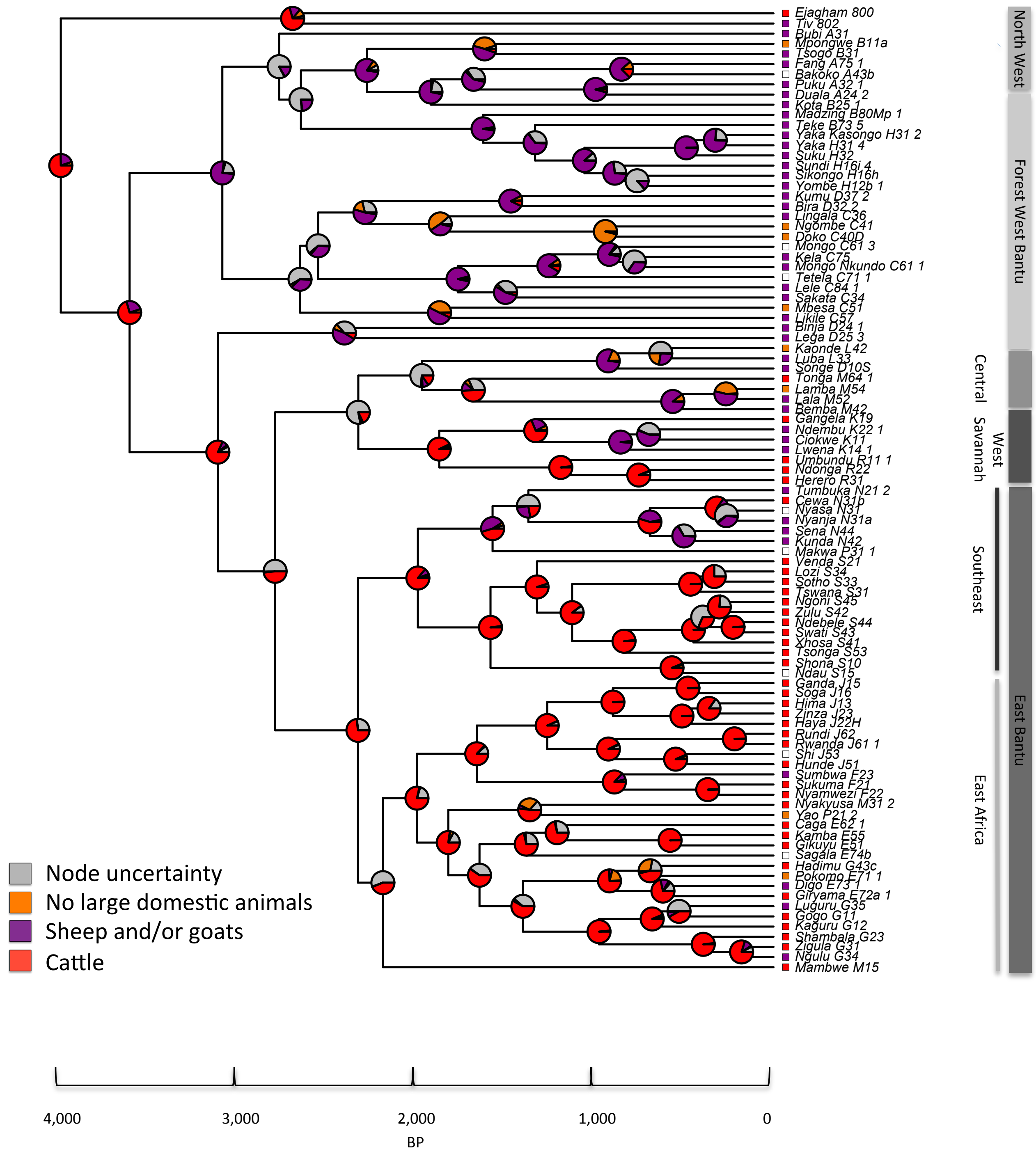

Figure 6.2. Plot of animal husbandry at ancestral nodes on the Bantu phylogeny. Pies show probability of state at ancestral nodes (grey shows the level of uncertainty for the node's presence in the tree). Squares show trait state at the tips (white = missing data).

The binary trait of cattle farming also shows very strong posterior probability of cattle at the root of the phylogeny (Table 6.2). Figure 6.3 shows a very similar pattern of change for the binary trait as for animal husbandry.

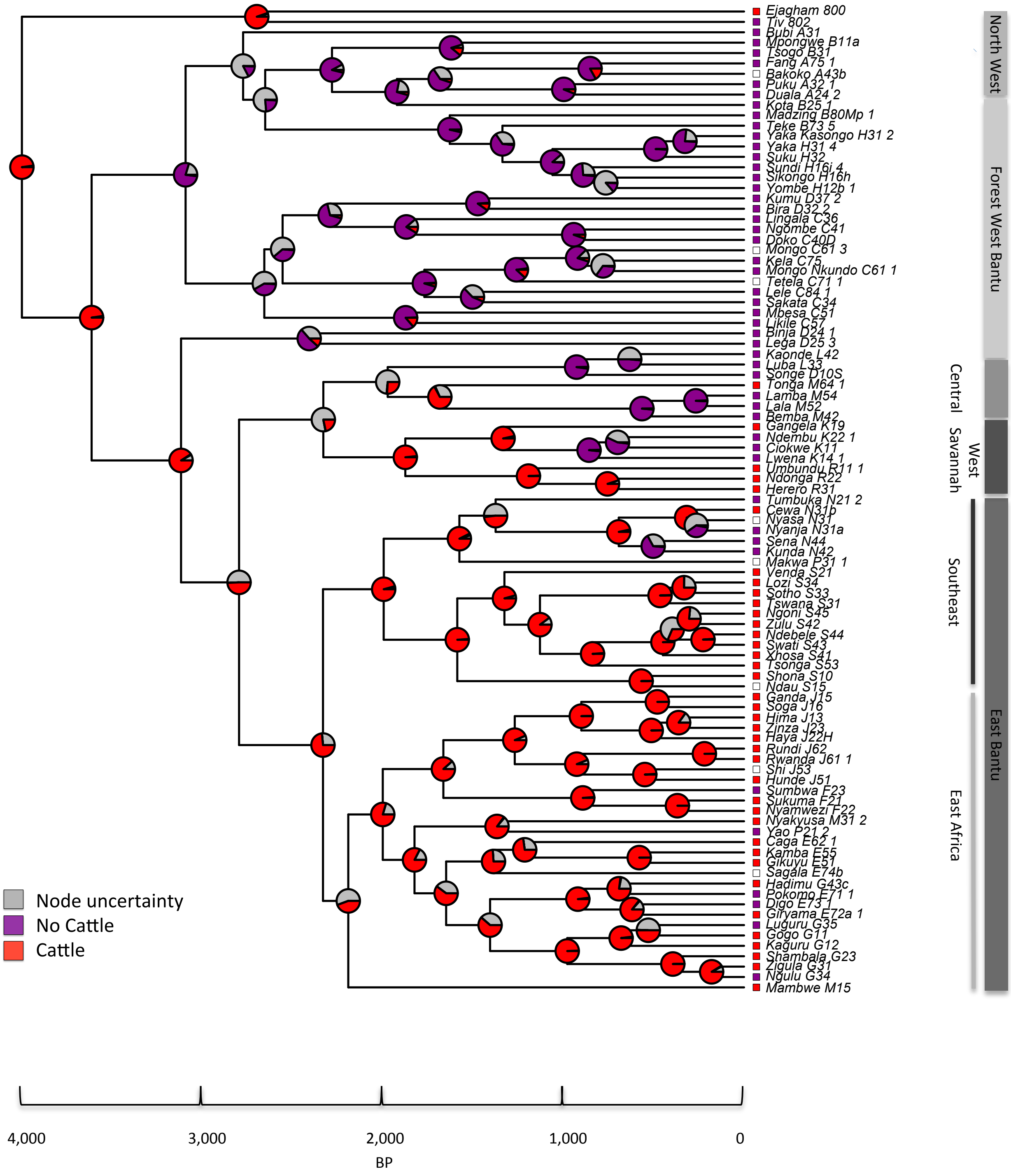

Figure 6.3. Plot of cattle farming at ancestral nodes on the Bantu phylogeny. Pies show probability of state at ancestral nodes (grey shows the level of uncertainty for the node's presence in the tree). Squares show trait state at the tips (white = missing data).

There was strong support for the farming of roots/tubers to be the ancestral state of the crop type trait at the root of the Bantu phylogeny (Table 6.2).

6.4.3 Co-evolution

Each of the tsetse fly groups transmits trypanosomiasis (sleeping sickness) to both cattle and human populations (Wint and Rogers 2000). There is decisive support for co-evolution between cattle farming and the presence of each of the tsetse fly groups (Table 6.3). However, Figure 6.4 suggests that it is only the *G. morsitans* tsetse fly group that causes cattle herding to be lost among Bantu societies. Cattle herders moved into areas with *G. morsitans* tsetse fly and then lost cattle, but did not lose cattle herding in areas without this tsetse fly group. Whereas, with the other two tsetse fly groups, cattle herding is as likely to be lost with or without tsetse fly presence. Since the *G. morsitans* tsetse fly group is associated with hot dry conditions, such as those on the savannah, it may have been the move into these savannah areas that is associated with the loss of cattle herding.

Table 6.3. Comparison of dependent and independent models shows co-evolution between traits. The Bayes Factor (BF) shows the weight of evidence to support the dependent model over the independent. Evidence for co-evolution: < 0.0 (none), 0 - 0.5 (insubstantial), 0.5 – 1.0 (substantial), 1.0 – 2.0 (strong), > 2.0 (decisive) (Kass and Raftery 1995). NB. * descent (patriliny) - patrilineal versus matrilineal or bi-lateral, + descent (matriliny) - matrilineal versus patrilineal or bi-lateral (to allow for a comparison with the results of Holden and Mace (2003, 2005)).

Co-evolution	**Dependent model**		**Independent model**		**Log10 Bayes Factor**
	Log likelihood	S.E.	Log likelihood	S.E.	
Cattle farming - Tsetse (*G.fusca*)	-74.27	0.03	-82.99	0.03	3.79
Cattle farming - Tsetse (*G. morsitans*)	-74.21	0.03	-85.84	0.03	5.05
Cattle farming - Tsetse (*G. palpalis*)	-70.17	0.04	-76.76	0.02	2.86
Descent (matriliny) - Cattle farming +	- 90.41	0.04	- 91.26	0.03	0.37
Descent (patriliny) - Cattle farming *	- 99.48	0.04	- 101.97	0.03	1.08
Descent - Crop type	- 107.61	0.03	- 111.10	0.02	1.52

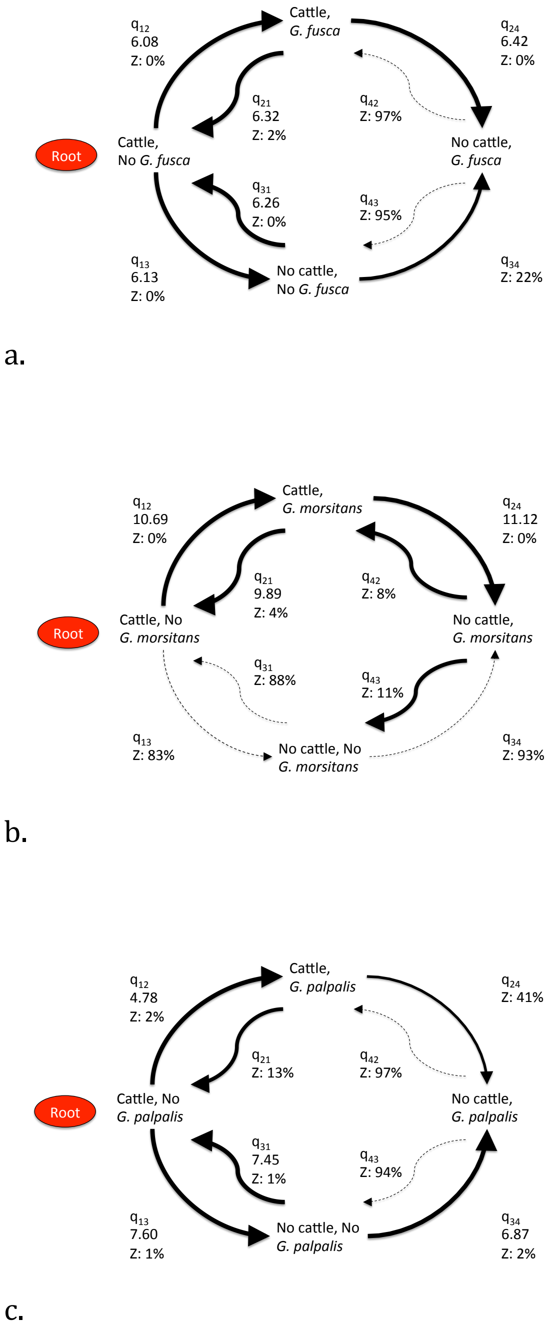

Figure 6.4. Co-evolution between tsetse fly group presence and cattle farming among Bantu populations: a. Cattle farming - Tsetse (*G.fusca*), b. Cattle farming - Tsetse (*G. morsitans*), c. Cattle farming - Tsetse (*G. palpalis*). Z denotes visits assigned to zero as a proportion of posterior probability distribution. Thickness of arrows reflects proportion of time transition rate is not assigned to zero. Dashed line denotes a zero rate in the RJ-derived model. Number below rate name (q_{ij}) is the mean transition rate where rate distribution is normal.

It has been argued that Bantu descent patterns were affected by the presence or absence of cattle farming (Holden and Mace 2003, Holden and Mace 2005). In order to make comparisons with the maximum likelihood analysis using a maximum parsimony Bantu phylogeny carried out by Holden and Mace (2003), co-evolution was tested for between descent (matriliny) and cattle herding. There was no substantial co-evolution between descent (matriliny) and cattle herding, with a Bayes Factor below 0.5 (Table 6.3). However, descent (patriliny) shows strong evidence of co-evolution with cattle farming.

Despite the low support for co-evolution between descent (matriliny) and cattle farming in the analysis reported here, there were some similarities between the model of evolution (Figure 6.5a) and the model suggested by Holden and Mace (2003). Cattle were gained in matriliny (q_{43}) but not in patriliny/bi-lateral descent (q_{21}), which was a zero rate in the RJ-derived model. However, matriliny was as likely to be gained in the presence of cattle (q_{13}) as in the absence of cattle (q_{24}) in the results reported here (Figure 6.5a), whereas Holden and Mace (2003) show a rate not significantly different from zero for the gain of matriliny in the presence of cattle.

The model of evolution between descent (patriliny) and cattle farming (Figure 6.5b) shows that there was neither a loss (q_{12}) nor a gain (q_{21}) of cattle within patriliny, which were zero rates in the RJ-derived model. Furthermore, matriliny/bi-lateral descent was more likely to be gained in the presence of cattle (q_{13}), which was never assigned to a zero rate, than in the absence of cattle (q_{24}), which was assigned a zero rate 27% of the time. While patriliny could be gained in the presence (q_{31}) or absence (q_{42}) of cattle the route to patriliny with cattle could only proceed via matriliny/bi-lateral descent with cattle (q_{31}). From patriliny with cattle at the root of the phylogeny matriliny/bi-lateral descent evolved first (q_{13}) followed by a loss of cattle (q_{34}). From this analysis it is suggested that changes in descent (route q_{13} & q_{34}) may drive the loss of cattle rather than the other way around (route q_{12} & q_{24}).

The model of co-evolution between descent and crop type (Figure 6.5c) among Bantu populations shows that the route from the ancestral state of patriliny and root/tuber cultivation to the derived state of matriliny/bi-lateral descent and grain cultivation is more likely to proceed via matriliny/bi-lateral descent and root cultivation (transitions q_{13} and q_{34}) than via patriliny and grain cultivation (transitions q_{12} and q_{24}). Descent changes before cultivation type, and therefore the loss of patriliny is not driven by changes in cultivation type.

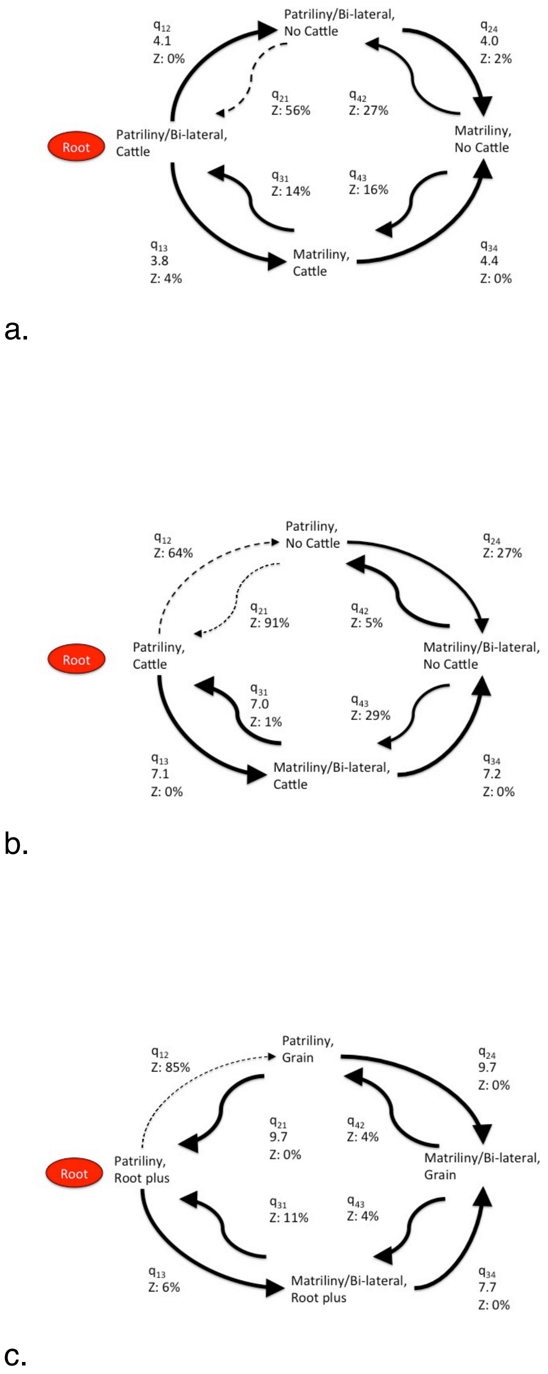

Figure 6.5. a. Co-evolution between descent (matriliny) and cattle farming among Bantu cultures, b. Co-evolution between descent (patriliny) and cattle farming among Bantu cultures, c. Co-evolution between descent (patriliny) and crop type among Bantu cultures. Z denotes visits assigned to a zero rate as a proportion of posterior probability distribution. Thickness of arrows reflects proportion of

time transition rate is not assigned to a zero rate. Dashed line denotes a zero rate in the RJ-derived model. Number below rate name (q_{ij}) is the mean transition rate where rate distribution is normal.

6.4.4 Phylogenetic and Spatial Effects

Since cattle farming and crop choice appear to follow the switch in descent pattern to matriliny, rather than precede it, further analyses were run including other cultural and ecological factors that may have an impact on descent, residence and marriage patterns among Bantu populations.

6.4.4.1 Descent

Chapter 5 has shown that among Bantu speaking cultures changes in descent patterns precede changes in both residence and marriage, therefore residence and marriage were not included in this analysis. A *stepAIC* procedure was used on the initial model (Equation 1), with traits being dropped sequentially, based on their AIC value (Table 6.4), to leave a final model with the best AIC value (Equation 2) suggesting that descent was influenced by a combination of goat density, and the presence of the Fusca and Morsitans tsetse fly groups.

Equation 1

Initial Model: Descent ≈ Biome + Temperature + Rainfall + Cattle + Human + Goats + Tsetse (*fusca*) + Tsetse (*palpalis*) + Tsetse (*morsitans*)

Table 6.4. StepAIC process for descent with variables removed sequentially. The AIC improves (lower value) at each step as a variable is removed from the model, with the improvement at each step reported.

Step	**AIC**	**Model improvement from Initial Model (AIC)**
Initial Model	123.54	-
- Rainfall	121.79	-1.75
- Biome	120.33	-3.21
- Cattle	118.94	-4.60
- Tsetse (palpalis)	118.64	-4.90
- Temperature	118.29	-5.25
- Human population density	117.64	-5.90

Equation 2

Final Model: Descent ≈ Tsetse (*morsitans*) - Goats - Tsetse (*fusca*)

Both goat density and the presence of the Fusca group of tsetse fly have a negative effect on the move from patrilineal to matrilineal descent, while the presence of the Morsitans tsetse fly group has a positive effect (Table 6.7). The AIC value of the final model of descent was improved by the inclusion of the phylogeny, and further improved by the inclusion of space. This is confirmed by the values for phylogeny ($\lambda = 0.528$) and space ($\phi = 0.416$) in the model with both parameters, suggesting that descent is influenced by both history and geography leaving very little influence to factors independent of those ($\Upsilon = 0.056$).

6.4.4.2 Residence

Chapter 5 has shown that among Bantu speaking cultures changes in residence patterns follow changes in descent but precede changes in marriage, therefore marriage was not included in this analysis. A *stepAIC* procedure was used on the initial model (Equation 3), with traits being dropped sequentially (Table 6.5) to leave the final model (Equation 4), suggesting that the move from patrilocal to matrilocal residence was influenced by a combination of descent, goat density, and the Morsitan tsetse fly group.

Equation 3

Initial Model: Residence ≈ Descent + Temperature + Rainfall + Cattle + Human + Goats + Tsetse(*fusca*) + Tsetse(*palpalis*) + Tsetse(*morsitans*) + Biome

Table 6.5. StepAIC process for residence with variables removed sequentially. The AIC improves (lower value) at each step as a variable is removed from the model, with the improvement at each step reported.

Step	**AIC**	**Model improvement from Initial Model (AIC)**
Initial Model	73.87	-
- Biome	71.87	-2.00
- Tsetse (palpalis)	70.12	-3.75
- Tsetse (fusca)	68.16	-5.71
- Cattle	67.25	-6.62
- Rainfall	66.23	-7.64
- Human population density	65.23	-8.64
- Temperature	64.35	-9.52

Equation 4

Final Model: Residence ≈ Descent + Tsetse (*morsitans*) - Goats

Both the change from patriliny to matrilineal descent and the presence of the Morsitans tsetse fly group had a positive effect on the move from patrilocal to matrilocal residence patterns among the Bantu, while goat density had a negative effect (Table 6.8). The inclusion of phylogeny improved the AIC value of the model but the inclusion of space had no effect. This is confirmed by the values for phylogeny ($\lambda = 0.71$) and space ($\phi = 0.00$), suggesting that there was an independent (Υ) effect on the move to matrilocal residence ($\Upsilon = 0.29$). The inclusion of descent in the final residence model supports the co-evolutionary analysis in Chapter 5.

6.4.4.3 Marriage

Chapter 5 has shown that among Bantu speaking culture changes in marriage patterns follow changes in both descent and residence, therefore both traits were included in this analysis. A *stepAIC* procedure was used on the initial model (Equation 5), with traits being sequentially dropped (Table 6.6) to leave the final model (Equation 6), suggesting that marriage was influenced by a combination of residence and average annual temperature.

Equation 5

Initial Model: Marriage ≈ Residence + Descent + Biome + Temperature + Rainfall + Cattle + Human + Goats + Tsetse (*fusca*) + Tsetse (*palpalis*) + Tsetse (*morsitans*)

Table 6.6. StepAIC process for marriage with variables removed sequentially. The AIC improves (lower value) at each step as a variable is removed from the model, with the improvement at each step reported.

Step	AIC	Model improvement from Initial Model (AIC)
Initial Model	62.57	-
- Tsetse (palpalis)	60.57	-2.00
- Tsetse (fusca)	58.57	-4.00
- Goats	56.60	-5.97
- Biome	54.77	-7.80
- Rainfall	53.82	-8.75
- Descent	53.64	-8.93
- Cattle	53.53	-9.04
- Tsetse (morsitans)	53.40	-9.17
- Human population density	53.31	-9.26

Equation 6

Final Model: Marriage ≈ Residence + Temperature

Both the change from patrilocal to matrilocal residence and higher average annual temperature had an influence on the switch from polygynous to monogamous marriage among Bantu societies (Table 6.9). Neither the inclusion of phylogeny nor geography improved the AIC value of the model. The inclusion of residence in the final marriage model, but not descent, suggests that co-evolution between marriage and descent seen in Chapter 5 was due to co-evolution between residence and the other two traits.

Table 6.7. General linear model (GLM), phylogenetic GLM (PGLM), and PGLM with spatial fit for descent final model. Composite parameters summarise the net relative impact of phylogeny, space and independent effects. The SpatialFit procedure estimates the λ value for the model as a measure of the impact of phylogeny as well Phi (ϕ), the impact of the geographic distribution of populations, and the impact of factors independent (Υ) of both (following Freckleton and Jetz 2009).

GLM														
			LogLh max	*AIC*	*Adj R2*	*df*	*Estimate*	*Std Err*	*F*	*t*	*p*			
Model			-57.88	126.85	0.11	86			4.53		0.005			
Goats							-0.009	0.004		-2.54	0.013			
Tsetse (*morsitans*)							0.330	0.199		1.66	0.101			
Tsetse (*fusca*)							-0.311	0.145		-2.15	0.034			
PGLM														
		λ	*LogLh max*	*AIC*	*Adj R2*	*df*	*Estimate*	*Std Err*	*F*	*t*	*p*			
Model		0.59	-50.65	112.39	0.13	86			5.25		0.002			
Goats							-0.005	0.004		-1.43	0.157			
Tsetse (*morsitans*)							0.523	0.212		2.47	0.016			
Tsetse (*fusca*)							-0.584	0.215		-2.72	0.008			
PGLM + Spatial Fit												***composite parameters***		
	ϕ	*λ*	*LogLh max*	*AIC*	*Adj R2*	*df*	*Estimate*	*Std Err*	*F*	*t*	*p*	*independent (ϒ)*	*phylogenetic (λ')*	*spatial (ϕ)*
Model	0.528	0.416	-49.33	109.76	0.05	86			2.55		0.061	0.056	0.416	0.528
Goats							-0.003	0.004		-0.70	0.485			
Tsetse (*morsitans*)							0.354	0.210		1.68	0.096			
Tsetse (*fusca*)							-0.394	0.195		-2.02	0.047			

Table 6.8. General Linear Model (GLM), Phylogenetic GLM (PGLM), and PGLM with spatial fit for Residence final model. Composite parameters summarise the net relative impact of phylogeny, space and independent effects. The SpatialFit procedure estimates the λ value for the model as a measure of the impact of phylogeny as well Phi (ϕ), the impact of the geographic distribution of populations, and the impact of factors independent (Υ) of both (following Freckleton and Jetz 2009).

GLM														
			LogLh max	*AIC*	*Adj R2*	*df*	*Estimate*	*Std Err*	*F*	*t*	*p*			
Model			-29.86	70.82	0.45	86			24.25		<0.001			
Descent							0.496	0.079		6.30	<0.001			
Tsetse (*morsitans*)							0.299	0.143		2.09	0.040			
Goats							-0.010	0.003		-3.56	0.001			
PGLM														
		λ	*LogLh max*	*AIC*	*Adj R2*	*df*	*Estimate*	*Std Err*	*F*	*t*	*p*			
Model		0.714	-26.75	64.60	0.33	86			15.24		<0.001			
Descent							0.401	0.080		5.03	<0.001			
Tsetse (*morsitans*)							0.196	0.167		1.18	0.242			
Goats							-0.009	0.003		-3.15	0.002			
PGLM + Spatial Fit												***composite parameters***		
	ϕ	*λ*	*LogLh max*	*AIC*	*Adj R2*	*df*	*Estimate*	*Std Err*	*F*	*t*	*p*	*independent (Υ)*	*phylogenetic (λ')*	*spatial (ϕ)*
Model	0.00	0.714	-26.75	64.60	0.33	86			15.24		<0.001	0.286	0.714	0
Descent							0.401	0.080		5.03	<0.001			
Tsetse (*morsitans*)							0.196	0.167		1.18	0.242			
Goats							-0.009	0.003		-3.15	0.002			

Table 6.9. General Linear Model (GLM), Phylogenetic GLM (PGLM), and PGLM with spatial fit for Marriage final model. Composite parameters summarise the net relative impact of phylogeny, space and independent effects. The SpatialFit procedure estimates the λ value for the model as a measure of the impact of phylogeny as well Phi (ϕ), the impact of the geographic distribution of populations, and the impact of factors independent (ϒ) of both (following Freckleton and Jetz 2009).

GLM														
			LogLh max	*AIC*	*Adj R2*	*df*	*Estimate*	*Std Err*	*F*	*t*	*p*			
Model			-16.18	40.41	0.15	86			8.31		0.001			
Residence							0.235	0.069		3.41	0.001			
Temperature							0.002	0.001		1.71	0.091			
PGLM														
		λ	*LogLh max*	*AIC*	*Adj R2*	*df*	*Estimate*	*Std Err*	*F*	*t*	*p*			
Model		0	-16.18	40.41	0.15	86			8.31		0.001			
Residence							0.235	0.069		3.41	0.001			
Temperature							0.002	0.001		1.71	0.091			
PGLM + Spatial Fit												***composite parameters***		
	ϕ	*λ*	*LogLh max*	*AIC*	*Adj R2*	*df*	*Estimate*	*Std Err*	*F*	*t*	*p*	*independent (ϒ)*	*phylogenetic (λ')*	*spatial (ϕ)*
Model	0	0	-16.18	40.41	0.15	86			8.31		0.001	1	0	0
Residence							0.235	0.069		3.41	0.001			
Temperature							0.002	0.001		1.71	0.091			

6.5 Discussion

Anthropologists have argued that residence patterns are fundamental to human social structures such that changes in residence drive changes in descent systems and other cultural traits (Murdock 1949, Levinson and Malone 1980). However, in Chapter 5 it was suggested, using phylogenetic analyses, that among Bantu societies, at least, descent patterns are fundamental; driving changes in both residence and marriage patterns. Bantu residence patterns also exert an effect on their marriage practices, but it was not clear whether it was residence or descent that directly drove changes in marriage. This Chapter has sought to establish the drivers of change for marriage, descent and residence among Bantu societies, examining history, geographic proximity and ecological traits in order to inform the debate about the ultimate causes of kinship changes across cultures.

Holden and Mace (2003) were the first to use phylogenetic techniques to address the causes of change in Bantu descent patterns. They used maximum likelihood methods and a maximum parsimony tree to suggest that the adoption of cattle herding among matrilineal Bantu societies had resulted in a switch to patrilineal descent (Holden and Mace 2003, Holden and Mace 2005). This was based on the premise that neither cattle herding nor either descent pattern was ancestral for the Bantu. Instead, in Chapter 5, it was suggested that patriliny was highly likely to be the descent pattern among the ancestral Bantu, and polygyny as the marriage pattern, with the analyses reported here further suggesting that cattle herding was also the ancestral Bantu state. This complex of polygyny, patriliny and cattle herding has also been reported for ancestral and contemporary populations elsewhere (Hartung 1976, Hartung 1982, Cowlishaw and Mace 1996).

Many researchers argue that rather than ancestral, cattle herding was adopted from their Cushitic neighbours in East Africa following the split in Bantu speaking societies about 3,000 years ago (Vansina 1990, Holden and Mace 2003, Hage and Marck 2011, Marck and Bostoen 2011). While it may not be possible for the RJ MCMC analyses reported here to distinguish between a borrowing event of this type and an ancestral root for cattle herding (Currie, Greenhill, and Mace 2010), the analyses incorporating geography do suggest that geographic proximity, which could facilitate borrowing, was important in the evolution of descent. On the other hand, Ehret (2002) argues that the ancestral Bantu population did herd cattle, although cattle herding might have been lost for those populations entering the forest due to the trypanosomiasis carried by tsetse fly found there. The analyses reported here suggest that it was the *G. morsitans* tsetse fly group, associated with savannah environments, that might have affected cattle herding among Bantu people, since the loss of cattle herding as a practice followed the move of populations to Morsitans tsetse fly group infected areas. Until other traits are identified that could be used to test for a borrowing event in East Africa, cattle herding among the ancestral Bantu remains a possibility.

Co-evolutionary analyses conducted here have shown that from a root of patrilineal descent and cattle herding, descent changed first to matriliny, followed by the loss of cattle herding. It was also shown that the switch from root crops to grain crops also followed the switch from patrilineal to matrilineal patterns of descent. Both of these analyses suggest that farming practices were not the cause of the change in descent patterns, but rather that the adoption of matrilineal descent facilitated the change in farming methods. The best-fit regression model for descent also suggests that cattle density was not a factor in the switch to matrilineal descent, supporting the co-evolutionary analyses. These two results question previous research suggesting that cattle herding was ‘the friend of patriliny’ (Aberle 1961 p. 680) and its loss may lead to a change in descent to matriliny. Instead, cattle herding practices may be influenced by the descent pattern within Bantu societies. This leaves the causes for the change in descent patterns, as well as residence and marriage patterns among Bantu societies, unclear.

If farming practices were not the cause but the result of changes in descent, it might be that other ecological factors predisposed Bantu populations to switch their descent and related cultural patterns. Using a range of ecological, livestock density, and human population data, multiple regression analyses were run on each of these cultural traits. The best prediction model for descent included only goats, and Morsitans and Fusca group tsetse fly density. The fit of this model was improved by the inclusion of the Bantu phylogeny, suggesting that although the causal factors for descent were ecological, cultural history also had an impact on the switch to matrilineal descent across cultures. The addition of the geographic variance-covariance matrix, which accounts for spatial autocorrelation across Bantu populations, improved the model fit further, but reduced the variance explained by the model. This may be accounted for by the three traits in the best-fit model for descent, namely the density of goats, Morsitans and Fusca group tsetse fly, which show a significant spatial element. This suggests that it was the move out of forested areas, inhabited by Fusca group tsetse fly, and into savannah areas, inhabited by Morsitans tsetse fly, that caused the shift to matrilineal descent. Once in savannah habitats, and following the shift to matriliny, the farming of cattle, goats and root crops may have given way to grain crops.

The shift to matrilineal descent preceded matrilocal residence among the Bantu according to the analyses in Chapter 5. Here it was shown that a drop in goat density and an increase in Morsitans group tsetse fly were also implicated in that shift. The fit of this model was improved by the inclusion of the Bantu phylogenetic matrix, although the addition of the spatial matrix had no impact on model fit. This suggests that as well as descent there were other features of cultural history that impacted on residence patterns. In addition, there were other factors independent of both phylogeny and geography that caused the move to matrilocality.

The co-evolutionary analyses in Chapter 5 could not distinguish between the impact of descent and residence on Bantu marriage patterns. This may have been because of the very strong co-evolution between those two traits themselves. Here it has been possible to suggest that it is residence that has the major role in the shift in Bantu marriage practice. Along with higher average annual temperatures, matrilocality is a causal factor for the shift from polygynous to monogamous marriage. High temperature on its own is unlikely to be a factor in the shift to monogamous marriage, instead it is likely to be a proxy for other underlying features associated hotter environments. Further analyses looking at factors that may be associated with hot environments may disentangle the underlying drivers of monogamous marriage. However, the addition of a phylogenetic or a spatial model had no impact on the best-fit model. This suggests that if there are other factors that influence Bantu cultures to practice monogamy they have neither an historical nor a spatial element.

The best-fit model for marriage suggests that human population density was not a causal factor for the switch to monogamous marriage as has been previously suggested (Low 2003, Low 2007). It may be that current population densities are not the right variable to use here, but since marriage has no phylogenetic signal it would seem to be a relevant measure. It may be that the binary marriage variable is concealing changes in marriage practice that are more subtle, such as a gradual reduction in the extent of polygyny. A continuous variable, the percentage of marriages that are polygynous, would be ideal, but this type of data is not currently available. Pathogen stress, as suggested by tsetse fly borne trypanosomes, which may be implicated in the emergence of matrilineal descent and matrilocal residence, was also not a causal factor for the switch to monogamous marriage among matrilocal Bantu societies. This suggests that previous studies (Low 1988, Low 1990), which found such an association may have missed the mediating role of cultural change that accompanied the ecological drivers, or else, other pathogens than trypanosomes should be included in future analyses.

The results reported here suggest a possible scenario for the emergence of monogamous marriage from a predominantly polygynous culture as practiced in early Bantu society. First, polygynous, patrilineal and patrilocal Bantu-speaking people expanded into the equatorial rainforest south of their ancestral homeland in the Benue Valley in eastern Nigeria (de Filippo *et al.* 2012). Later, as populations emerged from those forested habitats there was a shift to matrilineal descent systems driven by the pressure of savannah tsetse fly, which led to an abandonment of cattle and root crop farming in favour of grain farming and a reduced reliance on goats. The change in descent led to a switch to matrilocality, which in turn led to a reduction in polygynous marriage and a shift to monogamous marriage among the Bantu cultures that remained near the equator, where savannah temperatures were highest.

These results suggest that descent among the Bantu is influenced by historical relatedness and geographic proximity, as well as ecological factors. Residence, on the other hand, is driven by descent, historical relatedness and ecology, with spatial proximity not affecting post-marital residence patterns. Marriage is not influenced by either the historical relatedness of cultures or their proximity, but rather by residence changes and ecology. That different cultural traits seem to be influenced by different factors suggests that the approaches used here can be invaluable in distinguishing between the various drivers of cultural change. Such knowledge may be useful to anthropological researchers, who could take this information into account when deciding on their approach to the study of cultural change among Bantu, and potentially other, societies.

Chapter 7 Discussion

7.1 Introduction

The inferences that can be made, about the evolution of social behaviour and the selective forces that contribute to social change, using the fossil record are limited (Nelson and Shultz 2010, Nelson *et al.* 2011, Shultz, Nelson, and Dunbar 2012). Therefore, since Darwin's time (Darwin 1968 [1859], Darwin 2004 [1871]), the comparative method has been used to investigate the evolution of social systems (Nunn 2011), yielding significant insights into how sociality has evolved (Janson 2000, Clutton-Brock and Janson 2012). However, it has also been long recognised that ignoring the relatedness between species can inflate correlation between traits. Because species may be similar because of a shared history, rather than independent evolution, the comparative approach is vulnerable to false positives (Galton 1889, Darwin 1968 [1859], Harvey and Pagel 1991, Mace and Pagel 1994). Corrections for non-independence of data, which account for the relatedness between species, are widely used across anthropology through the incorporation of phylogenies into comparative analyses. Nevertheless, the full potential of the phylogenetic approach has often been over-looked (Nunn 2011). Phylogenetic comparative methods enable inferences to be made about the ancestral states of a trait, as well as the most likely model of how that trait evolved through time (Pagel 1999a, Pagel, Meade, and Barker 2004). Furthermore, evolutionary hypotheses, both in humans and non-human animals, can be tested by detecting correlated evolution between traits as well as identifying the timing of trait evolution in order to propose causality (Pagel and Meade 2006).

In this thesis, a Bayesian phylogenetic comparative approach was used to investigate the evolution of primate social and mating systems (Chapter 3 & 4) and the evolution of residence, descent, and marriage systems in humans, using Bantu-speaking cultures as a model (Chapter 5 & 6). Hypotheses for the drivers of evolutionary change in important aspects of primate and human social systems were also evaluated using this approach. In this final chapter I will discuss the broader implications of these findings for socioecological theory, and our understanding of infanticide, human evolution and cultural evolution.

7.2 Socioecology

While primatologists have incorporated phylogenies into comparative analyses as a control for the relatedness between species, they have shown a reluctance to investigate the impact of phylogeny on the evolution of primate social systems (Nunn 2011). This is despite the inconsistencies in the socioecological model highlighted by a number of researchers (Janson 2000, Clutton-Brock and Janson 2012), significant enough that some believe the model should be abandoned altogether (Thierry 2008). However, the use of phylogenies has helped to explain some of these problems of model fit (Di Fiore and Rendall 1994, Rendall and Di Fiore 2007), as well as to test some of the central hypotheses of the model successfully (Sillen-Tullberg and Møller 1993, Pagel 1994b, Pagel and Meade 2006, Nunn 2011).

The results reported in this thesis (and see Shultz, Opie, and Atkinson 2011, Opie, Atkinson, and Shultz 2012) have been a further contribution to understanding the role of phylogenetic history in the evolution of primate sociality. One of the consequences of socioecology's focus on the social behaviour of extant primates, without looking at their phylogenetic history, has been to give the impression that the social systems of primates are highly flexible in response to changes in the environment (Wrangham 1980, Sterck, Watts, and van Schaik 1997). Chapter 3 showed that instead of being flexible, three fundamental primate social traits are in fact highly constrained by phylogenetic inertia: social organisation, dispersal patterns and mating systems. This suggests that rather than primates being able to adopt social behaviour that suits the environment that they occupy, they may instead occupy habitats that are suited to the social behaviour that they have inherited. These results support suggestions that the socioecological model requires a fundamental realignment, such that both historical and environmental influences are included as key factors determining social systems (Di Fiore and Rendall 1994, Janson 2000, Thierry 2008). Testing for phylogenetic inertia in other social traits, such as social structure, and relations within groups, will build up a picture of which primate traits are flexible to short-term environmental change, and which are not.

The strong phylogenetic signal for social traits investigated here has made it possible to use the recently developed Bayesian phylogenetic methods to establish, for the first time, the evolutionary history of primate sociality. The results reported in this thesis (Chapter 3) have shown the ancestral states and evolutionary models for three fundamental social traits: social organisation, dispersal patterns, and mating systems, and provide the first steps in building a comprehensive picture of how primate sociality evolved. From a solitary social state with polygynandrous mating and bi-sexual dispersal patterns in the ancestral primate, multi-male/multi-female sociality evolved early in haplorhine primates, while uni-male systems and pair living evolved much later. Harem polygyny evolved with uni-male sociality and monogamy with pair living in haplorhines, but mating systems changed in many strepsirrhine species while they remained solitary foragers. Bi-sexual dispersal patterns persisted across most of the primate phylogeny, changing to sex-based dispersal late in primate evolution. This result supports those who have argued that old world monkeys, with male-biased dispersal, should not be viewed as typical primates (Di Fiore and Rendall 1994, Strier 1994).

Furthermore, the strong phylogenetic signal in the social traits reported here might also have implications for primate conservation efforts. A few primate taxa are flexible between their social organisation state depending on ecological factors, such as the Callitrichids and some Lemur species, while other taxa appear to have social systems that are well suited to a wide variety of environments, such as the

Cercopithecines. But most primate taxa, with strong phylogenetic inertia in their social behaviour, do not change their social systems to deal with short-term environmental change. Many primate species are already highly endangered by habitat loss (Chapman and Peres 2001), but it is not just a question of whether primates can adjust to the new food sources which are available (Isabirye-Basuta and Lwanga 2008), and the changing predation threat, but also whether their social behaviour is suited to their new or changing environment, that will ultimately determine their survival. Conservation efforts, based on the view that primates can adapt flexibly to environmental change, may fail; more effort should be focused on preserving existing primate habitats.

The phylogenetic comparative methods used here also enabled a number of hypotheses about the evolution of sociality to be tested. No evidence was found for the central idea of Wrangham's socioecological model (Wrangham 1980), that social organisation co-evolved with, and was driven by, dispersal (Chapter 3) (and see Shultz, Opie, and Atkinson 2011). A next step could be to investigate primate social structure, i.e. the nature of relationships between members of a group (Kappeler and van Schaik 2002). In particular, it would be useful to test the hypothesis that primate dispersal patterns determine the relations between females in a group (Clutton-Brock and Lukas 2012). Dispersal patterns have long been seen as crucial determinants of primate (Sterck, Watts, and van Schaik 1997), and animal (Nowak, Tarnita, and Wilson 2010) social systems, but it is not clear which aspects of sociality are affected by or affect them.

While social organisation did not co-evolve with dispersal patterns in primates, social organisation was found to co-evolve with activity pattern, with sociality emerging from solitary living following the switch to diurnal living, about 52 million years ago in anthropoids (Shultz, Opie, and Atkinson 2011). It is suggested that groups then formed in order to protect individuals against the increased predation threat posed by daylight foraging (van Schaik 1983). It is, however, not known why primates switched to a diurnal activity pattern in the first place. An intriguing possibility is that diurnal living in primates may have evolved following the appearance of fruiting angiosperms, so that some primates switched to being diurnal to make use of the new food sources of leaves, fruit and especially figs (Fleming and John Kress 2011), best gathered in daylight, and may be linked to the evolution of trichromatic colour vision that enables discrimination between red and green (Dominy and Lucas 2001).

7.3 Infanticide

One of the most intractable problems for primatology to explain is the emergence of monogamy across all primate clades. Researchers have variously suggested that monogamy arose in primates because of female ranging patterns, concealed oestrous signals, paternal care and infanticide (Kleiman 1977, Alexander 1979, Turke 1984, van Schaik and Dunbar 1990, Komers and Brotherton 1997, van Schaik and Kappeler 2003), but no consensus has been achieved. The results reported here (Chapter 4), show that, while female ranging patterns, oestrous signal and paternal care co-evolved with primate mating systems, it was the presence of infanticide that drove the evolution of monogamy across primates. Given the strength of this result and the increase in infanticide risk as relative lactation length increased across anthropoid evolution, infanticide may also be implicated in the emergence of the other derived primate mating system, harem polygyny. A phylogenetic analysis could infer the drivers of the evolution of harem polygyny in primates and test whether infanticide was also the cause of this mating system. Furthermore, it has been proposed that the mating systems of other taxa, such as equids, carnivores, and sciurognath rodents, may also be shaped by infanticide risk (van Schaik 2000b). A phylogenetic analysis of the drivers of mating system change in these taxa could determine whether infanticide has a major impact on mating systems across mammalian species, as in primates, or whether other factors are implicated, such as female space use (Komers and Brotherton 1997, Brotherton and Komers 2003).

From the results reported here, it appears that the weaning ratio was held at or near to one in prosimian primates, indicating that infanticide risk was kept at bay throughout their evolution. Among anthropoids, on the other hand, there was a run-away increase in infanticide risk as relative lactation periods increased. The results of Chapters 3 and 4 taken together, suggest that among anthropoid primates, following the switch to diurnal living, predation encouraged the formation of multi-male/multi-female groups (van Schaik 1983). Large groups required larger brains to deal with the increased complexity of group social relations (Dunbar 1995c), which resulted in infants being born altricial, and requiring longer lactation periods to grow large brains (Ross and MacLarnon 2000). Longer relative lactation periods resulted in increased infanticide risk. Given the large impact that infanticide can have on reproductive success, accounting for between 34% and 64% of all infant deaths (Watts 1989, Sommer 1994) in some species, it can be expected that female anthropoids would have developed a number of counter strategies (van Schaik, van Noordwijk, and Nunn 1999).

The first approach taken by females was to confuse paternity, by mating promiscuously, it is suggested (Hrdy 1979), such that all males that had mated with an oestrous female would have some prospect of being the father of the subsequent offspring and therefore had a stake in its survival (van Schaik 2000b). It has been suggested that conspicuous oestrous swellings (Pagel 1994b, Pagel and Meade 2006) and female mating calls (van Schaik 2000b) were adaptations that evolved to enable a female to advertise her fertile period, encouraging multiple males to mate with her, as a way of confusing paternity and reducing infanticide risk. Furthermore, it has been proposed that concealed ovulation may also have evolved to confuse oestrous signals and therefore paternity (Hrdy 1979, Sillen-Tullberg and Møller 1993). The results reported here confirm that concealed ovulation evolved in polygynandrous species following the emergence of infanticide, but before the switch to monogamous mating (Chapter 4).

An alternative approach for dealing with the increased infanticide risk faced by anthropoid females was for a female to look to a male to protect her infants from other infanticidal males (van Schaik 2000b). This suggestion is supported by the results presented in this thesis (Chapter 4), showing that monogamy only evolved in species with infanticide. Furthermore, in anthropoids, the switch to harem polygyny appears to have occurred after the evolution of male infanticide (Chapter 4) and is associated with concealed or slight signs of ovulation rather than conspicuous sexual swellings (Pagel and Meade 2006). The protection strategy, where a female develops a bond with a single male, mating exclusively or predominantly with him, results in high degrees of paternity certainty. However, this means that the male needs to stay close to the female long-term to protect their infants from all other males, who would be sure that the infants were not their offspring. The protection strategy appears to be successful among those species that switched to monogamy, since it has been shown that monogamy without infanticide is a stable state (Chapter 4). Furthermore, monogamy is associated with a reduction in relative lactation periods, which lowered infanticide risk. Shorter lactation may possibly be due to the input of paternal care such as infant carrying, or simply due to male vigilance allowing the female to feed uninterrupted, as has been shown in some monogamous ungulates (Dunbar and Dunbar 1974). Why some species switched from the ancestral mating state of polygynandry to harem polygyny rather than monogamy requires further investigation. However, whether monogamy or polygyny, the drawback of the protection strategy, which ensures high levels of paternity certainty, is that infants are vulnerable following the death or displacement of the male. It has been shown that infants are vulnerable to attack from an incoming male, following the displacement or death of the male, in species where paternity certainty is high, such as langurs (Sommer 1994), gibbons (Borries, Savini, and Koenig 2010), gorillas (Harcourt and Greenberg 2001) and humans (Daly, Wilson, and Weghorst 1982).

7.4 Human Evolution

The results reported in this thesis suggest that infanticide is a crucial factor in the evolution of mating systems across the primate order. This raises the possibility that infanticide may also have had an important effect on mating systems during human evolution. Apes have the longest relative lactation periods of any primate, due to the requirements of growing very large brains, meaning that ape infants face extreme levels of infanticide risk. Ape mating systems may be a response to this considerable threat to reproductive success. Since orangutans, gorillas and humans have opted for a protection strategy (van Schaik 2000b), it might be expected that the ancestral great ape may also have had a mating system based on this strategy, with *Pan* changing to a paternity confusion strategy. This supposition could be tested with future phylogenetic analyses. Thus, it might be that hominins would have also persisted with the protection strategy, leading to the uni-male systems of harem polygyny or monogamy, as seen in humans today. This would be consistent with a recent study of the second-to-fourth digit ratio (2D:4D), which is a biomarker for prenatal androgen effects. In this study it was shown that 2D:4D covaries with intra-sexual competition and mating systems across haplorhines (Nelson *et al.* 2011). The ratio for hominin species, within the range of extant gibbons, humans and gorillas, suggest that they were either monogamous or polygynous.

Indeed, the marriage system of early modern human hunter-gatherers has been reconstructed as monogamous with occasional polygyny (Walker *et al.* 2011). Additionally, mitochondrial and autosomal genetic markers have been used to infer matrilocal residence patterns as the ancestral pattern for African hunter-gatherers (Destro-Bisol *et al.* 2003, Destro-Bisol *et al.* 2004, Destro-Bisol 2005), and these residence patterns are associated with monogamy (Burton *et al.* 1996). The infanticide risk faced by modern humans has changed from the risk faced by the ancestral African great ape. On the one hand, allocare in humans has reduced both weaning times and inter-birth intervals (Opie and Power 2008), while on the other, investing fathers require paternity certainty before heavy provisioning of infants from weaning to adolescence (Daly, Wilson, and Weghorst 1982), leaving humans with high levels of infanticide risk. The marriage practices of modern day human populations, either monogamy or polygyny, are consistent with a protection strategy, such that children may be 40 times more likely to be physically abused in households including a stepparent, following the departure of a natural parent (Daly and Wilson 1985).

7.5 Cultural Evolution

The emergence of farming has been associated with a switch from monogamous to polygynous marriage, especially among pastoralists (Hartung 1982). Here it has been shown that, in early Bantu-speaking farming cultures (~ 4,000 years B.P.), polygyny was closely associated with patrilineal inheritance and patrilocal residence (Chapter 5). But where cultural and environmental factors led to a switch from patrilineal to matrilineal inheritance, societies subsequently changed to matrilocal residence, and then some switched to monogamy (Chapter 6). To test whether this switch to monogamy, following changes to matriliny and matrilocality, are applicable more widely, it would be useful to do similar analyses on societies from other language families. For example, some work has already been done with Indo-European cultures (Pagel and Meade 2005, Fortunato 2011b, Fortunato 2011c), but the results suggest that the ancestral state of marriage among these agricultural-based societies was monogamous, associated with patriliny and patrilocality. It may be that the spread of Christianity in the last two millennia has masked the earlier signal, or that the Bantu and Indo-European marriage and kinship trajectories are different. Further analysis, particularly investigating the potential co-evolution between marriage practice and the spread of Christianity, might help to resolve this question, as well as the association between monogamy and patriliny in industrial societies. Coevolution has also been tested between residence and descent among Austronesian societies, with residence suggested as the driver of inheritance rules (Fortunato and Jordan 2010). Further analyses using data on the marriage systems in Austronesia could be used to test whether the Bantu or Indo-European pattern is more widely applicable. As more language trees become available the approach taken in this thesis can be extended and evolutionary analyses of marriage and kinship undertaken across more language families so that results can be compared.

The results in this thesis (Chapters 5 & 6) have further contributed to a body of work in cultural phylogenetics that is tackling important questions in cultural history that are beyond the scope of traditional approaches (Richerson 2012). While change in marriage practice is driven by changes in residence, in the Bantu, there was no association found between marriage and kinship terms. This is surprising since kinship terminology indicates suitable marriage partners across many cultures (Allen 2008). However, the co-evolution of residence and kinship found here (Chapter 5) may suggest a more complex system, whereby residence drives both marriage and kinship terms, while there is no direct association between them. Chapter 6 suggested that descent among the Bantu was not driven by subsistence patterns, but instead drove them. This result concurs with some previous research (Low 1990), but conflicts with others (Fortunato and Jordan 2010), suggesting that further work is needed to unravel the way history and environment can interact in driving cultural change. Furthermore, tsetse fly distribution was used here as an example of pathogen stress, suggested to influence marriage systems (Low 1988), a result that was supported here. Other pathogens could be included in further research to examine the interaction with culture and assess the impact that pathogen reduction programmes may have on future cultural change.

Across anthropology, the increased use of cultural phylogenetics has been one of the main factors leading to a revival in the study of kinship (Allen *et al.* 2008), which had previously been abandoned by many anthropologists (Parkin 1997). As outlined in Chapter 1, many questions in cultural evolution have been investigated using phylogenetic methods (Gray and Atkinson 2003, Holden and Mace 2003, Pagel and Meade 2005, Fortunato, Holden, and Mace 2006, Jordan *et al.* 2009, Fortunato and Jordan 2010, Walker *et al.* 2011, Bouckaert *et al.* 2012), including those reported here. Since it is the evolving nature of human culture (Darwin 2004 [1871]) that separates humans from other animals (Pagel 2012a), it has been argued that the same phylogenetic tools, used for biological evolutionary studies, can also be used for the study of cultural history (Mace and Pagel 1994).

However, this view, that culture can be studied using a similar approach to the study of biological evolution, has led to some controversy within anthropology (Mesoudi, Whiten, and Laland 2006, Ingold 2007, Mesoudi 2011). Indeed, there has been reluctance among anthropologists, sociologists and historians, those who have led the study of cultural history during the twentieth century, to embrace the view that culture evolves in a Darwinian sense (Richerson 2012). However, the continued success of phylogenetics to answer some fundamental questions of cultural evolution may begin to persuade researchers of the value of this approach. The questions about cultural change that can be studied using an ethnographic approach within an individual culture (Parkin 2009) are of a different nature to those that can be studied by cross-cultural analysis. Furthermore, by assessing the phylogenetic signal in cultural data, decisions can be taken on the most appropriate approach for the analysis of specific traits. The phylogeographic tools, recently developed (Freckleton and Jetz 2009, Bouckaert *et al.* 2012), allow for the contribution of history, geography and environmental drivers of cultural change to be identified and analysed (Chapter 6). This means it is possible to partial out the effects of different factors involved in driving cultural change. For example, here (Chapter 6) it was shown that changes in marriage patterns across Bantu populations were not driven by historical inertia or spatial proximity, and therefore, more work needs to be done to identify ecological drivers without an historical or geographic element that may be implicated in the change to monogamy. On the other hand, changes in inheritance patterns were strongly influenced by both historical inertia and spatial proximity with ecological factors independent of phylogeny and geography playing little part. Future research into specific cultural traits can use such information to identify the data that is required to test hypotheses about cultural change. For example, among Indo-European speakers, as well as some other language families, the spread of religion may play a vital role in influencing changes in marriage and kinship practice. The role of historical and spatial inertia on different aspects of religion may determine the choice of traits to analyse.

7.6 Summary

This thesis has demonstrated the use of phylogenetic comparative methods in the study of the social systems of human and non-human primates. The results show that primate societies, like human kinship systems, are strongly influenced by history, not responding to short-term changes in the environment (Chapter 3 & 5). However, while primate mating systems also show phylogenetic inertia human marriage does not, suggesting that moves between polygyny and monogamy in humans can take place in response to short-term cultural or ecological change. Chapter 3 detailed the evolutionary history of primate social organisation, dispersal patterns and mating systems, and showed that social organisation did not co-evolve with dispersal patterns. In Chapter 4 an analysis of the causes of monogamy in primates, including humans, concluded that while paternal care and discrete female ranging co-evolved with mating systems, infanticide was the driver of monogamy. Chapter 5 used Bantu societies to study the history of marriage and kinship systems suggesting that it was descent that drove residence and marriage patterns. The finer grained analyses in Chapter 6 were able to look in more detail at the drivers of change suggesting that changes in descent patterns were the result of both historical and spatial processes, while changes in residence, due to descent and other historical change, drove the emergence of monogamy as Bantu-speaking cultures expanded across sub-Saharan Africa. The phylogenetic analyses, such as those undertaken in this thesis, provide for a richer understanding of the way sociality evolves than has been hitherto possible. This approach enables the identification of the drivers of social change that may have far reaching implications for the understanding of past and future social trends.

Bibliography

2011. "ArcGIS Desktop," 10 edition. Redlands, CA: Environmental Systems Research Institute.

Aberle, D. F. 1961. "Matrilineal descent in cross-cultural comparison," in *Matrilineal Kinship*. Edited by D. Schneider and K. Gough, pp. 655–730. Berkeley: University of California Press.

Alberts, S. C., and J. Altmann. 1995. Balancing costs and opportunities: dispersal in male baboons. *American Naturalist* 145:279-306.

Alexander, R. D. 1974. The evolution of social behavior. *Annual Review of Ecology and Systematics* 5:325-383.

Alexander, R. D. 1979. "Sexuality and sociality in humans and other primates," in *Human Sexuality*. Edited by A. Katchadourian, pp. 81-97. Berkeley: University of California Press.

Alexander, R. D., J. L. Hoogland, R. D. Howard, K. M. Noonan, and P. W. Sherman. 1979. "Sexual dimorphisms and breeding systems in pinnipeds, ungulates, primates and humans," in *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective*. Edited by N. A. Chagnon and W.Irons, pp. 402-435. North Scituate, Mass.: Duxbury Press.

Allen, N. J. 2008. "Tetradic theory and the origin of human kinship systems," in *Early Human Kinship: From Sex to Social Reproduction*. Edited by N. J. Allen, H. Callan, R. I. M. Dunbar, and W. James, pp. 96-112. Oxford: Blackwells.

Allen, N. J. 2012. "personal communication."

Allen, N. J., H. Callan, R. I. M. Dunbar, and W. James. Editors. 2008. *Early Human Kinship: From Sex to Social Reproduction*. Oxford: Blackwell.

Arnold, C., L. J. Matthews, and C. L. Nunn. 2010. The 10k trees website: a new online resource for primate phylogeny. *Evolutionary Anthropology* 19:114-118.

Atkinson, Q., G. Nicholls, D. Welch, and R. Gray. 2005. From words to dates: water into wine, mathemagic or phylogenetic inference? *Transactions of the Philological Society* 103:193-219.

Atkinson, Q. D., A. Meade, C. Venditti, S. J. Greenhill, and M. D. Pagel. 2008. Languages evolve in punctuational bursts. *Science* 319:588.

Atz, J. W. 1970. "The application of the idea of homology to behavior," in *Development and the Evolution of Behavior*. Edited by L. R. Aronson, E. Tobach, D. S. Lehrman, and J. S. Rosenblatt, pp. 53-74. San Francisco, California: Freeman.

Barkow, J. H., L. Cosmides, and J. Tooby. 1992. *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*. Oxford: Oxford University Press.

Barrett, L., R. I. M. Dunbar, and J. E. Lycett. 2002. *Human Evolutionary Psychology*. Basingstoke: Palgrave.

Bastin, Y., A. Coupez, and M. Mann. 1999. Continuity and divergence in the Bantu languages: perspectives from a lexicostatistic study. *Annales, Sciences humaines* 162:315–317.

Bateman, A. J. 1948. Intrasexual selection in drosophila. *Heredity* 2:349-368.

Bayon, G., B. Dennielou, J. Etoubleau, E. Ponzevera, S. Toucanne, and S. Bermell. 2012. Intensifying weathering and land use in Iron Age central Africa. *Science* 335:1219-1222.

Bettridge, C., J. Lehmann, and R. I. M. Dunbar. 2010. Trade-offs between time, predation risk and life history, and their implications for biogeography: A systems modelling approach with a primate case study. *Ecological Modelling* 221:777-790.

Betzig, L. 1997. *Human Nature: A Critical Reader*. Oxford: Oxford University Press.

Blomberg, S. P., T. Garland, and A. R. Ives. 2003. Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. *Evolution* 57:717-745.

Blurton Jones, N. G., L. C. Smith, J. F. O'Connell, K. Hawkes, and C. L. Kamuzora. 1992. Demography of the Hadza, an increasing and high density population of savanna foragers. *American Journal of Physical Anthropology* 89:159-181.

Boas, F. 1932. The aims of anthropological research. *Science* 76:605-613.

Boas, F. 1938 [1911]. *The Mind of Primitive Man*. New York: Macmillan.

Borgerhoff Mulder, M. 1990. Kipsigis women's preferences for wealthy men: evidence for female choice in mammals? *Behavioral Ecology and Sociobiology* 27:255-264.

Borgerhoff Mulder, M. 2001. Using phylogenetically based comparative methods in anthropology: More questions than answers. *Evolutionary Anthropology* 10:99-111.

Borries, C., K. Launhardt, C. Epplen, J. Î. T. Epplen, and P. Winkler. 1999. DNA analyses support the hypothesis that infanticide is adaptive in langur monkeys. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 266:901-904.

Borries, C., T. Savini, and A. Koenig. 2010. Social monogamy and the threat of infanticide in larger mammals. *Behavioral Ecology and Sociobiology*:1-9.

Bouckaert, R., P. Lemey, M. Dunn, S. J. Greenhill, A. V. Alekseyenko, A. J. Drummond, R. D. Gray, M. A. Suchard, and Q. D. Atkinson. 2012. Mapping the origins and expansion of the Indo-European language family. *Science* 337:957-960.

Boyd, R., and P. Richerson. 1985. *Culture and the Evolutionary Process*. Chicago: Chicago University Press.

Brotherton, P. N. M., and P. E. Komers. 2003. "Mate guarding and the evolution of social monogamy in mammals," in *Monogamy: Mating Strategies and Partnerships in Birds, Humans and Other Mammals*. Edited by U. H. Reichard and C. Boesch, pp. 42-58. Cambridge: Cambridge University Press.

Brotherton, P. N. M., and M. B. Manser. 1997. Female dispersion and the evolution of monogamy in the dik-dik. *Animal Behaviour* 54:1413-1424.

Burton, M. L., C. C. Moore, J. W. M. Whiting, A. K. Romney, D. F. Aberle, J. A. Barcelo, M. M. Dow, J. I. Guyer, D. B. Kronenfeld, J. E. Levy, and J. Linnekin. 1996. Regions based on social structure. *Current Anthropology* 37:87-123.

Buss, D. M. 1994. *The Evolution of Desire: Strategies of Human Mating*. New York: Basic Books.

Buss, D. M., and D. P. Schmitt. 1993. Sexual strategies theory: an evolutionary perspective on human mating. *Psychological Review* 100:204-232.

Byrne, R. W., and A. Whiten. 1988. *Machiavellian Intelligence: Social Expertise and The Evolution of Intelligence in Monkeys, Apes and Humans*. Oxford, UK: Oxford University Press.

Campbell, C. J., A. Fuentes, K. C. MacKinnon, M. Panger, and S. K. Bearder. 2007. *Primates in Perspective*. Oxford: Oxford University Press.

Carpenter, C. R. 1934. *A Field Study of the Behavior and Social Relations of Howling Monkeys*. Baltimore: Johns Hopkins Press.

Cavalli-Sforza, L. L., and M. W. Feldman. 1981. *Cultural Transmission and Evolution: A Quantitative Approach*. Princeton: Princeton University Press.

Cavalli-Sforza, L. L., P. Menozzi, and A. Piazza. 1994. *The History and Geography of Human Genes*. Princeton: Princeton University Press.

Center for International Earth Science Information Network (CIESIN), and Centro Internacional de Agricultura Tropical (CIAT). 2005. "Gridded Population of the World, Version 3 (GPWv3)." Edited by C. U. Socioeconomic Data and Applications Center (SEDAC). New York: Palisades.

Chagnon, N. A., and W. Irons. Editors. 1979. *Evolutionary Biology and Human Social Behavior*. North Scituate, MA: Duxbury Press.

Chalmers, N. R. 1968. The social behaviour of free living mangabeys in Uganda. *Folia Primatologica* 8:263-281.

Chapman, C. A., and C. A. Peres. 2001. Primate conservation in the new millennium: The role of scientists. *Evolutionary Anthropology* 10:16-33.

Chapman, C. A., and J. M. Rothman. 2009. Within-species differences in primate social structure: evolution of plasticity and phylogenetic constraints. *Primates* 50:12-22.

Charnov, E. L., and D. Berrigan. 1993. Why do female primates have such long lifespans and so few babies? *or* life in the slow lane. *Evolutionary Anthropology* 1:191-194.

Clutton-Brock, T., and P. Harvey. 1976. "Evolutionary rules and primate societies," in *Growing Points in Ethology*. Edited by P. P. G. Bateson and R. A. Hinde, pp. 195-237. Cambridge: Cambridge University Press.

Clutton-Brock, T., and C. Janson. 2012. Primate socioecology at the crossroads: past, present, and future. *Evolutionary Anthropology* 21:136-150.

Clutton-Brock, T. H., and P. H. Harvey. 1977. Primate ecology and social organization. *Journal of Zoology* 183:1-39.

Clutton-Brock, T. H., and D. Lukas. 2012. The evolution of social philopatry and dispersal in female mammals. *Molecular Ecology* 21:472-492.

Cohas, A., and D. Allaine. 2009. Social structure influences extra-pair paternity in socially monogamous mammals. *Biology Letters* 5:313-316.

Cornwallis, C. K., S. A. West, K. E. Davis, and A. S. Griffin. 2010. Promiscuity and the evolutionary transition to complex societies. *Nature* 466:969-U91.

Cowlishaw, G. 1997. Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. *Animal Behaviour* 53:667-686.

Cowlishaw, G., and R. Mace. 1996. Cross-cultural patterns of marriage and inheritance: a phylogenetic approach. *Ethology and Sociobiology* 17:87-97.

Crook, J., and J. Gartlan. 1966. Evolution of primate societies. *Nature* 210:1200-1203.

Currie, T. E., S. J. Greenhill, R. D. Gray, T. Hasegawa, and R. Mace. 2010. Rise and fall of political complexity in island South-East Asia and the Pacific. *Nature* 467:801-804.

Currie, T. E., S. J. Greenhill, and R. Mace. 2010. Is horizontal transmission really a problem for phylogenetic comparative methods? A simulation study using continuous cultural traits. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:3903-3912.

Curry, O., and R. I. M. Dunbar. 2011. Altruism in networks: the effect of connections. *Biology Letters* 7:651-653.

Dalerum, F. 2007. Phylogenetic reconstruction of carnivore social organizations. *Journal of Zoology* 273:90-97.

Daly, M., and M. Wilson. 1985. Child abuse and other risks of not living with both parents. *Ethology and Sociobiology* 6:197-210.

Daly, M., M. Wilson, and S. J. Weghorst. 1982. Male sexual jealousy. *Ethology and Sociobiology* 3:11-27.

Darwin, C. 1968 [1859]. *The Origin of Species by Means of Natural Selection*. London: Penguin Books.

Darwin, C. 2004 [1871]. *The Descent of Man, and Selection in Relation to Sex*. London: Penguin Books.

Dawkins, R. 1976. *The Selfish Gene*. Oxford: Oxford University Press.

Denham, W. W. 1971. Energy relations and some basic properties of primate social organization. *American Anthropologist* 73:77-95.

Destro-Bisol, G. 2005. Genetic variation and social structure: a case-study from Africa. *Human Evolution* 20:93-98.

Destro-Bisol, G., Coia V, Donati F, Battaggia C, Spedini G, Arredi B, Caglia A, Capelli C, and T.-S. C. 2003. Evidence of differential evolution of male and female lineages in African hunter-gatherers and food producers. *American Journal of Physical Anthropology suppl.* 36:88.

Destro-Bisol, G., F. Donati, V. Coia, I. Boschi, F. Verginelli, A. Caglia, S. Tofanelli, G. Spedini, and C. Capelli. 2004. Variation of female and male lineages in sub-Saharan populations: the importance of sociocultural factors. *Mol Biol Evol* 21:1673-1682.

DeVore, I., and S. L. Washburn. 1963. "Baboon ecology and human evolution," in *African Ecology and Human Evolution*. Edited by F. Howell and F. Bourliere, pp. 335-367. Chicago: Aldine.

Di Fiore, A., and D. Rendall. 1994. Evolution of social organization: a reappraisal for primates by using phylogenetic methods. *Proceedings of the National Academy of Sciences of the United States of America* 91:9941-9945.

Diamond, J., and P. Bellwood. 2003. Farmers and their languages: the first expansions. *Science* 300:597-603.

Divale, W. 1974. Migration, external warfare and matrilocal residence. *Behavior Science Research* 9:75-133.

Divale, W. 1984. *Matrilocal Residence in Pre-literate Societies*. Ann Arbor, MI: UMI Research Press.

Dixson, A. F. 1998. *Primate Sexuality: Comparative Studies of the Prosimians, Monkeys, Apes, and Human Beings*. Oxford: Oxford University Press.

Dominy, N. J., and P. W. Lucas. 2001. Ecological importance of trichromatic vision to primates. *Nature* 410:363-366.

Drummond, A., and A. Rambaut. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology* 7:214.

Dunbar, R. I. M. 1988. *Primate Social Systems*. London: Chapman & Hall.

Dunbar, R. I. M. 1992. Time: a hidden constraint on the behavioural ecology of baboons. *Behavioral Ecology and Sociobiology* 31:35-49.

Dunbar, R. I. M. 1995a. The mating system of callitrichid primates: I. conditions for the coevolution of pair bonding and twinning. *Animal Behaviour* 50:1057-1070.

Dunbar, R. I. M. 1995b. The mating system of callitrichid primates: II. the impact of helpers. *Animal Behaviour* 50:1071-1089.

Dunbar, R. I. M. 1995c. Neocortex size and group size in primates: a test of the hypothesis. *Journal of Human Evolution* 28:287-296.

Dunbar, R. I. M. 2000. "Male mating strategies: a modeling approach," in *Primate Males: Causes and Consequences of Variation in Group Composition*. Edited by P. M. Kappeler, pp. 259-268. Cambridge: Cambridge University Press.

Dunbar, R. I. M., and E. P. Dunbar. 1974. Social organization and ecology of the klipspringer (*Oreotragus oreotragus*) in Ethiopia. *Zeitschrift für Tierpsychologie* 35:481-93.

Ehret, C. 1998. *An African Classical Age: Eastern and Southern Africa in World History, 1000 B.C. to A.D. 400*. Charlottesville: University Press of Virginia.

Ehret, C. 2002. "The Civilizations of Africa: a History to 1800," pp. 480. Charlottesville: University Press of Virginia.

Emlen, S. T., and L. W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215-223.

Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist* 125:1-15.

de Filippo, C., K. Bostoen, M. Stoneking, and B. Pakendorf. 2012. Bringing together linguistic and genetic evidence to test the Bantu expansion. *Proceedings of the Royal Society B: Biological Sciences* 279:3256-3263.

Fleming, T. H., and W. John Kress. 2011. A brief history of fruits and frugivores. *Acta Oecologica* 37:521-530.

Ford, J. 1963. The distribution of the vectors of African pathogenic trypanosomes. *Bulletin of the World Health Organization* 28:653.

Fortunato, L. 2011a. Reconstructing the history of marriage and residence strategies in Indo-European speaking societies. *Human Biology* 83:129-135.

Fortunato, L. 2011b. Reconstructing the history of marriage strategies in Indo-European speaking societies: monogamy and polygyny. *Human Biology* 83:87-105.

Fortunato, L. 2011c. Reconstructing the history of residence strategies in Indo-European speaking societies: neo-, uxori-, and virilocality. *Human Biology* 83:107-128.

Fortunato, L., and M. Archetti. 2010. Evolution of monogamous marriage by maximization of inclusive fitness. *Journal of Evolutionary Biology* 23:149-156.

Fortunato, L., C. Holden, and R. Mace. 2006. From bridewealth to dowry? A Bayesian estimation of ancestral states of marriage transfers in Indo-European groups. *Human Nature* 17:355-376.

Fortunato, L., and F. Jordan. 2010. Your place or mine? A phylogenetic comparative analysis of marital residence in Indo-European and Austronesian societies. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:3913-3922.

Freckleton, R. P., P. H. Harvey, and M. D. Pagel. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. *American Naturalist* 160:712-726.

Freckleton, R. P., and W. Jetz. 2009. Space versus phylogeny: disentangling phylogenetic and spatial signals in comparative data. *Proceedings of the Royal Society B: Biological Sciences* 276:21-30.

Galton, F. 1889. *Natural Inheritance*. London: Macmillan.

Garcia-Pena, G. E., G. H. Thomas, J. D. Reynolds, and T. Szekely. 2009. Breeding systems, climate, and the evolution of migration in shorebirds. *Behavioral ecology* 20:1026-1033.

Ghiglieri, M. P. 1987. Sociobiology of the great apes and the hominid ancestor. *Journal of Human Evolution* 16:319-357.

Gittleman, J., C. Anderson, M. Kot, and H. Luh. 1996. "Comparative tests of evolutionary lability and rates using molecular phylogenies," in *New Uses for New Phylogenies*. Edited by P. Harvey, A. L. Brown, J. M. Smith, and S. Nee, pp. 289–307. Oxford: Oxford University Press.

Gordon, H. O. 1969. On the evolution of mating systems in birds and mammals. *American Naturalist* 103:589-603.

Goss-Custard, J. D., R. I. M. Dunbar, and F. P. G. Aldrich-Blake. 1972. Survival, mating and rearing strategies in the evolution of primate social structure. *Folia Primatologica* 17:1-19.

Gray, J. P. 1999. A corrected ethnographic atlas. *World Cultures* 10:24-136.

Gray, R. D., and Q. D. Atkinson. 2003. Language-tree divergence times support the Anatolian theory of Indo-European origin. *Nature* 426:435-439.

Gray, R. D., A. J. Drummond, and S. J. Greenhill. 2009. Language phylogenies reveal expansion pulses and pauses in Pacific settlement. *Science* 323:479-483.

Gray, R. D., and F. M. Jordan. 2000. Language trees support the express-train sequence of Austronesian expansion. *Nature* 405:1052-1055.

Greenberg, J. H. 1963. *The Languages of Africa*. Bloomington: Indiana University Press.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28:1140-1162.

Guthrie, M. 1967-1971. *Comparative Bantu: an introduction to the comparative linguistics and prehistory of the Bantu languages*. Vol. 1-4. Farnborough, UK: Gregg International.

Hage, P., and J. Marck. 2002. Proto-Micronesian kin terms, descent groups, and interisland voyaging. *Oceanic Linguistics* 41:159-170.

Hage, P., and J. Marck. 2003. Matrilineality and the Melanesian origin of Polynesian Y chromosomes. *Current Anthropology* 44:121-127.

Hage, P., and J. Marck. 2011. "Proto-Bantu descent groups," in *Kinship, Language, and Prehistory: Per Hage and the Renaissance in Kinship Studies*. Edited by D. Jones and M. Bojka, pp. 75-78. Salt Lake City: The University of Utah Press.

Hamilton, W. D. 1964a. The genetical evolution of social behaviour. I. *Journal of Theoretical Biology* 7:1-16.

Hamilton, W. D. 1964b. The genetical evolution of social behaviour. II. *Journal of Theoretical Biology* 7:17-52.

Hammer, M. F., T. M. Karafet, A. J. Redd, H. Jarjanazi, S. Santachiara-Benerecetti, H. Soodyall, and S. L. Zegura. 2001. Hierarchical patterns of global human Y-Chromosome diversity. *Mol Biol Evol* 18:1189-1203.

Harcourt, A. H., and J. Greenberg. 2001. Do gorilla females join males to avoid infanticide? A quantitative model. *Animal Behaviour* 62:905-915.

Harcourt, A. H., P. H. Harvey, S. Larson, and R. Short. 1981. Testis weight, body weight and breeding system in primates. *Nature* 293:55-57.

Harcourt, A. H., A. Purvis, and L. Liles. 1995. Sperm competition: mating system, not breeding season, affects testes size of primates. *Functional Ecology* 9:468-476.

Harmon, L. J., J. T. Weir, C. D. Brock, R. E. Glor, and W. Challenger. 2008. GEIGER: investigating evolutionary radiations. *Bioinformatics* 24:129-131.

Hartung, J. 1976. Natural selection and inheritance of wealth. *Current Anthropology* 17:607-622.

Hartung, J. 1982. Polygyny and inheritance of wealth. *Current Anthropology* 23:1-11.

Hartung, J. 1997. "If I had it to do over," in *Human Nature*. Edited by L. Betzig, pp. 344 - 348. New York: Oxford University Press.

Harvey, P., and S. Nee. 1997. "The phylogenetic foundations of behavioural ecology," in *Behavioral Ecology: an evolutionary approach*, 4th edition. Edited by J. Krebs and N. Davies, pp. 334-349. Oxford: Blackwell Science.

Harvey, P. H., and M. D. Pagel. 1991. *The Comparative Method in Evolutionary Biology*. Oxford: Oxford University Press.

Hawkes, K. 2003. Grandmothers and the evolution of human longevity. *American Journal of Human Biology* 15:380-400.

Hawkes, K., J. F. O'Connell, N. G. B. Jones, H. Alvarez, and E. L. Charnov. 1998. Grandmothering, menopause, and the evolution of human life histories. *Proceedings of the National Academy of Sciences of the United States of America* 95:1336-1339.

Henrich, J., R. Boyd, and P. Richerson. 2008. Five misunderstandings about cultural evolution. *Human Nature* 19:119-137.

Henrich, J., R. Boyd, and P. J. Richerson. 2012. The puzzle of monogamous marriage. *Philosophical Transactions of the Royal Society of London. Series B, Biological sciences* 367:657-69.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25:1965-1978.

Hill, K. R., R. S. Walker, M. Bozicevic, J. Eder, T. Headland, B. Hewlett, A. M. Hurtado, F. Marlowe, P. Wiessner, and B. Wood. 2011. Co-residence patterns in hunter-gatherer societies show unique human social structure. *Science* 331:1286-1289.

Holden, C., and R. Mace. 1997. Phylogenetic analysis of the evolution of lactose digestion in adults. *Human Biology* 69:605-628.

Holden, C., and R. Mace. 2003. Spread of cattle led to the loss of matrilineal descent in Africa: a coevolutionary analysis. *Proceedings of the Royal Society of London Series B-Biological Sciences* 270:2425-2433.

Holden, C., and R. Mace. 2005. "'The cow is the enemy of matriliny': using phylogenetic methods to investigate cultural evolution in Africa," in *The Evolution of Cultural Diversity: a Phylogenetic Approach*. Edited by R. Mace, C. Holden, and S. Shennan, pp. 217 – 234. Walnut Creek, CA: Left Coast Press.

Holden, C. J. 2002. Bantu language trees reflect the spread of farming across sub-Saharan Africa: a maximum-parsimony analysis. *Proceedings of the Royal Society B-Biological Sciences* 269:793-799.

Holden, C. J., A. Meade, and M. Pagel. 2005. "Comparison of maximum parsimony and Bayesian Bantu language trees," in *The Evolution of Cultural Diversity: a Phylogenetic Approach*. Edited by R. Mace, C. Holden, and S. Shennan, pp. 53-65. Walnut Creek, CA: Left Coast Press.

Howell, N. 2000. *Demography of the Dobe! Kung*. New York: Aldine De Gruyter.

Hrdy, S. B. 1977. *The Langurs of Abu: female and male strategies of reproduction*. Cambridge, MA: Harvard University Press.

Hrdy, S. B. 1979. Infanticide among animals: A review, classification, and examination of the implications for the reproductive strategies of females. *Ethology and Sociobiology* 1:13-40.

Hrdy, S. B. 1981. *The Woman That Never Evolved*. Cambridge, MA: Harvard University Press.

Hrdy, S. B., C. Janson, and C. Van Schaik. 1994. Infanticide: let's not throw out the baby with the bath water. *Evolutionary Anthropology* 3:151-154.

Huelsenbeck, J. P., F. Ronquist, R. Nielsen, and J. P. Bollback. 2001. Bayesian inference of phylogeny and its impact on evolutionary biology. *Science* 294:2310-2314.

Huxley, J. 1942. *Evolution: The Modern Synthesis*. London: Allen & Unwin.

Ingold, T. 2007. The trouble with 'evolutionary biology'. *Anthropology Today* 23:13-17.

Isabirye-Basuta, G., and J. Lwanga. 2008. Primate populations and their interactions with changing habitats. *International Journal of Primatology* 29:35-48.

Isbell, L. A., and D. van Vuren. 1996. Differential costs of locational and social dispersal and their consequences for female group-living primates. *Behaviour* 133:1-36.

Isbell, L. A., and T. P. Young. 2002. Ecological models of female social relationships in primates: similarities, disparities, and some directions for future clarity. *Behaviour* 139:177-202.

Janson, C., and C. van Schaik. 2000. "The behavioral ecology of infanticide," in *Infanticide by Males and its Implications*. Edited by C. van Schaik and C. Janson. Cambridge: Cambridge University Press.

Janson, C. H. 2000. Primate socio-ecology: the end of a golden age. *Evolutionary Anthropology* 9:73-86.

Johnson, J. B., and K. S. Omland. 2004. Model selection in ecology and evolution. *Trends in Ecology & Evolution* 19:101-108.

Jolly, A. 1966. Lemur social behavior and primate intelligence - step from prosimian to monkey intelligence probably took place in a social context. *Science* 153:501-508.

Jordan, F. M., R. D. Gray, S. J. Greenhill, and R. Mace. 2009. Matrilocal residence is ancestral in Austronesian societies. *Proceedings of the Royal Society B-Biological Sciences*.

Kamilar, J. M., and J. L. Marshack. 2012. Does geography or ecology best explain ‘cultural’ variation among chimpanzee communities? *Journal of Human Evolution* 62:256-260.

Kamilar, J. M., K. M. Muldoon, S. M. Lehman, and J. P. Herrera. 2012. Testing Bergmann's rule and the resource seasonality hypothesis in Malagasy primates using GIS-based climate data. *American Journal of Physical Anthropology* 147:401-408.

Kanazawa, S., and M. C. Still. 1999. Why monogamy? *Social Forces* 78:25-50.

Kappeler, P. M. 1998. Nests, tree holes, and the evolution of primate life histories. *American Journal of Primatology* 46:7-33.

Kappeler, P. M., and C. P. van Schaik. 2002. Evolution of primate social systems. *International Journal of Primatology* 23:707-740.

Kass, R. E., and A. E. Raftery. 1995. Bayes factors. *Journal of the American Statistical Association* 90:773-795.

Kitchen, A., C. Ehret, S. Assefa, and C. J. Mulligan. 2009. Bayesian phylogenetic analysis of Semitic languages identifies an Early Bronze Age origin of Semitic in the Near East. *Proceedings of the Royal Society B-Biological Sciences* 276:2703-2710.

Kleiman, D. G. 1977. Monogamy in mammals. *The Quarterly Review of Biology* 52:39-69.

Klein, L. L., and D. J. Klein. 1975. "Social and ecological contrasts between four taxa of neotropical primates," in *Socioecology and Psychology of Primates*. Edited by R. Tuttle, pp. 59-85. The Hague: Mouton.

Koenig, A. 2002. Competition for resources and its behavioral consequences among female primates. *International Journal of Primatology* 23:759-783.

Koenig, A., and C. Borries. 2006. "The predictive power of socioeciological models: a reconsideration of resource characteristics, agonism, and dominance hierarchies," in *Feeding Ecology in Apes and Other Primates*. Edited by G. Hohmann, M. Robbins, and C. Boesch, pp. 263–284. Cambridge: Cambridge University Press.

Komers, P. E., and P. N. M. Brotherton. 1997. Female space use is the best predictor of monogamy in mammals. *Proceedings of the Royal Society B-Biological Sciences* 264:1261-1270.

Korstjens, A. H., I. L. Verhoeckx, and R. I. M. Dunbar. 2006. Time as a constraint on group size in spider monkeys. *Behavioral Ecology and Sociobiology* 60:683-694.

Krebs, J., and N. Davies. 1997. *Behavioral Ecology: an Evolutionary Approach*, 4th edition. Oxford: Wiley-Blackwell.

Kummer, H. 1968. *Social Organization of Hamadryas Baboons: a Field Study*. Chicago & London: University of Chicago Press

Lack, D. 1968. *Ecological Adaptations for Breeding in Birds*. London: Methuen & Co.

Lee, P. C. 1999. "Comparative ecology of postnatal growth and weaning among haplorhine primates," in *Comparative Primate Socioecology*. Edited by P. Lee, pp. 111–139. Cambridge: Cambridge University Press.

Lehmann, J., A. Korstjens, and R. I. M. Dunbar. 2007. Fission–fusion social systems as a strategy for coping with ecological constraints: a primate case. *Evolutionary Ecology* 21:613-634.

Lehmann, J., A. H. Korstjens, and R. I. M. Dunbar. 2008. Time and distribution: a model of ape biogeography. *Ethology Ecology & Evolution* 20:337-359.

Lesthaeghe, R. J. 1989. *Reproduction and Social Organization in Sub-Saharan Africa*. Berkeley: University of California Press.

Levinson, D., and M. J. Malone. 1980. *Toward Explaining Human Culture: A critical review of the findings of worldwide cross-cultural research*. New Haven, CT: HRAF Press.

Lewis, M. P. 2009. "Ethnologue: Languages of the World," 16 edition. Dallas, Texas: SIL International.

Low, B. S. 1988. "Pathogen stress and polygyny in humans," in *Human Reproductive Behaviour: A Darwinian Perspective*. Edited by L. Betzig, M. Borgerhoff Mulder, and P. W. Turke, pp. 115-128. Cambridge: Cambridge University Press.

Low, B. S. 1990. "Human responses to environmental extremeness and uncertainty: A cross-cultural perspective," in *Risk and Uncertainty in Tribal and Peasant Economies*. Edited by E. Cashdan, pp. 229-255. Boulder, Colorado: Westview Press.

Low, B. S. 2003. "Ecological and social complexities in human monogamy," in *Monogamy: Mating Strategies and Partnerships in Birds, Humans and Other Mammals*. Edited by U. H. Reichard and C. Boesch, pp. 161–176. Cambridge: Cambridge University Press.

Low, B. S. 2007. "Ecological and socio-cultural impacts on mating and marriage systems," in *Oxford Handbook of Evolutionary Psychology*. Edited by R. I. M. Dunbar and L. Barrett, pp. 449–462. Oxford: Oxford University Press.

Mace, R., and C. Holden. 1999. "Evolutionary ecology and cross-cultural comparison: the case of matrilineal descent in sub-Saharan Africa," in *Comparative Primate Socioecology*. Edited by P. C. Lee, pp. 387-405. Cambridge: Cambridge University Press.

Mace, R., and M. Pagel. 1994. The comparative method in anthropology. *Current Anthropology* 35:549-564.

Maddison, W. P. 1990. A method for testing the correlated evolution of two binary characters: are gains or losses concentrated on certain branches of a phylogenetic tree? *Evolution* 44:539-557.

Malinowski, B. 1970 [1944]. *A Scientific Theory of Culture and Other Essays*. Chapel Hill: University of North Carolina Press.

Marck, J., and K. Bostoen. 2011. "Proto-Oceanic society (Austronesian) and proto-East Bantu society (Niger-Congo) residence, descent, and kin terms, ca. 1000 BC," in *Kinship, Language, and Prehistory: Per Hage and the Renaissance in Kinship Studies*. Edited by D. Jones and M. Bojka, pp. 83-94. Salt Lake City: The University of Utah Press.

Marlowe, F. W. 2000. Paternal investment and the human mating system. *Behavioural Processes* 51:45-61.

Maynard Smith, J. 1977. Parental investment: a prospective analysis. *Animal Behaviour* 25:1-9.

Mesoudi, A. 2011. *Cultural Evolution: how Darwinian theory can explain human culture and synthesize the social sciences*: University of Chicago Press.

Mesoudi, A., A. Whiten, and K. Laland. 2007. Science, evolution and cultural anthropology: a response to Ingold. *Anthropology Today* 23:18-18.

Mesoudi, A., A. Whiten, and K. N. Laland. 2006. Towards a unified science of cultural evolution. *Behavioral and Brain Sciences* 29:329-347.

Metropolis, N., A. W. Rosenbluth, M. N. Rosenbluth, A. H. Teller, and E. Teller. 1953. Equation of state calculations by fast computing machines. *Journal of Chemical Physics* 21:1087.

Mitani, J. C., and P. S. Rodman. 1979. Territoriality: the relation of ranging pattern and home range size to defendability, with an analysis of territoriality among primate species. *Behavioral Ecology and Sociobiology* 5:241-251.

Mitchell, J. 1956. *The Yao Village: A Study in the Social Structure of a Nyasaland Tribe*. Manchester: Manchester University Press.

Montano, V., G. Ferri, V. Marcari, C. Batini, O. Anyaele, G. Destro-Bisol, and D. Comas. 2011. The Bantu expansion revisited: a new analysis of Y chromosome variation in Central Western Africa. *Molecular Ecology* 20:2693-2708.

Morgan, L. H. 1964 [1877]. *Ancient Society*. Cambridge: Belknap Press.

Müller, A. E., and U. Thalmann. 2000. Origin and evolution of primate social organisation: a reconstruction. *Biological Reviews* 75:405-435.

Murdock, G. P. 1949. *Social Structure*. New York: MacMillan.

Murdock, G. P. 1954. *Outline of World Cultures*. New Haven, CT: Human Relations Area Files.

Murdock, G. P. 1967. Ethnographic atlas - a summary. *Ethnology* 6.

Murdock, G. P., and D. R. White. 1969. Standard cross-cultural sample. *Ethnology* 8:329-369.

Nelson, E., C. Rolian, L. Cashmore, and S. Shultz. 2011. Digit ratios predict polygyny in early apes, Ardipithecus, Neanderthals and early modern humans but not in Australopithecus. *Proceedings of the Royal Society B: Biological Sciences* 278:1556-1563.

Nelson, E., and S. Shultz. 2010. Finger length ratios (2D:4D) in anthropoids implicate reduced prenatal androgens in social bonding. *American Journal of Physical Anthropology* 141:395-405.

Nowak, M. A., C. E. Tarnita, and E. O. Wilson. 2010. The evolution of eusociality. *Nature* 466:1057-1062.

Nunn, C. L. 1999. The evolution of exaggerated sexual swellings in primates and the graded-signal hypothesis. *Animal Behaviour* 58:229-246.

Nunn, C. L. 2000. "Collective benefits, free-riders, and male extra-group conflict," in *Primate Males: Causes and Consequences of Variation in Group Composition*. Edited by P. M. Kappeler, pp. 192. Cambridge: Cambridge University Press.

Nunn, C. L. 2011. *The Comparative Method in Evolutionary Anthropology and Biology*. Chicago: The University of Chicago Press.

O'Connell, J. F., K. Hawkes, and N. G. Blurton Jones. 1999. Grandmothering and the evolution of *Homo erectus*. *Journal of Human Evolution* 36:461-485.

Olson, V. A., T. J. Webb, R. P. Freckleton, and T. Szekely. 2009. Are parental care trade-offs in shorebirds driven by parental investment or sexual selection? *Journal of Evolutionary Biology* 22:672-682.

Opie, C., Q. Atkinson, and S. Shultz. 2012. The evolutionary history of primate mating systems. *Communicative & Integrative Biology* 5:1-4.

Opie, K., and C. Power. 2008. "Grandmothering and female coalitions: a basis for matrilineal priority?," in *Early Human Kinship: From Sex to Social Reproduction*. Edited by N. J. Allen, H. Callan, R. I. M. Dunbar, and W. James, pp. 168-186. Oxford: Blackwell.

Ossi, K., and M. K. Jason. 2006. Environmental and phylogenetic correlates of eulemur behavior and ecology. *Behavioral Ecology and Sociobiology* 61:53-64.

Pagel, M. 2012a. Adapted to culture. *Nature* 482:297-299.

Pagel, M. 2012b. *Wired for Culture: The Natural History of Human Cooperation*: Allen Lane.

Pagel, M. D. 1994a. Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. *Proceedings of the Royal Society of London Series B-Biological Sciences* 255:37-45.

Pagel, M. D. 1994b. The evolution of conspicuous oestrous advertisement in Old World monkeys. *Animal Behaviour* 47:1333-1341.

Pagel, M. D. 1997. Inferring evolutionary processes from phylogenies. *Zoologica Scripta* 26:331-348.

Pagel, M. D. 1999a. Inferring the historical patterns of biological evolution. *Nature* 401:877-884.

Pagel, M. D. 1999b. The maximum likelihood approach to reconstructing ancestral character states of discrete characters on phylogenies. *Systematic Biology* 48:612-622.

Pagel, M. D., and A. Meade. 2005. "Bayesian estimation of correlated evolution across cultures: a case study of marriage systems and wealth transfer at marriage," in *The Evolution of Cultural Diversity: a Phylogenetic Approach*.

Edited by R. Mace, C. Holden, and S. Shennan, pp. 235-56. London: University College London Press.

Pagel, M. D., and A. Meade. 2006. Bayesian analysis of correlated evolution of discrete characters by reversible-jump Markov chain Monte Carlo. *American Naturalist* 167:808-825.

Pagel, M. D., A. Meade, and D. Barker. 2004. Bayesian estimation of ancestral character states on phylogenies. *Systematic Biology* 53:673-684.

Palombit, R. A. 1999. Infanticide and the evolution of pair bonds in nonhuman primates. *Evolutionary Anthropology* 7:117-129.

Paradis, E., J. Claude, and K. Strimmer. 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* 20:289-290.

Parkin, R. 1997. *Kinship: An Introduction to Basic Concepts*. Oxford: Blackwell.

Parkin, R. 2009. What Shapiro and McKinnon are all about, and why kinship still needs anthropologists. *Social Anthropology* 17:158-170.

Pérez-Barbería, F. J., S. Shultz, and R. I. M. Dunbar. 2007. Evidence for coevolution of sociality and relative brain size in three orders of mammals. *Evolution* 61:2811-2821.

Plavcan, J. M. 2000. Inferring social behavior from sexual dimorphism in the fossil record. *Journal of Human Evolution* 39:327-344.

Plavcan, J. M., C. A. Lockwood, W. H. Kimbel, M. R. Lague, and E. H. Harmon. 2005. Sexual dimorphism in Australopithecus afarensis revisited: How strong is the case for a human-like pattern of dimorphism? *Journal of Human Evolution* 48:313-320.

Posada, D., and T. R. Buckley. 2004. Model selection and model averaging in phylogenetics: advantages of akaike information criterion and bayesian approaches over likelihood ratio tests. *Systematic Biology* 53:793-808.

Purvis, A. 1995. A composite estimate of primate phylogeny. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 348:405-421.

Purvis, A., J. L. Gittleman, G. Cowlishaw, and G. M. Mace. 2000. Predicting extinction risk in declining species. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 267:1947-1952.

Purvis, A., and A. Rambaut. 1995. Comparative-analysis by independent contrasts (CAIC) - an Apple-Macintosh application for analyzing comparative data. *Computer Applications in the Biosciences* 11:247-251.

Purvis, A., and A. J. Webster. 1999. Phylogenetically independent comparisons and primate phylogeny. *Comparative Primate Socioecology*:44-70.

Pusey, A., and C. Packer. 1987. "Dispersal and philopatry," in *Primate Societies*. Edited by B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham, and T. Struhsaker, pp. 250-266. Chicago: University of Chicago Press.

R Development Core Team. 2008. "R: A language and environment for statistical computing." Vienna, Austria: R Foundation for Statistical Computing.

Radcliffe-Brown, A. R. 1950. "Introduction," in *African Systems of Kinship and Marriage*. Edited by A. R. Radcliffe-Brown and D. Forde. Oxford: Oxford University Press.

Radcliffe-Brown, A. R. 1952. *Structure and Function in Primitive Society*. London: Routledge.

Rambaut, A., and A. Drummond. 2007. Tracer v1.4. *Available from* http://beast.bio.ed.ac.uk/Tracer.

Reader, S. M., and K. N. Laland. 2002. Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Sciences* 99:4436-4441.

Rendall, D., and A. Di Fiore. 1995. The road less travelled: phylogenetic perspectives in primatology. *Evolutionary Anthropology* 4:43-52.

Rendall, D., and A. Di Fiore. 2007. Homoplasy, homology, and the perceived special status of behavior in evolution. *Journal of Human Evolution* 52:504-521.

Reno, P. L., R. S. Meindl, M. A. McCollum, and C. O. Lovejoy. 2003. Sexual dimorphism in Australopithecus afarensis was similar to that of modern humans. *Proceedings of the National Academy of Sciences of the United States of America* 100:9404-9409.

Reno, P. L., R. S. Meindl, M. A. McCollum, and C. O. Lovejoy. 2005. The case is unchanged and remains robust: Australopithecus afarensis exhibits only moderate skeletal dimorphism. A reply to. *Journal of Human Evolution* 49:279-288.

Richerson, P. 2012. Evolution: custom built. *Nature* 482:304-305.

Richerson, P., and R. Boyd. 2005. *Not By Genes Alone*. Chicago: University of Chicago Press.

Ronquist, F. 2004. Bayesian inference of character evolution. *Trends in Ecology & Evolution* 19:475-481.

Ross, C., and A. MacLarnon. 2000. The Evolution of non-maternal care in anthropoid primates: a test of the hypotheses. *Folia Primatologica* 71:93-113.

Ruhlen, A. 1987. *A Guide to the World's Languages: I. Classification*. London: Edward Arnold.

van Schaik, C. P. 1983. Why are diurnal primates living in groups? *Behaviour* 87:120-144.

van Schaik, C. P. 1989. "The ecology of social relationships amongst female primates," in *Comparative Socioecology: The Behavioural Ecology of Humans and other Mammals*. Edited by V. Standen and R. A. Foley. Oxford: Blackwell.

van Schaik, C. P. 2000a. "Infanticide by male primates: the sexual selection hypothesis revisited," in *Infanticide by Males and its Implications*. Edited by C. P. van Schaik and C. Janson, pp. 27–60. Cambridge: Cambridge University Press.

van Schaik, C. P. 2000b. "Social counterstrategies against infanticide by males in primates and other mammals," in *Primate Males: Causes and Consequences of Variation in Group Composition*. Edited by P. Kappeler, pp. 34–52. Cambridge: Cambridge University Press.

van Schaik, C. P. 2000c. "Vulnerability to infanticide by males: patterns among mammals," in *Infanticide by Males and its Implications*. Edited by C. P. van Schaik and C. H. Janson. Cambridge: Cambridge University Press.

van Schaik, C. P., and R. I. M. Dunbar. 1990. The evolution of monogamy in large primates: a new hypothesis and some crucial tests. *Behaviour* 115:30-61.

van Schaik, C. P., and J. A. R. A. M. van Hooff. 1983. On the ultimate causes of primate social systems. *Behaviour* 85:91-117.

van Schaik, C. P., and C. H. Janson. Editors. 2000. *Infanticide by Males and its Implications*. Cambridge: Cambridge University Press.

van Schaik, C. P., and P. M. Kappeler. 1997. Infanticide risk and the evolution of male-female association in primates. *Proceedings of the Royal Society B: Biological Sciences* 264:1687.

van Schaik, C. P., and P. M. Kappeler. 2003. "The evolution of social monogamy in primates," in *Monogamy: Mating Strategies and Partnerships in Birds, Humans and Other Mammals*. Edited by U. H. Reichard and C. Boesch, pp. 59–80. Cambridge: Cambridge University Press.

van Schaik, C. P., M. A. van Noordwijk, and C. L. Nunn. 1999. "Sex and social evolution in primates," in *Comparative Primate Socioecology*. Edited by P. C. Lee, pp. 204-240. Cambridge: Cambridge University Press.

Sear, R., R. Mace, and I. A. McGregor. 2000. Maternal grandmothers improve nutritional status and survival of children in rural Gambia. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 267:1641-1647.

Seielstad, M. T., E. Minch, and L. L. Cavalli-Sforza. 1998. Genetic evidence for a higher female migration rate in humans. *Nat Genet* 20:278-280.

Shultz, S., and R. I. M. Dunbar. 2007. The evolution of the social brain: anthropoid primates contrast with other vertebrates. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 7:2429-2436.

Shultz, S., and R. I. M. Dunbar. 2010. Social bonds in birds are associated with brain size and contingent on the correlated evolution of life-history and increased parental investment. *Biological Journal of the Linnean Society* 100:111-123.

Shultz, S., E. Nelson, and R. I. M. Dunbar. 2012. Hominin cognitive evolution: identifying patterns and processes in the fossil and archaeological record. *Philosophical Transactions of the Royal Society B: Biological Sciences* 367:2130-2140.

Shultz, S., C. Opie, and Q. D. Atkinson. 2011. Stepwise evolution of stable sociality in primates. *Nature* 479:219-222.

Silk, J. B. 2011. The path to sociality. *Nature* 479:182-183.

Sillen-Tullberg, B., and A. P. Møller. 1993. The relationship between concealed ovulation and mating systems in anthropoid primates: a phylogenetic analysis. *American Naturalist* 141:1-25.

Smuts, B., D. Cheney, R. Seyfarth, R. Wrangham, and T. Struhsaker. 1987. *Primate Societies*. Chicago: University of Chicago Press.

Snaith, T. V., and C. A. Chapman. 2007. Primate group size and interpreting socioecological models: Do folivores really play by different rules? *Evolutionary Anthropology* 16:94-106.

Sommer, V. 1994. "Infanticide among the langurs of Jodhpur: testing the sexual selection hypothesis with a long-term record," in *Infanticide and Parental Care*. Edited by S. Parmigiani and F. vom Saal, pp. 155-198. Chur, CH: Harwood.

Sterck, E. H. M., D. P. Watts, and C. P. van Schaik. 1997. The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology* 41:291-309.

Strier, K. B. 1994. Myth of the typical primate. *American Journal of Physical Anthropology* 37:233-271.

Struhsaker, T. T. 1969. Correlates of ecology and social organization among African cercopithecines. *Folia Primatologica* 11:80-118.

Sussman, R. 1992. Male life history and intergroup mobility among ringtailed lemurs (Lemur catta). *International Journal of Primatology* 13:395-413.

Sussman, R. W., J. M. Cheverud, and T. Q. Bartlett. 1995. Infant killing as an evolutionary strategy: reality or myth? *Evolutionary Anthropology* 3:149 – 151.

Swadesh, M. 1955. Towards greater accuracy in lexicostatistic dating. *International Journal of American Linguistics* 21:121-137.

Terborgh, J., and C. H. Janson. 1986. The socioecology of primate groups. *Annual Review of Ecology and Systematics* 17:111-136.

Thierry, B. 2008. Primate socioecology, the lost dream of ecological determinism. *Evolutionary Anthropology* 17:93-96.

Tinbergen, N. 1963. On aims and methods of ethology. *Zeitschrift für Tierpsychologie* 20:410-433.

Trivers, R. L. 1972. "Parental investment and sexual selection," in *Sexual Selection and the Descent of Man, 1871-1971*. Edited by B. Campbell, pp. 136-179. Chicago: Aldine.

Turke, P. W. 1984. Effects of ovulatory concealment and synchrony on protohominid mating systems and parental roles. *Ethology and Sociobiology* 5:33-44.

Tylor, E. B. 1973 [1873]. *Primitive Culture*. Vol. 1 & 2. London: J. Murray.

Vansina, J. 1990. *Paths in the Rainforest*. Madison: University of Wisconsin Press.

Vansina, J. 1995. New linguistic evidence and the Bantu expansion. *Journal of African History* 36:173-195.

Venables, W. N., and B. D. Ripley. 2002. *Modern Applied Statistics with S*, 4 edition. New York: Springer.

Walker, R. S., and M. J. Hamilton. 2011. Social complexity and linguistic diversity in the Austronesian and Bantu population expansions. *Proceedings of the Royal Society B-Biological Sciences* 278:1399-1404.

Walker, R. S., K. R. Hill, M. V. Flinn, and R. M. Ellsworth. 2011. Evolutionary history of hunter-gatherer marriage practices. *PLoS ONE* 6:e19066.

Walker, R. S., and L. A. Ribeiro. 2011. Bayesian phylogeography of the Arawak expansion in lowland South America. *Proceedings of the Royal Society B-Biological Sciences* 278:2562-2567.

Walker, R. S., S. Wichmann, T. Mailund, and C. J. Atkisson. 2012. Cultural phylogenetics of the Tupi language family in Lowland South America. *PLoS ONE* 7.

Watts, D. P. 1989. Infanticide in mountain gorillas: new cases and a reconsideration of the evidence. *Ethology* 81:1-18.

Weakliem, D. L. 1999. A Critique of the Bayesian information criterion for model selection. *Sociological Methods & Research* 27:359-397.

White, D. R. 1988. Rethinking polygyny - co-wives, codes, and cultural systems. *Current Anthropology* 29:529-572.

White, D. R., and M. L. Burton. 1988. Causes of polygyny: ecology, economy, kinship, and warfare. *American Anthropologist* 90:871-887.

Whittingham, M. J., P. A. Stephens, R. B. Bradbury, and R. P. Freckleton. 2006. Why do we still use stepwise modelling in ecology and behaviour? *Journal of Animal Ecology* 75:1182-1189.

Wilson, E. O. 1975. *Sociobiology : The New Synthesis* Cambridge, Mass: Belknap Press of Harvard University Press.

Wint, G. R. W., and T. P. Robinson. 2007. *Gridded livestock of the world 2007*. Food and Agriculture Organization of the United Nations.

Wint, W., and D. Rogers. 2000. *Consultants' report predicted distributions of tsetse in Africa*. Food and Agriculture Organisation of the United Nations.

Wittenberger, J. F., and R. L. Tilson. 1980. The evolution of monogamy: hypotheses and evidence. *Annual Review of Ecology and Systematics* 11:197-232.

Wrangham, R. 1979. On the evolution of ape social systems. *Social Science Information* 18:336-368.

Wrangham, R. W. 1980. An ecological model of female-bonded primate groups. *Behaviour* 75:262-300.

Wrangham, R. W. 1987a. "Evolution of social structure," in *Primate Societies*. Edited by B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham, and T. Struhsaker, pp. 282-296. Chicago: University of Chicago Press.

Wrangham, R. W. 1987b. "The significance of African apes for reconstructing human social evolution," in *The Evolution of Human Behavior: Primate Models*. Edited by W. G. Kinzey, pp. 51-71. Albany: State University of New York Press.

WWF. 2012. "Terrestrial Ecoregions of the World." Edited by WWF. Gland, Switzerland.

Appendices

1. Shultz, S., C. Opie, and Q. D. Atkinson. 2011. Stepwise evolution of stable sociality in primates. Nature 479:219-222.

2. Opie, C., Q. Atkinson, and S. Shultz. 2012. The evolutionary history of primate mating systems. Communicative & Integrative Biology 5:0--1.

LETTER

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Stepwise evolution of stable sociality in primates

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Although much attention has been focused on explaining and describing the diversity of social grouping patterns among primates[1–3], less effort has been devoted to understanding the evolutionary history of social living[4]. This is partly because social behaviours do not fossilize, making it difficult to infer changes over evolutionary time. However, primate social behaviour shows strong evidence for phylogenetic inertia, permitting the use of Bayesian comparative methods to infer changes in social behaviour through time, thereby allowing us to evaluate alternative models of social evolution. Here we present a model of primate social evolution, whereby sociality progresses from solitary foraging individuals directly to large multi-male/multi-female aggregations (approximately 52 million years (Myr) ago), with pair-living (approximately 16 Myr ago) or single-male harem systems (approximately 16 Myr ago) derivative from this second stage. This model fits the data significantly better than the two widely accepted alternatives (an unstructured model implied by the socioecological hypothesis or a model that allows linear stepwise changes in social complexity through time). We also find strong support for the co-evolution of social living with a change from nocturnal to diurnal activity patterns, but not with sex-biased dispersal. This supports suggestions that social living may arise because of increased predation risk associated with diurnal activity. Sociality based on loose aggregation is followed by a second shift to stable or bonded groups. This structuring facilitates the evolution of cooperative behaviours[5] and may provide the scaffold for other distinctive anthropoid traits including coalition formation, cooperative resource defence and large brains.

Anthropoids differ from other social vertebrates in the prevalence of stable groups and bonded relationships between individuals[6]. Explaining how primate social systems evolved is central to understanding the evolution of our closest relatives and the emergence of early human social behaviour[7]. Conventional explanations have appealed more to adaptive reasoning than phylogenetic history to account for patterns of sociality[4]. Adaptive arguments often invoke the socioecological model[8], which predicts that individuals readily alter patterns of aggregation in response to ecological conditions[3,9]. This focus has resulted in less emphasis on the historical processes and phylogenetic constraints that have informed other areas of evolutionary biology[10].

However, behaviour, like morphology, physiology and life history, is heritable[11] and shaped by historical processes. Primate social behaviour is no exception; Old World primates, particularly cercopithecines, have highly inflexible social structures, and social traits cluster according to taxonomic grouping across the order[4]. Strong historical constraints make it crucial to incorporate phylogeny when testing adaptive explanations, but also create the possibility of explicitly modelling the evolutionary pathways leading to extant primate grouping patterns.

To evaluate the evolution of stable sociality in primates, we mapped the composition of foraging groups (solitary, family groups, harems or multi-male; see Supplementary Information for further discussion of alternative classification schemes) for 217 species onto a primate consensus tree (Fig. 1 and Supplementary Information) derived from genetic data[12]. We then evaluated the strength of phylogenetic inertia in the data (historical non-independence) using Pagel's lambda (λ)[13]. A λ value of 0 implies evolution independent of the phylogenetic tree, whereas a value of 1 indicates that the probability of shared inheritance between species is proportional to their relatedness. Social grouping patterns showed a strong phylogenetic signal ($\lambda_{\max} = 0.983$, maximum likelihood ($\mathrm{LL}_{\max}$) $= -150.038$) (significantly different from a λ value of 0 ($\mathrm{LL}_0 = -332.63$, $P < 0.001$), but not significantly different from a λ value of 1 ($\mathrm{LL}_1 = -141.12$, $P = 0.189$)). Flexible social structure is characteristic of only two groups, the Callitrichidae and Lemuridae (Fig. 1).

This strong phylogenetic signal allows a reconstruction of the evolutionary pathways leading to extant primate grouping patterns. Theoretical models suggest two possibilities. First, the socioecological model posits that grouping patterns are driven by individual responses to resource availability[3,9]. Under this 'unstructured' model, if grouping patterns are facultative, transitions between all possible social states (and polymorphic states within species) should be equally likely. Second, primate social complexity has been proposed to increase in a stepwise fashion from solitary individuals, through small groups to large, socially complex groups[14–16]. From this 'increasing complexity' model we would predict that pair-living was the earliest form of social group, followed by more complex grouping patterns. Support for such a model of social evolution through pair-bonds has been found in birds[17,18] and insects[19].

We used a Bayesian framework, implemented in BayesTraits[20], to evaluate four alternative models of social evolution (Fig. 2), including the two described above, on a posterior distribution of primate trees. The simplest model estimates a single rate of transition between all social states, representing an unstructured 'null' model of social change in which all state changes occur at the same underlying rate. We contrast this with a second, parameter-rich model in which rates are allowed to vary across all transitions. This model implies that some transitions are more likely than others, for example the rate from solitary to pair-living may be different from the rate from pair-living to solitary or to some other state—but does not make assumptions about what this structure will be. The third model simulates increasing complexity by restricting possible transitions to stepwise changes up and down a chain linking solitary to pair-living, to small harem groups and finally to large multi-male/multi-female groups. The fourth model is derived from the data and identifies likely transitions using the reversible-jump procedure in BayesTraits, which searches the posterior distribution of possible models by linking (setting to equal) or removing (setting to zero) transition rate parameters.

The model with the highest posterior support in the reversible-jump analysis (Supplementary Table 1) suggests that social evolution proceeds from solitary to multi-male/multi-female groups and then either to pair-living or harems. Back transitions occur from harems to multi-male groups, whereas transitions between pair-living and harems do not occur. Transitions from solitary to social are not reversed; such that once a lineage becomes social it remains so. We used Bayes Factors[20–22] to test whether there is sufficient signal in the primate sociality data to support decisively any of the four alternative models. Table 1 shows that the reversible-jump-derived model is not only the

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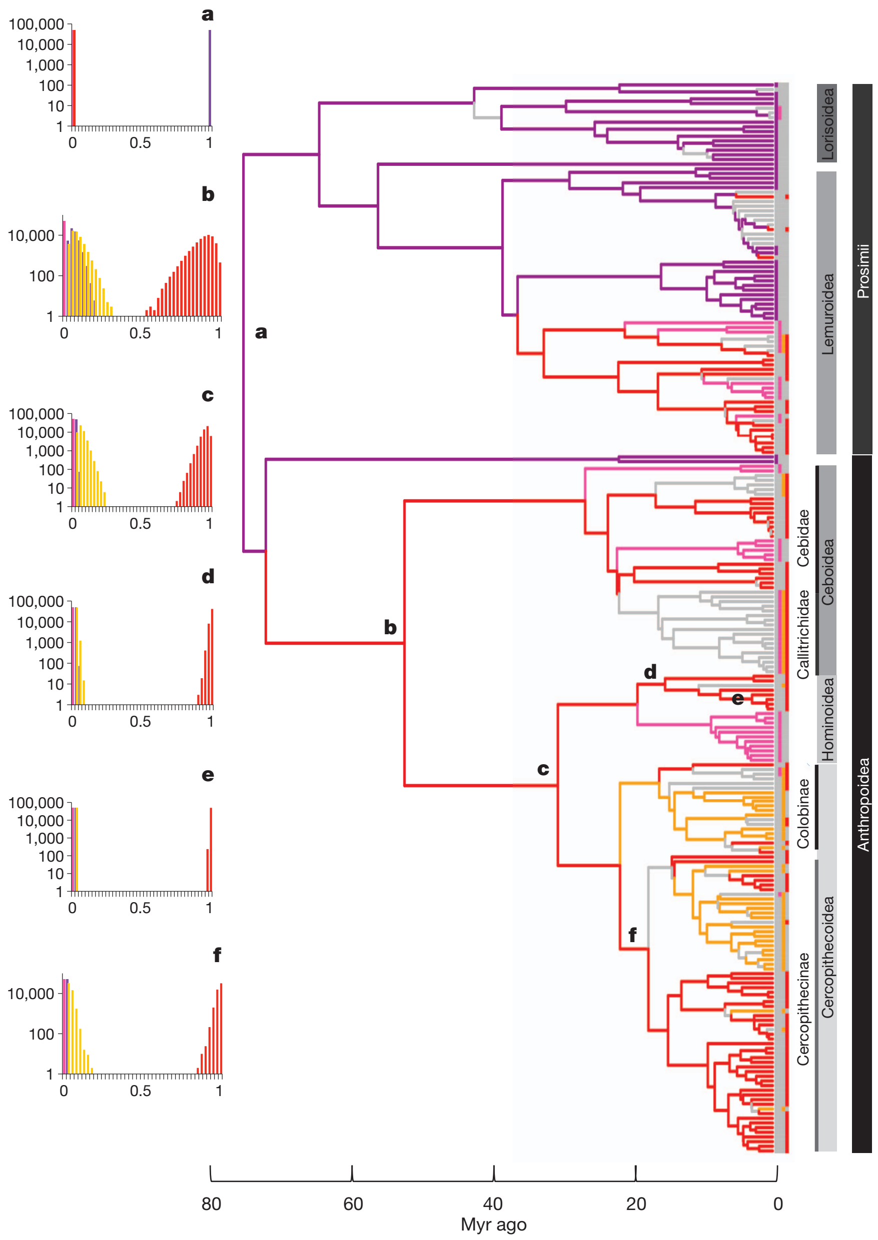

Figure 1 | Primate phylogeny showing ancestral state reconstructions for sociality under the reversible-jump Markov chain Monte Carlo-derived model of evolution. The tree topology is the maximum clade credibility tree from the 10kTrees Project[12] posterior distribution with branch lengths drawn proportional to time. Branches and tips are coloured for solitary (purple), uni-male (orange), multi-male (red), pair-living (pink) where the combined probability of the state and the branch is greater than or equal to 0.7. Where the combined probability is less than 0.7, the branch is grey. Histograms represent the posterior probability distribution of each social state at the nodes indicated (**a**, primate root; **b**, anthropoid root, **c**, catarrhine root; **d**, great ape root; **e**, *Pan*–*Homo* split; **f**, Old World monkey root).

best fit to the data, but is also decisively better at explaining the data than the equal rates, the fully parameterized or the increasing complexity models.

We used the reversible-jump-derived model of social evolution to reconstruct the evolutionary history of social organization across the primate tree (Fig. 1). Ancestral node reconstructions reveal that the transition from solitary foraging at the primate root (74 Myr ago) to social aggregations was established at the anthropoid root (52 Myr ago) and the root of the Indriidae and Lemuridae (32 Myr ago) in prosimians. Other forms of social grouping evolved later in primates; harems appeared at the root of the Colobinae (16 Myr ago), followed soon after in the Cercopithecini (14 Myr ago). Pair-living arose at the root of the Callitrichidae (16 Myr ago), Hylobatidae (8.6 Myr ago), *Avahi* (6.4 Myr ago), hapalemurs (6.3 Myr ago), *Aotus* (4.8 Myr ago) and *Callicebus* (4.5 Myr ago). Thus, the fundamental shift to sociality occurred with the appearance of aggregations, followed later by derived grouping structures, including pair-living.

We next examined two possible catalysts of primate social evolution. First, the switch to social living is presumed to occur under increased predation pressure[1] coinciding with the shift from nocturnal to diurnal activity. We used a test of co-evolution in BayesTraits[20] to assess whether changes in activity patterns predict the major transition to social living. There was decisive support[22] for the dependent model (that is, co-evolution between activity and sociality, Fig. 3a) over the independent model (mean $LL_{D(dependent)} = -33.03 \pm 0.08$ s.e.m. compared with $LL_{I(independent)} = -41.71 \pm 0.04$ s.e.m.; Bayes Factor 3.39; Supplementary Table 2), supporting the proposed link between the evolution of activity patterns and social living. Additionally, both

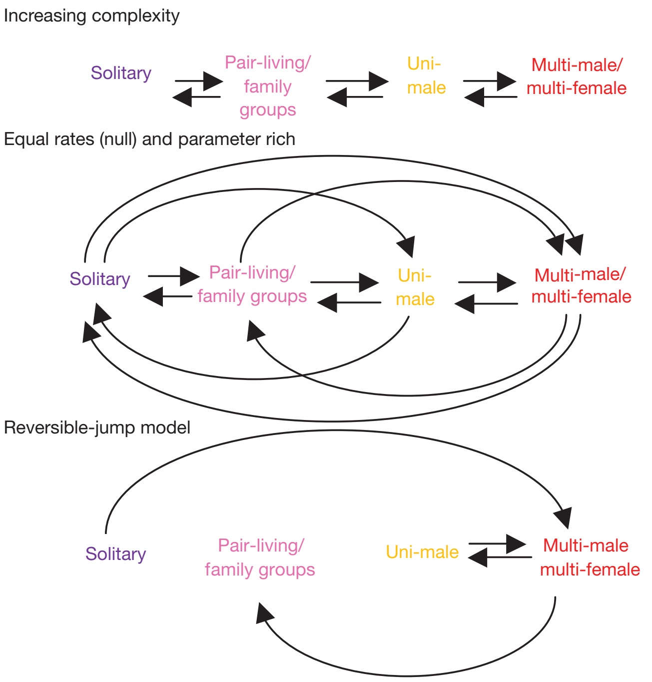

Figure 2 | Alternative evolutionary models of primate social evolution. Arrows represent allowable transitions between modes of social living under each model. Under the complexity and parameter-rich model, transition rates represented by each arrow can vary. Under the equal rates model, all rates are fixed to a single optimized rate parameter. The reversible-jump-derived model is a significantly better fit to the data than the alternative models.

intermediate states (social/nocturnal and solitary/diurnal) are unstable as the transition rate from these states to social/diurnal is an order of magnitude higher than any other transition. This suggests that the switch from a solitary, nocturnal lifestyle to diurnal social living represents a major shift in the primate adaptive landscape. Group living has long been argued to provide anti-predator benefits[1], and the shift to diurnal social living in primates would have opened up a vast new adaptive space in a highly visual world[23].

The second possible catalyst is the switch to sex-biased dispersal, whereby one sex (typically males) disperses further from the natal range than the other. This is assumed to be an ancestral or default mammalian characteristic[24]. Changes in dispersal behaviour may be important in the evolution of sociality because in its extreme form, philopatry, one sex foregoes dispersal and remains in the natal range resulting in kin structured groups. A switch to sex-biased dispersal could therefore facilitate kin selection and the emergence of cooperative social groups[25–27]. The extension of the mother–daughter bond to groups of related females also has been proposed as the fundamental relationship underpinning mammalian sociality[28]. We used Discrete to evaluate whether sex-biased dispersal precedes the shift to sociality in primates. Although we find support for co-evolution between social grouping and dispersal patterns (mean $LL_D = -73.27 \pm 0.03$ s.e.m. versus $LL_I = -74.66 \pm 0.05$ s.e.m.; Bayes Factor 1.21; Fig. 3b), the association is much weaker than between sociality and activity patterns and independent models are sampled above chance (Supplementary Table 3).

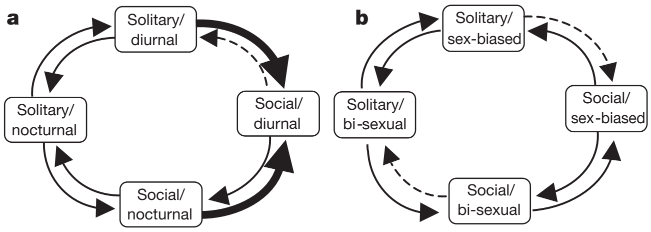

Figure 3 | Estimated transition rates for co-evolution of social living. Estimated transition rates with (**a**) activity and (**b**) dispersal patterns. Thin lines, an estimated median transition rate >0 but <0.01; heavy lines, a rate >0.01; dashed lines, a median estimated zero transition rate. Full estimated rates are reported in Supplementary Information.

Additionally, contrary to the assumption of sex-biased dispersal being a primate (and mammalian) default[24], the ancestral state for primates is bi-sexual dispersal (posterior probability of 0.93) and the estimated transition rates indicate that sex-biased natal dispersal follows the shift to sociality rather than precedes it (Fig. 3b).

Dispersal changes, therefore, do not trigger social living, but as they follow the emergence of social living they could be associated with a secondary transition to stable groups. A similar suggestion was put forward in a controversial model for the evolution of cooperative sociality in eusocial insects[5]. The model argues that aggregating individuals first create population structure. Stable groups then emerge secondarily through increased persistence resulting from silenced dispersal in at least one sex. To test whether this model explains the evolution of stable primate groups, we classified species as solitary, unstable social or stable social (the later defined as species with natal philopatry coupled with no/limited secondary dispersal or those with stable, long-term pair bonds). We then used the reversible jump procedure to identify the most likely model for the evolution of group stability; our model suggests that solitary living is the ancestral state, followed by unstable groups, and with a final transition to stable social groups (marginal $LL = -65.2 \pm 0.019$, Supplementary Table 4). This model is a better fit to the data than either an equal rates ($LL = -71.59 \pm 0.021$, Bayes Factor = 2.77) or a parameter-rich model, where transitions are allowed between all states ($LL = -69.08 \pm 0.052$; Bayes Factor = 1.66; Fig. 4). It thus appears that although the evolution of social groups does not occur through increasing complexity as defined by group size, there is strong support for a model of stepwise transitions leading from solitary living to unstable social aggregations, followed by a second step to stable groups based on either kinship or reproductive ties. Although transitions to social grouping are not uncommon in vertebrates, this secondary transition to stable grouping is, and may hold the key to the evolution of cooperative sociality characteristic of anthropoid primates, particularly humans.

Our analyses demonstrate a model of primate social evolution, which highlights the initial switch from solitary foraging to multi-male/multi-female aggregations. Although we cannot directly test adaptive explanations, our findings show this switch co-evolved with a change from a nocturnal to a diurnal lifestyle, supporting the role of predation in driving social evolution. Although group size has often been used as a proxy of social complexity in primates, relationship or group stability represents a more important indication of social

Table 1 | Comparison of alternative model performance

Model	Rank	Parameters	Mean likelihood	Log_{10}[Bayes Factor]
Reversible-jump Markov chain Monte Carlo-derived model	1	4	−64.84	-
Parameter-rich (unconstrained) model	2	12	−72.13	5.03
Equal rate 'null' model	3	1	−76.82	5.24
Increasing complexity	4	6	−77.55	6.5

Table shows number of model parameters, model rank, likelihood and log_{10}[Bayes Factors] (see Supplementary Information). The Bayes Factor indicates relative support for the reversible-jump-derived model over alternatives (0–0.5 minimal; 0.5–1.0 substantial; 1.0–2.0 strong; >2.0 decisive)[21].

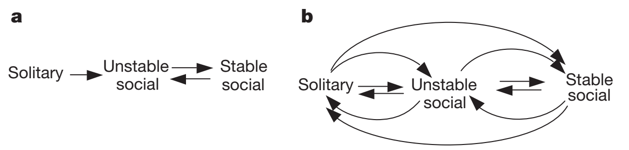

Figure 4 | Alternative evolutionary models for the evolution of stable grouping patterns. **a**, The model with the highest posterior support for the evolution of stable or bonded social groups. The model implies that stable social groups evolve from sociality through unstable social groups. **b**, Alternative models allow transitions between all possible states, either all constrained to the same rate (equal rates model) or allowed to vary (parameter-rich model).

complexity[6]. Our models suggest that the initial switch to sociality involved loose or unstable multi-male/multi-female aggregations (as exemplified in diurnal lemurs) followed by secondary transitions to bonded social relationships between mothers and daughters[28] (philopatry) or reproductive adults[6] (pair-living). This secondary transition may be a key step towards facilitating cooperative social behaviour. In non-primates, social structuring is most commonly characterized by aggregations, with bonding associated with pair-living (for example, birds, ungulates, carnivores), and kin-based groups limited to a few taxa such as elephants and cetaceans[6,29]. Kin-based structuring parallels that seen in eusocial insects. Testing these evolutionary models in other phyla would reveal whether the pathways suggested for primate evolution are more widely characteristic of cooperative sociality.

METHODS SUMMARY

To account for uncertainty in the underlying phylogeny, model testing was undertaken across a Bayesian posterior distribution of 10,000 ultrametric primate trees derived from genetic data as part of version 2 of the 10kTrees Project[12]. The maximum clade credibility tree we present was inferred from the complete 10kTrees sample using TreeAnnotator[30]. Pagel's lambda was estimated using the Ape and Geiger (see Supplementary Information) packages in R.

BayesTraits[20] uses an Markov chain Monte Carlo method to derive posterior distributions of log-likelihoods, the rate parameters of models of evolution, and trait values at ancestral nodes on the phylogeny. Transition rates between all states were constrained to be equal for the unstructured model (producing a simple one-parameter model). Rates were allowed to vary freely to parameterize the flexible model. All rates in the increasing complexity model except the forward and backward transitions between solitary/pair-living, pair-living/uni-male and uni-male/multi-male groups were restricted to zero. Model transition rates were also determined using the reversible-jump procedure in BayesTraits. Reversible-jump models were ranked in order of their posterior probability to identify the top ranked model. Model performance was compared using a $\log_{10}$[Bayes Factor][21]. Co-evolution between behavioural traits was assessed using the Discrete package in BayesTraits. Social organization was classed as solitary (0) or social (1) (including pair-living); activity pattern as nocturnal (0) and diurnal (1); natal dispersal as bi-sexual (0) or sex-biased (1) (see Supplementary Materials for further details).

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

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1. van Schaik, C. P. Why are diurnal primates living in groups? *Behaviour* **87,** 120–144 (1983).
2. Terborgh, J. & Janson, C. H. The socioecology of primate groups. *Annu. Rev. Ecol. Syst.* **17,** 111–135 (1986).
3. Sterck, H. M., Watts, D. P. & van Schaik, C. P. The evolution of female social relationships in nonhuman primates. *Behav. Ecol. Sociobiol.* **41,** 291–309 (1997).
4. Di Fiore, A. & Rendall, D. Evolution of social organization: a reappraisal for primates by using phylogenetic methods. *Proc. Natl Acad. Sci. USA* **91,** 9941–9945 (1994).
5. Nowak, M. A., Tarnita, C. E. & Wilson, E. O. The evolution of eusociality. *Nature* **466,** 1057–1062 (2010).
6. Shultz, S. & Dunbar, R. I. M. The evolution of the social brain: anthropoid primates contrast with other vertebrates. *Proc. R. Soc. Lond. B* **274,** 2429–2436 (2007).
7. Elton, S. Forty years on and still going strong: the use of hominin-cercopithecid comparisons in palaeoanthropology. *J. R. Anthropol. Inst.* **12,** 19–38 (2006).
8. Jarman, P. J. The social organisation of antelope in relation to their ecology. *Behaviour* **48,** 215–268 (1974).
9. Kappeler, P. M. & van Schaik, C. P. Evolution of primate social systems. *Int. J. Primatol.* **23,** 707–740 (2002).
10. Gould, S. J. & Lewontin, R. C. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proc. R. Soc. Lond. B* **205,** 581–598 (1979).
11. Stirling, D. G., Réale, D. & Roff, D. A. Selection, structure and the heritability of behaviour. *J. Evol. Biol.* **15,** 277–289 (2002).
12. Arnold, C., Matthews, L. J. & Nunn, C. L. The 10kTrees website: a new online resource for primate phylogeny, *Evol. Anthropol.* **19,** 114–118 (2010).
13. Pagel, M. Inferring the historical patterns of biological evolution. *Nature* **401,** 877–884 (1999).
14. Dunbar, R. I. M. in *Primate Males: Causes and Consequences of Variation in Group Composition* (ed. Kappeler, P. M.) 259–268 (Cambridge Univ. Press, 2000).
15. Nunn, C. L. & van Schaik, C. P. in *Reconstructing Behavior in the Primate Fossil Record* (eds Plavcan, J. M., Kay, R. F., Jungers, W. L. & van Schaik, C. P.) 159–216 (Plenum, 2001).
16. Müller, A. E. & Thalmann, U. Origin and evolution of primate social organisation: a reconstruction. *Biol. Rev. Camb. Philos. Soc.* **75,** 405–435 (2000).
17. Cornwallis, C. K., West, S. A., Davis, K. E. & Griffin, A. S. Promiscuity and the evolutionary transition to complex societies. *Nature* **466,** 969–972 (2010).
18. Shultz, S. & Dunbar, R. I. M. Life-history, social bonding and adaptive peak shifts in avian brain evolution. *Biol. J. Linn. Soc.* **100,** 111–123 (2010).
19. Hughes, W. O. H., Oldroyd, B. P., Beekman, M. & Ratnieks, F. L. W. Ancestral monogamy shows kin selection is key to the evolution of eusociality. *Science* **320,** 1213–1216 (2008).
20. Pagel, M. & Meade, A. Bayesian analysis of correlated evolution of discrete characters by reversible-jump Markov chain Monte Carlo. *Am. Nat.* **167,** 808–825 (2006).
21. Rambaut, A. & Drummond, A. J. Tracer v1.4. *Tracer* ⟨http://beast.bio.ed.ac.uk/Tracer⟩ (2007).
22. Kass, R. E. & Raftery, A. E. Bayes Factors. *J. Am. Stat. Assoc.* **90,** 773–795 (1995).
23. Barton, R. A. Visual specialization and brain evolution in primates. *Proc. R. Soc. Lond. B* **265,** 1933–1937 (1998).
24. Greenwood, P. J. Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* **28,** 1140–1162 (1980).
25. Frank, S. A. *Foundations of Social Evolution* (Princeton Univ. Press, 1998).
26. Hamilton, W. D. The genetical evolution of social behaviour. II. *J. Theor. Biol.* **7,** 17–52 (1964).
27. Gompper, M. E., Gittleman, J. L. & Wayne, R. K. Genetic relatedness, coalitions and social behaviour of white-nosed coatis, *Nasua narica*. *Anim. Behav.* **53,** 781–797 (1997).
28. Broad, K. D., Curley, J. P. & Keverne, E. B. Mother–infant bonding and the evolution of mammalian social relationships. *Phil. Trans. R. Soc. B* **361,** 2199–2214 (2006).
29. Shultz, S. & Dunbar, R. I. M. Encephalization is not a universal macroevolutionary phenomenon in mammals but is associated with sociality. *Proc. Natl Acad. Sci. USA* **107,** 21582–21586 (2010).
30. Drummond, A. & Rambaut, A. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evol. Biol.* **7,** 214 (2007).

Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions S.S. designed the study, compiled the data and executed analyses. C.O. executed analyses. Q.A. was involved in study design and advised on statistical analyses. All authors contributed to the manuscript.

Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of this article at www.nature.com/nature. Correspondence and requests for materials should be addressed to S.S. (susanne.shultz@anthro.ox.ac.uk).

METHODS

Primate data. Primates were classified as solitary, pair-living and group-living[9]; group-living were further split into single and multi-male groups (Supplementary Fig. 1). Data were compiled mainly from secondary literature or review articles[3,16,31–35] and several online sites (pin.primate.wisc.edu, www.theprimata.com). The species were coded as follows: solitary ($n = 40$), pair-living ($n = 53$), single-male, multi-female ($n = 67$) or multi-male, multi-female ($n = 121$). Dispersal was classified as male-biased ($n = 86$), female-biased ($n = 14$) or bi-sexual dispersal ($n = 105$). Recent papers have argued that dispersal is more flexible than classification schemes acknowledge[36]. However, here we attempt to capture the characteristic dispersal behaviour for each species. Activity was classified as diurnal or nocturnal; cathermeral species were classed as polymorphic for activity. Species were also classified in multiple states when variation between or within populations was reported. One classification decision we faced was how to categorize species that spent most of their time foraging solitarily but were either known to have extended and stable social groups or had stable sleeping associations (for example, *Loris*, *Microcebus*, *Galago*, *Pongo*). Although no primate is truly solitary, these species are particularly problematical as a few well-documented studies suggest stable community structures in nocturnal species, yet they do not form stable foraging parties[37]. The same discussion about whether orang-utans are social or solitary has longed plagued primatologists. For this reason, we used multiple classifications for these species: (1) solitary foragers, (2) polymorphic (solitary foraging plus social category), and (3) solitary foraging except for *Pongo*. This way we were able to evaluate the impact their classification had on model performance. The classification scheme that primarily relied on social grouping classification, with the exception of *Pongo*, had the highest mean likelihood ($\mathrm{LL} = -64.80$), followed by the polymorphic classification scheme ($\mathrm{LL} = -66.14$), and finally the scheme that classified *Pongo* as solitary ($\mathrm{LL} = -71.71$). *Pongo* classification affects model fit as they would be the only example of an anthropoid primate to revert from social to solitary living. We evaluated the posterior probability of predicted rate classes (zero versus non-zero) for each transition across all three classification schemes (Supplementary Fig. 2). Finally, we classified stability based on reported adult dispersal or migration events for both males (typically secondary dispersal after joining new groups) and females (classified as post-partum dispersal). This classification is more subjective than the previous traits as the data are limited and often descriptive. We classified pair-living species as stable if group turnover events were typically associated with death or severe injury to one of the adults (rather than regular emigration by resident adults). For group-living species, we defined stability as at least one sex typically remaining in the group throughout adulthood (resulting in kin-based groups). The primary references that the classifications were based on are found in the Supplementary Table 6.

Tree. The primate phylogeny was based on a sample of 10,000 ultrametric trees from version 2 of the 10kTrees Project[12]. This provides a posterior distribution of phylogenies using Bayesian inference from six mitochondrial (CYTB, COX1, COX2, 12S rRNA, 16S rRNA and a gene cluster) and three autosomal genes (MC1R, CCR5, SRY) for 230 primate species. The nodes of the consensus tree are dated using mean molecular branch lengths from the Bayesian analysis and six known fossil calibration points[12]. The consensus tree is a maximum credibility tree and was inferred from the complete 10,000 tree sample using TreeAnnotator[30]. As BayesTraits[20] (http://www.evolution.rdg.ac.uk/SoftwareMain.html) allows missing data, we included all species from the tree block rather than pruning the tree to fit the data.

Phylogenetic signal. Phylogenetic signal in data indicates that related species are more similar in a particular trait than would be expected by chance (that is, the trait of a daughter species is not independent of that of the parent). To quantify phylogenetic signal in our primate sociality data, we used the fitDiscrete function in the Geiger[38] package in R to calculate the maximum likelihood value of Pagel's lambda[13,39] on the maximum credibility tree. A λ value of 1 is consistent with a model of evolution along the phylogeny (that is, a probability of shared inheritance proportional to relatedness), whereas a λ value of 0 suggests evolution independent of the phylogenetic tree[40]. A likelihood ratio test was used to compare the fitted maximum likelihood value of λ with a model implying no phylogenetic signal ($\lambda = 0$) to a model of evolution along the tree ($\lambda = 1$). The likelihood ratio test follows a χ^2 distribution, with one degree of freedom. Polymorphisms were collapsed such that flexible species were assigned an additional flexible social category.

Model settings and performance. To identify the model best supported by the data for each analysis (social evolution, stability, social-activity and social-dispersal models, plus the social-stability data sets), we used the Discrete and Multistate option in BayesTraits[20]. We began with the reversible-jump procedure, using a uniform hyper before seed exponential rate priors with mean and variance ranging between 0 and 2 (ref. 41). We initially explored using a uniform hyperprior to seed exponential rate priors with mean and variance ranging between 0 and 2. Model performance was robust to choice of hyper prior. 'Rate dev' settings were set to achieve acceptance values within 20–40% (for most models this was 0.02, 0.05 or 0.1). To establish whether the models had converged, we evaluated the posterior distribution and trace of harmonic mean log-likelihoods; we assumed convergence when this distribution was approximately normal, the likelihood traces did not show large jumps across runs. Models visited by the Markov chain were ranked in order of their posterior probability (Supplementary Tables 1–4). The posterior sample of transition rates for the social evolution model is shown in Supplementary Fig. 3.

Each Markov chain Monte Carlo simulation was run five times for 30 million iterations sampled every 100, with the first 25 million iterations discarded as the burn-in period. Examination of the post-burn-in log-likelihood and rate parameters across the Markov chain plotted in Tracer[21] indicated that runs had reached convergence by this time (25 million iterations) and effective sample sizes for the parameters of interest were all above 2,000. We report the posterior distribution for rate parameters, marginal log-likelihoods[21] and states at ancestral nodes from the run with the median likelihood.

Model comparison: social evolution. We constructed four different models of social organization. First, all rates were set equal, simulating equal likelihood for all transitions. Second, rates were allowed to vary freely without constraint to produce a 'flexible' model. Third, we ran a 'complexity' model where transitions were restricted so that movements were only allowed between solitary and pair-living, pair-living and uni-male harems, and uni-male harems and multi-male social organization. Finally, the model structure with the highest posterior support from the reversible-jump analysis was run, allowing transitions from solitary to multi-male and from multi-male to pair-living and to uni-male and back. All other rates were set to zero. Final models were run using uniform rate priors (0–0.3) across a range informed by either the reversible-jump analyses for the data driven models or maximum likelihood analyses for theoretical models. Examination of posterior distributions indicated that the rates were well within the prior bounds. Stability of the models was checked by evaluating variance in the mean log-likelihood values over five iterations of the final analyses.

To compare alternative models of social evolution, we calculated both the marginal likelihood and Bayes Factor (the ratio of the marginal likelihoods) using Tracer[21]. The Bayes Factor (BF) shows the weight of evidence to support one model over another, from 0 to 0.5 (minimal), to 0.5–1.0 (substantial), to 1.0–2.0 (strong), to greater than 2.0 (decisive)[22].

Ancestral states. We used BayesTraits to infer the posterior probability of social behaviours at each ancestral node in the primate tree under the model with the highest posterior probability from the reversible-jump analysis. Although the results presented in Supplementary Fig. 1 are drawn on the maximum clade credibility tree, the analysis was performed across the posterior distribution of 10,000 primate trees. The ancestral state probabilities for each branch of the tree are the combined posterior probability of each state on that branch with the posterior probability that the branch itself exists.

Correlated evolution. The Discrete package in BayesTraits enables analysis of the co-evolution of two binary traits over a phylogeny. We ran two Discrete analyses to test the hypotheses that either dispersal or activity patterns determine social organization in primates by investigating the correlation and relative timing of changes in social organization with those in dispersal and activity. We ran the Discrete analysis with social organization as solitary (0) or social (1) (including pair-living), dispersal as bi-sexual (0) or either female or male (1) and activity as nocturnal (0) or diurnal (1) with cathermeral as (01). Model parameters and performance were established using the procedures described above. Exponential rate priors were seeded from a uniform hyper prior with mean and variance ranging between 0 and 2 (ref. 41). The posterior sample of reversible-jump Markov chain Monte Carlo models for social-activity analyses is shown in Supplementary Table 2, and for social-dispersal analyses in Supplementary Table 3. A Bayes Factor[21] comparison was made between the independent and the dependent reversible-jump hyperprior model runs such that independent evolution could be rejected if there was support for the dependent model. In addition to a Bayes Factor comparison, we also investigated the number of visits to independent models in the dependent run to assess whether this was above chance[20]. Mean and median transition rates for the two dependent analyses are reported in Supplementary Table 5.

31. Campbell, C. J., Fuentes, A., MacKinnon, K. C., Panger, M. & Bearder, S. K. *Primates in Perspective* (Oxford Univ. Press, 2007).
32. Dixson, A. *Primate Sexuality: Comparative Studies of the Prosimians, Monkeys, Apes, and Human Beings* (Oxford Univ. Press, 1998).
33. Dunbar, R. I. M. *Primate Social Systems* (Chapman & Hall, 1988).
34. Smuts, B., Cheney, D., Seyfarth, R., Wrangham, R. & Struhsaker, T. *Primate Societies* (Univ. Chicago Press, 1987).
35. Isbell, L. A. & van Vuren, D. Differential costs of locational and social dispersal and their consequences for female group-living primates. *Behaviour* **133,** 1–36 (1996).

36. Jack, K. M. & Isbell, L. A. Dispersal in primates: advancing an individualized approach. *Behaviour* **146,** 429–436 (2009).
37. Schulke, O. & Ostner, J. Big times for dwarfs: social organization, sexual selection, and cooperation in the Cheirogaleidae. *Evol. Anthropol.* **14,** 170–185 (2005).
38. Harmon, L. J., Weir, J. T., Brock, C. D., Glor, R. E. & Challenger, W. GEIGER: investigating evolutionary radiations. *Bioinformatics* **24,** 129–131 (2008).
39. Pagel, M. D. Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. *Proc. R. Soc. Lond. B* **255,** 37–45 (1994).
40. Freckleton, R. P., Harvey, P. H. & Pagel, M. D. Phylogenetic analysis and comparative data: a test and review of evidence. *Am. Nat.* **160,** 712–726 (2002).
41. Pagel, M. D., Meade, A. & Barker, D. Bayesian estimation of ancestral character states on phylogenies. *Syst. Biol.* **53,** 673–684 (2004).

SHORT COMMUNICATION

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The evolutionary history of primate mating systems

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Keywords: primates, mating systems, monogamy, polygyny, polygynandry, phylogeny, Bayesian phylogenetics

Unlike bones, behavior does not fossilise, so it is hard to infer the evolutionary history of social traits. However, we have shown elsewhere that Bayesian phylogenetic methods allow the investigation of ancestral states and models of evolution of social grouping behavior in primates. Here, we extend this analysis to another significant aspect of primate social life, which may be subject to different evolutionary pressures - mating systems. We show that mating systems evolved from a polygynandrous state at the root of the phylogeny to the two derived states of harem-polygyny and monogamy. Unlike social organization, where there were no transitions from uni-male groups to pairs, here we found positive transition rates from both polygynous mating states into monogamy. There were no transitions out of monogamy to another mating state. Both derived mating systems evolved late in primate evolution. Nocturnal primates remained solitary foragers while their mating systems evolved from polygynandry to harem-polygyny and monogamy. However, among diurnal primates the derived mating states evolved at the same time as the derived states of social organization.

Although rare among mammals, sociality is common among primates.[1] In a recent study we showed how group living evolved in primates following a switch to diurnal activity patterns.[2] However, primate societies are shaped not only by the groups that animals live in, but also by the mating strategies that they employ. Therefore, for a full understanding of the evolutionary history of primate social systems both need to be investigated.

We have shown previously that for social traits with a strong phylogenetic signal, such as social organization or dispersal patterns, it is possible to infer models of evolution, transition rates between states and ancestral states at nodes on the primate phylogeny.[2] Here we use Bayesian phylogenetic methods[3] to infer ancestral states and evolutionary pathways for mating systems in primates, complementing our previous investigation of social organization and allowing the comparison of these two features of primate life.

An analysis using Ape[4] in R gave a Lambda value of 0.996, not significantly different from 1 (p = 0.679), suggesting a strong phylogenetic signal in the mating system data among primates.

We ran RJ MCMC analyses in BayesTraits[5] with mating system classified as both a binary trait (polygyny/monogamy) and a three state trait (harem-polygyny/polygynandry/monogamy). The analysis for the binary classification supports polygyny as the ancestral primate mating system at the root of the phylogeny (polygyny mean probability = 0.974 +/- 0.001; monogamy mean = 0.026 +/- 0.001). For the three state trait the root was polygynandry (polygynandry mean = 0.853 +/- 0.003; harem-polygyny mean = 0.109 +/- 0.002; monogamy mean = 0.038 +/- 0.001).

The best fitting model from the RJ procedure (with 71% of the posterior probability distribution) revealed that from polygynous mating at the root of the phylogeny there was a strong transition rate to monogamy, but a zero reverse rate (**Fig. 1A**). We also split the polygynous mating state into harem-polygyny and polygynandry to understand the dynamics of mating change better.[6] From polygynandry at the root of the phylogeny there were strong transition rates into both harem-polygyny and monogamy, and a non-zero but weaker rate from harem-polygyny to monogamy (best fitting model from the RJ procedure, with 33% of the posterior probability distribution). All other rates were zero (**Fig. 1B**).

Across the whole posterior probability distribution, for the three state analysis, the mode transition rate out of monogamy was zero, while the transitions from harem-polygyny to monogamy and back to polygynandrous mating were zero for 18% and 41% of the time respectively (**Fig. 1B**). Transitions from polygynandrous mating to the other two states were never zero.

Harem-polygyny evolved earliest among strepsirrhines, first at the root of the Loris sub-family *Perodicticinae* (~42mya) and later at the root of the Lepilemurs (~36mya) (**Fig. 2**). Monogamy evolved in a number of Lemur families from ~28mya. Among haplorrhines monogamy emerged first at the root of *Callicebus* (~26mya), followed by *Aotus* and the Callitrichids (~22mya) and then Gibbons (~19mya). Harem-polygyny evolved later among Anthropoids, at the root of the *Trachypithecus* genus (~16mya), and later still at the root of the *Cercopithecus* genus (~11mya).

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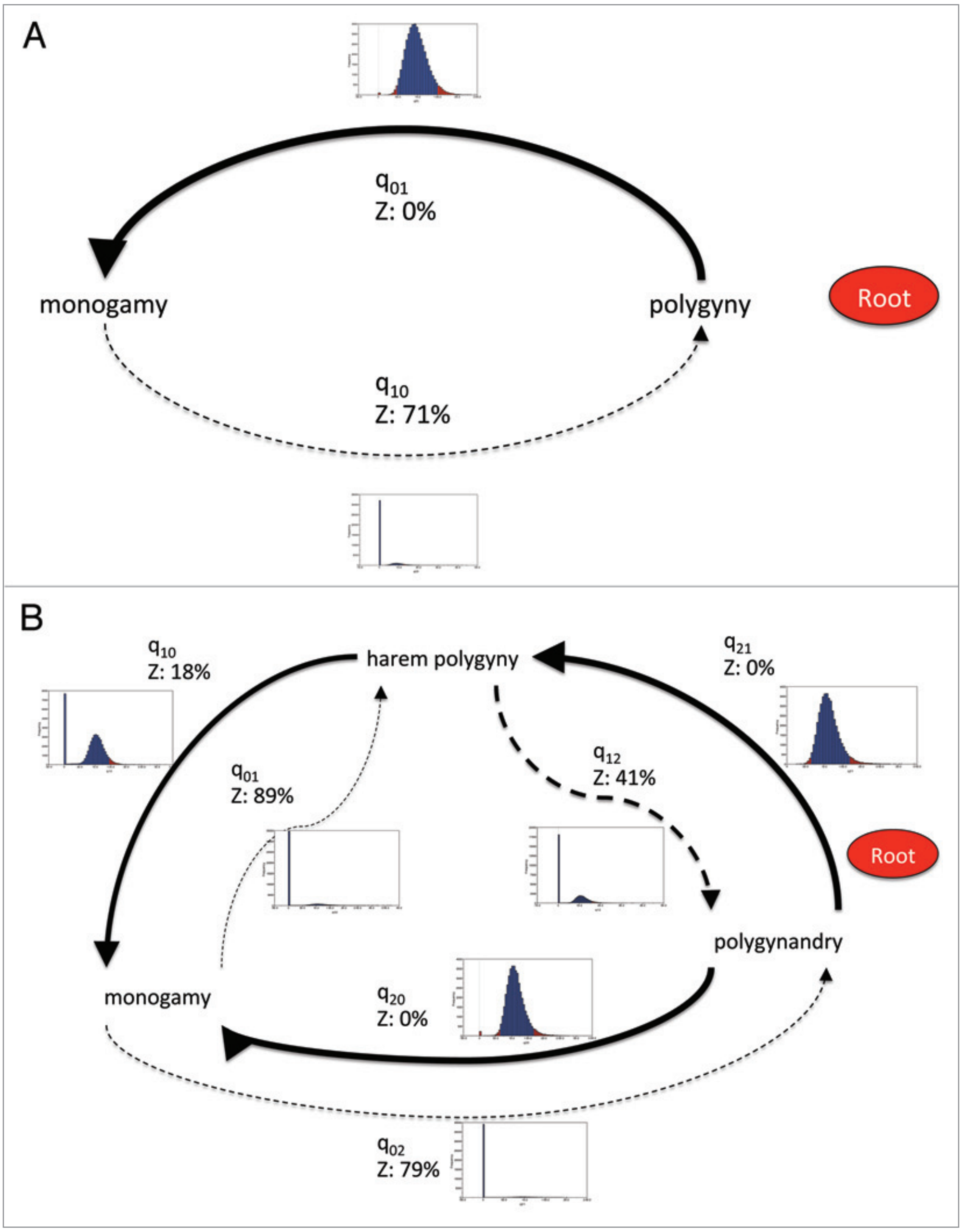

Figure 1. Model of evolution of primate mating systems showing posterior distribution of transition rates between states. A. Monogamy and polygyny. B. Monogamy, harem-polygyny and polygynandry. Thickness of arrows reflects proportion of time the transition rate is not zero. Z denotes a zero transition rate as a proportion of posterior probability distribution. A dashed line denotes a zero transition rate in the RJ derived model. Graphs show posterior probability distribution of each transition rate.

Like social organization[2] mating system data in primates show a strong phylogenetic signal, indicating that it is possible to make inferences about the evolution of this trait across the primate tree. This also suggests that history plays a significant role in the current distribution of both these social traits across species. The model of evolution for primate mating systems is similar to that for primate social organization,[2] once multi-male/multi-female groups were established, with transitions to both monogamy and harem-polygyny. The pathways differ in that monogamy was found to evolve from both harem-polygyny and polygynandry.

As with social organization, once monogamy was established (or pair living, in the case of social organization) there were no further transitions. This may be because the cognitive changes to enable the behavioral co-ordination required for stable monogamy are hard to reverse,[7] and also because the factors leading to the evolution of monogamy persisted over time.[8,9] Harem-polygyny

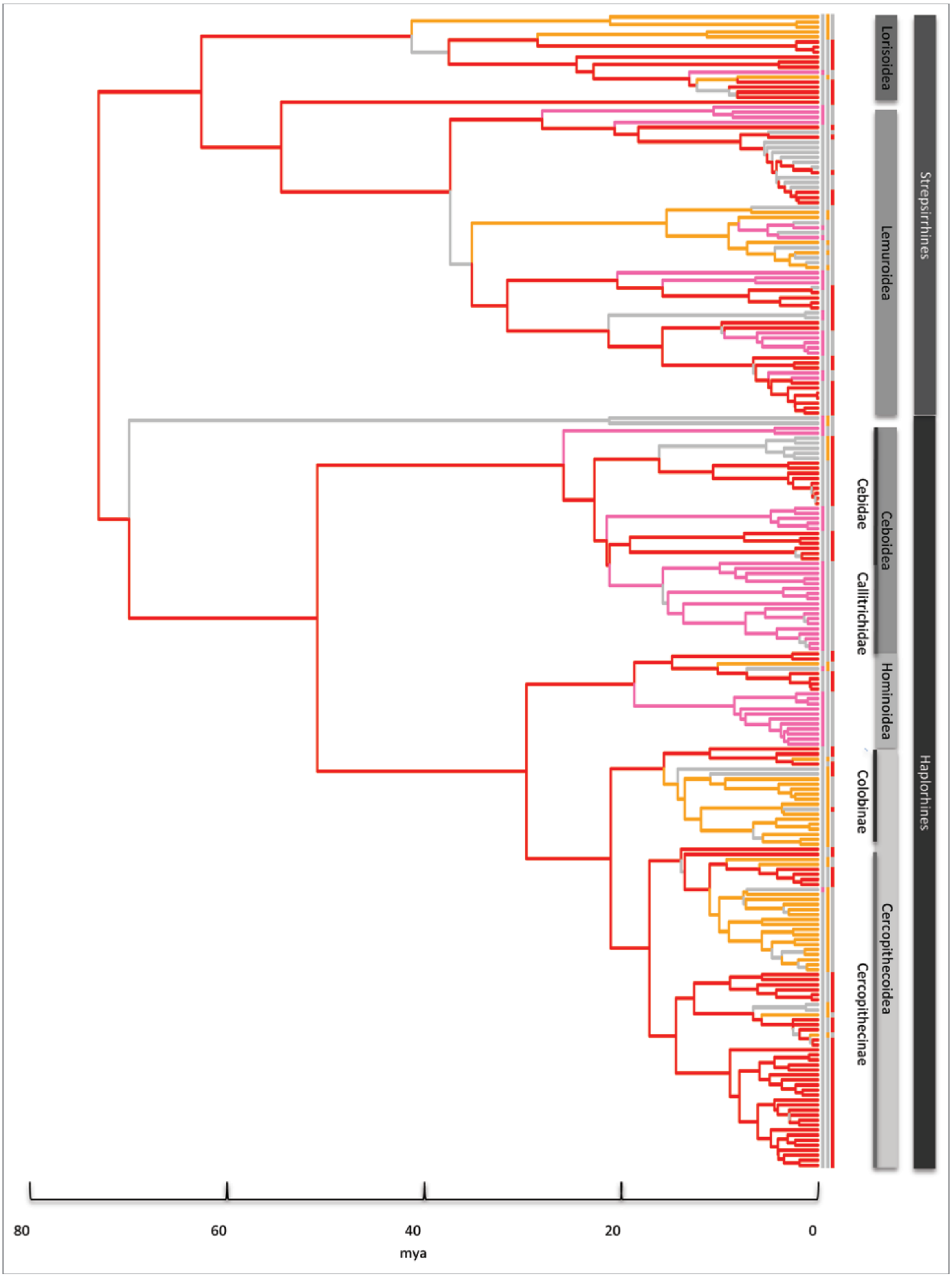

Figure 2. Primate phylogeny with ancestral states for mating systems derived from RJ MCMC model of evolution. The tree topology is the maximum clade credibility tree from the 10k Trees Project[13] posterior distribution with branch length drawn proportional to time. Branches and tips are colored for polygynandry (red), harem-polygyny (orange) and monogamy (pink) where the combined probability of the state and the branch is greater than or equal to 0.7. Where the combined probability is less than 0.7 the branch is gray.

also evolved directly from polygynandry, but there were back transitions. In contrast, there were no direct transitions into harem-polygyny from monogamy suggesting that rather than a 'combination of pairs'[10] harem-polygyny can be better described as 'degraded' polygynandry. An interesting question for future work is the extent to which this is due to ecological and physiological conditions, such as small female groups and asynchronous estrus, enabling a single male to monopolise mating within a group of females.[11,12] Co-evolutionary models could be used to test the factors leading to the emergence of harem-polygyny.

The derived states of mating system and social organization evolved at a similar time across diurnal primate clades such that they matched through most of primate evolutionary history. However, among those primates that remained nocturnal, solitary social organization persisted even when mating systems changed from the ancestral state of polygynandry to the derived states of harem-polygyny or monogamy.

Methods

Model testing was performed across a Bayesian posterior distribution of 10,000 ultrametric primate trees derived from genetic data (version 2 of the 10kTrees Project) to account for uncertainty in the underlying phylogeny.[13] We present a maximum clade credibility tree that was inferred from the complete 10kTrees sample using TreeAnnotator.[14] Pagel's Lambda was estimated in R, using the Ape[4] and Geiger[15] packages. We used a reversible-jump (RJ) Markov chain Monte Carlo (MCMC) analysis in the Multistate procedure of BayesTraits (available from www.evolution.rdg.ac.uk)[5,16] to derive the posterior distribution of log-likelihoods, the rate parameters of models of evolution, and trait values at ancestral nodes on the primate phylogeny including the root, where the frequency in the posterior distribution represents the posterior belief in that outcome. Primate mating systems were classified as monogamous (0) harem-polygynous (1) or polygynandrous (2), polymorphic species were coded accordingly, with data taken from the literature (see SI for[2]). The term monogamy is used in the sense of social monogamy, which may vary from genetic monogamy in a number species.

References

1. Krebs J, Davies N. *Behavioral ecology: an evolutionary approach*. 4th edn, (Wiley-Blackwell, 1997).
2. Shultz S, Opie C, Atkinson QD. Stepwise evolution of stable sociality in primates. *Nature* **479**, 219-222,http://www.nature.com/nature/journal/v479/n7372/abs/nature10601.html - supplementary-information (2011).
3. Huelsenbeck JP, Ronquist F, Nielsen R, Bollback JP. Bayesian inference of phylogeny and its impact on evolutionary biology. Science 2001; 294:2310-4; http://dx.doi.org/10.1126/science.1065889; PMID:11743192.
4. Paradis E, Claude J, Strimmer K. APE: Analyses of Phylogenetics and Evolution in R language. Bioinformatics 2004; 20:289-90; http://dx.doi.org/10.1093/bioinformatics/btg412; PMID:14734327.
5. Pagel MD, Meade A. Bayesian analysis of correlated evolution of discrete characters by reversible-jump Markov chain Monte Carlo. Am Nat 2006; 167:808-25; PMID:16685633; http://dx.doi.org/10.1086/503444.
6. Kappeler PM, van Schaik CP. Evolution of primate social systems. Int J Primatol 2002; 23:707-40; http://dx.doi.org/10.1023/A:1015520830318.
7. Shultz S, Dunbar RIM. The evolution of the social brain: anthropoid primates contrast with other vertebrates. Proc Biol Sci 2007; 274:2429-36; PMID:17652066; http://dx.doi.org/10.1098/rspb.2007.0693.
8. van Schaik CP, Kappeler PM. in *Monogamy: mating strategies and partnerships in birds, humans and other mammals* (eds U.H. Reichard & C. Boesch) Ch. 4, 59–80 (Cambridge University Press, 2003).
9. Opie C, Atkinson QD, Dunbar RIM, Shultz S. The evolution of pair living in primates. (*in prep*).
10. Harcourt AH, Greenberg J. Do gorilla females join males to avoid infanticide? A quantitative model. Anim Behav 2001; 62:905-15; http://dx.doi.org/10.1006/anbe.2001.1835.
11. Dunbar RIM. *Primate Social Systems*. (Chapman & Hall, 1988).
12. Dunbar RIM. in *Primate Males: causes and consequences of variation in group composition* (ed Peter M. Kappeler) 259-268 (Cambridge University Press, 2000).
13. Arnold C, Matthews LJ, Nunn CL. The 10k trees website: a new online resource for primate phylogeny. Evol Anthropol 2010; 19:114-8; http://dx.doi.org/10.1002/evan.20251.
14. Drummond AJ, Rambaut A. BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evol Biol 2007; 7:214; PMID:17996036; http://dx.doi.org/10.1186/1471-2148-7-214.
15. Harmon LJ, Weir JT, Brock CD, Glor RE, Challenger W. GEIGER: investigating evolutionary radiations. Bioinformatics 2008; 24:129-31; PMID:18006550; http://dx.doi.org/10.1093/bioinformatics/btm538.
16. Pagel MD, Meade A, Barker D. Bayesian estimation of ancestral character states on phylogenies. Syst Biol 2004; 53:673-84; PMID:15545248; http://dx.doi.org/10.1080/10635150490522232.