Male infanticide leads to social monogamy in primates

Christopher Opie[a,1], **Quentin D. Atkinson**[b], **Robin I. M. Dunbar**[c], **and Susanne Shultz**[d]

[a]Department of Anthropology, University College London, London WC1H 0BW, United Kingdom; [b]School of Psychology, University of Auckland, Auckland 1142, New Zealand; [c]Department of Experimental Psychology, University of Oxford, Oxford OX1 1UD, United Kingdom; and [d]Computational and Evolutionary Biology Research Group, Faculty of Life Sciences, University of Manchester, Manchester M13 9PT, United Kingdom

Edited by C. Owen Lovejoy, Kent State University, Kent, OH, and approved June 28, 2013 (received for review May 1, 2013)

Although common in birds, social monogamy, or pair-living, is rare among mammals because internal gestation and lactation in mammals makes it advantageous for males to seek additional mating opportunities. A number of hypotheses have been proposed to explain the evolution of social monogamy among mammals: as a male mate-guarding strategy, because of the benefits of biparental care, or as a defense against infanticidal males. However, comparative analyses have been unable to resolve the root causes of monogamy. Primates are unusual among mammals because monogamy has evolved independently in all of the major clades. Here we combine trait data across 230 primate species with a Bayesian likelihood framework to test for correlated evolution between monogamy and a range of traits to evaluate the competing hypotheses. We find evidence of correlated evolution between social monogamy and both female ranging patterns and biparental care, but the most compelling explanation for the appearance of monogamy is male infanticide. It is only the presence of infanticide that reliably increases the probability of a shift to social monogamy, whereas monogamy allows the secondary adoption of paternal care and is associated with a shift to discrete ranges. The origin of social monogamy in primates is best explained by long lactation periods caused by altriciality, making primate infants particularly vulnerable to infanticidal males. We show that biparental care shortens relative lactation length, thereby reducing infanticide risk and increasing reproductive rates. These phylogenetic analyses support a key role for infanticide in the social evolution of primates, and potentially, humans.

Social monogamy, or pair-living, is much more common among birds (90% of species) (1) than mammals (less than 3% of species) (2). In many bird species, the successful rearing of offspring requires investment of both pair-members in incubation and provisioning, effectively constraining the adults to stay in a pair (3). In mammals, by contrast, female internal gestation and lactation characteristically results in highly skewed parental investment, with males continuing to search for additional reproductive partners after each successful mating. Because of this behavior, the typical mammal mating system can be characterized as polygynandry, whereby multiple males mate with multiple females within a breeding season (4–6). Because social monogamy in mammals is relatively uncommon and appears to require a fundamental change in male reproductive strategy, understanding its evolution has generated a great deal of interest. Additionally, the evolutionary history of social monogamy in mammals may help uncover the selective pressures that led to the formation of long-term pair bonds in humans.

Three separate hypotheses have been proposed to explain the evolution of social monogamy: parental care, mate guarding, and infanticide risk. First, social monogamy may arise where the cost of raising offspring is high, such that a female must rely on the help of others, particularly for carrying infants (2, 7). For example, the females of socially monogamous New World primates (callitrichids and *Aotus*) typically give birth to twins and cannot cope with infant carrying without the help of a male (2). Although some socially monogamous mammal species are associated with high levels of care (8–10), biparental care has been discounted as a general explanation because it is not ubiquitous in socially monogamous mammals (11). It may be that rather than high-cost offspring giving rise to monogamy, monogamy enables the production of high-cost offspring. Second, social monogamy may arise when females occupy small but discrete ranges, making it difficult for males to monopolize more than one female. Males may choose to form a pair to guard the female from rival males seeking to mate with her (6, 11). It has been argued that this was the route to social monogamy among small ungulates (12), and a similar suggestion has been used to explain monogamy in other mammals, including primates (6, 11). Finally, social monogamy might arise where the risks of infanticide are high and resident males can provide protection against infanticidal males (13–16). Where lactation is longer than gestation, females are expected to avoid suckling two infants of different ages simultaneously by delaying the return to oestrus after parturition. Where oestrus is delayed, it can pay a male, who is not the father, to kill an unweaned infant so that the female returns to oestrus sooner (17). There remains no consensus over which of the above hypotheses best explains monogamy in primates. Some researchers have proposed that a combination of explanations may be plausible (16), but others doubt whether it is possible to test between these hypotheses effectively or to infer the historical origin of social monogamy (18).

Social monogamy is more common in primates than in other mammalian orders, accounting for more than a quarter of species across all of the major primate clades (Dataset S1). Social monogamy in primates evolved directly from polygynandry and appeared relatively late (16 Mya) in primate history (19, 20). Interestingly, social monogamy appears to be a stable state; once monogamy evolves there are few transitions back into polygynous mating systems (19). Primates, therefore, represent an intriguing case for understanding the factors associated with the evolution of social monogamy.

Here we use likelihood-based phylogenetic comparative methods in a Bayesian framework (21) to examine each of the three hypotheses for the origin of social monogamy, testing for correlated evolution between mating systems and a key dichotomized marker trait for each hypothesis: paternal care, female ranging patterns, and male infanticide. Given previous disagreement about potential explanations for social monogamy, we predicted that there would be evidence for correlated evolution between social monogamy and each of the putative markers; however, our temporal discrete analyses can also identify the likely factors driving the switch to monogamy versus the responses following that switch. For discrete traits, we compare the fit of the dependent model of evolution between mating systems and these traits to a model in which the traits are constrained to evolve independently. In addition to correlated evolution, we use

---

Author contributions: C.O. and S.S. designed research; C.O. performed research; Q.D.A. contributed new reagents/analytic tools; C.O. analyzed data; and C.O., Q.D.A., R.I.M.D., and S.S. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

[1]To whom correspondence should be addressed. E-mail: kit.opie@ucl.ac.uk.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1307903110/-/DCSupplemental.

ancestral-state reconstructions and model rate parameters to examine whether certain traits preceded monogamy and whether they tended to make the appearance of monogamy more likely. For example, if a trait evolved after the emergence of social monogamy and is more likely to arise in the presence of monogamy, it could be seen as the result of pair-living. Conversely, if a trait is the key functional driver or sufficient condition for the evolution of monogamy, we expect its appearance to be rapidly and regularly followed by the emergence of monogamy.

Results

We find decisive support for correlated evolution between social monogamy and paternal care, female ranging patterns, and male infanticide (Table 1). This supports our intuition that these traits represent a suite of social behaviors linked to social monogamy. However, the demonstration of correlation between traits does not identify any direction of causality. The ancestral state reconstructions (*SI Appendix* and Figs. S4–S7) and model rates (Fig. 1) suggest that only male infanticide precedes the initial shift to social monogamy. Paternal care only evolves after a switch to social monogamy and not in polygynous mating systems (Fig. 1*A*). Moreover, once paternal care evolves within social monogamy it is unlikely to be lost. This finding suggests that biparental care was not a factor driving the shift to monogamy. Within a few lineages, discrete female ranges arose independently of social monogamy; however, a rapid subsequent switch to discrete ranges following the evolution of social monogamy suggests they might contribute to its maintenance, but were not a causal factor in its appearance (Fig. 1*B*).

In contrast, as well as strong correlated evolution between male infanticide and mating systems, male infanticide precedes the switch to social monogamy (Fig. 1*C* and Table 1). First, there is little support for a transition from polygyny to monogamy with low infanticide; social monogamy is inferred to have been far more likely to evolve from polygyny in the presence of high infanticide. Second, once social monogamy evolves there is a high probability of a subsequent reduction in male infanticide and a smaller probability of transitions back to polygyny with infanticide remaining high. Taken together, these data suggest that social monogamy with high infanticide is an unstable state, whereas social monogamy with low infanticide is a very stable one.

In addition, socially monogamous species have lower risk of infanticide, in terms of the proportion of the breeding cycle devoted to lactation (the "weaning proportion"), than do polygynous species (Table 2). This finding hints at one mechanism by which social monogamy may reduce infanticide risk: social monogamy facilitates a shorter lactation period compared with gestation, thereby reducing infanticide risk. There was a strong reduction in the weaning proportion with the emergence of social monogamy in most clades (*SI Appendix* and Fig. S8). Furthermore, a Markov Chain Monte Carlo (MCMC) phylogenetic t test of paternal care with weaning proportion shows that species without paternal care have a significantly higher weaning proportion than those with paternal care (Table 2).

Discussion

Our results uncover the evolutionary relationship between social monogamy and its hypothesized causes. The evolution of both discrete female ranges and paternal care followed the shift to social monogamy rather than preceded it. Thus, there is little evidence to suggest that discrete female ranges are the cause of social monogamy in primates (contra refs. 6 and 11).

Similarly, although paternal care and social monogamy showed strong correlated evolution, paternal care (as seen in the callitrichids and *Aotus*) followed the appearance of social monogamy (15, 22). Biparental care in birds also appears to be a secondary adaptation following pair formation (23). In primates, paternal care is associated with a shortening of interbirth intervals and an increase in reproductive rates similar to that seen in birds and other mammals (2, 7, 15, 24). In socially monogamous primate species, such as *Aotus* and the callitrichids, paternal care shortens the lactation period, presumably because females can increase the resources devoted to lactation when relieved of some of the costs of infant care. Although this behavior can make monogamy more profitable (15), it appears not to be the cause of monogamy.

Of the traits we tested, high male infanticide alone consistently preceded the appearance of social monogamy across primates. Our analyses suggest that socially monogamous species are much more likely to have low male infanticide rates (Fig. 1*C*), presumably as social monogamy provides an effective counter-strategy. Social monogamy can reduce the incidence of infanticide because one or both pair-members can defend infants (13, 15). Shortened lactation time associated with biparental care may, however, play a particularly important role by hastening oestrus resumption, and so further mitigating infanticide risk (25). Both partners may, therefore, initially benefit from male protection of unweaned infants and in some species there is a secondary benefit of increasing reproductive rates via biparental care (15).

This association between infanticide and social monogamy raises the question of why more primate species are not monogamous. This question becomes particularly relevant when considering the extraordinarily high rates of infanticide in species such as gorillas and langurs, where it has been estimated that infanticide accounts for between 34% (in gorillas, *Gorilla gorilla beringei*) and 64% (in langurs, *Semnopithecus entellus*) of all infant deaths (26, 27). One would expect a strong pressure for these species to opt for social monogamy if it is an effective defense against infanticide. However, a switch to social monogamy may only be possible where ecological conditions permit. Other factors play a role in determining optimal grouping patterns: predation pressure drives up group size (28, 29) and resource distribution and habitat use also impact on group size and structure (30, 31). Hanuman langurs and gorillas incur high levels of mortality from infanticide but also live in a habitat with high predation risk. The pressure to maintain cohesive social groups as an antipredator defense may render social monogamy a nonstarter.

Table 1. Likelihoods for dependent and independent models of correlated evolution between mating system and other traits

	Dependent model		Independent model		
Coevolution analysis	Log likelihood	SE	Log likelihood	SE	Log_{10} Bayes factor
Paternal care	−83.10	±0.02	−0.92.82	±0.05	4.22
Discrete female ranges	−95.60	±0.03	−119.40	±0.02	10.34
Infanticide	−163.55	±0.04	−174.55	±0.04	4.78

The $\log_{10}$ Bayes factor indicates the relative support for the dependent model over the independent model. Values <1 suggest little support, 1–2 strong support and >2 decisive support for the dependent over the independent model (54).

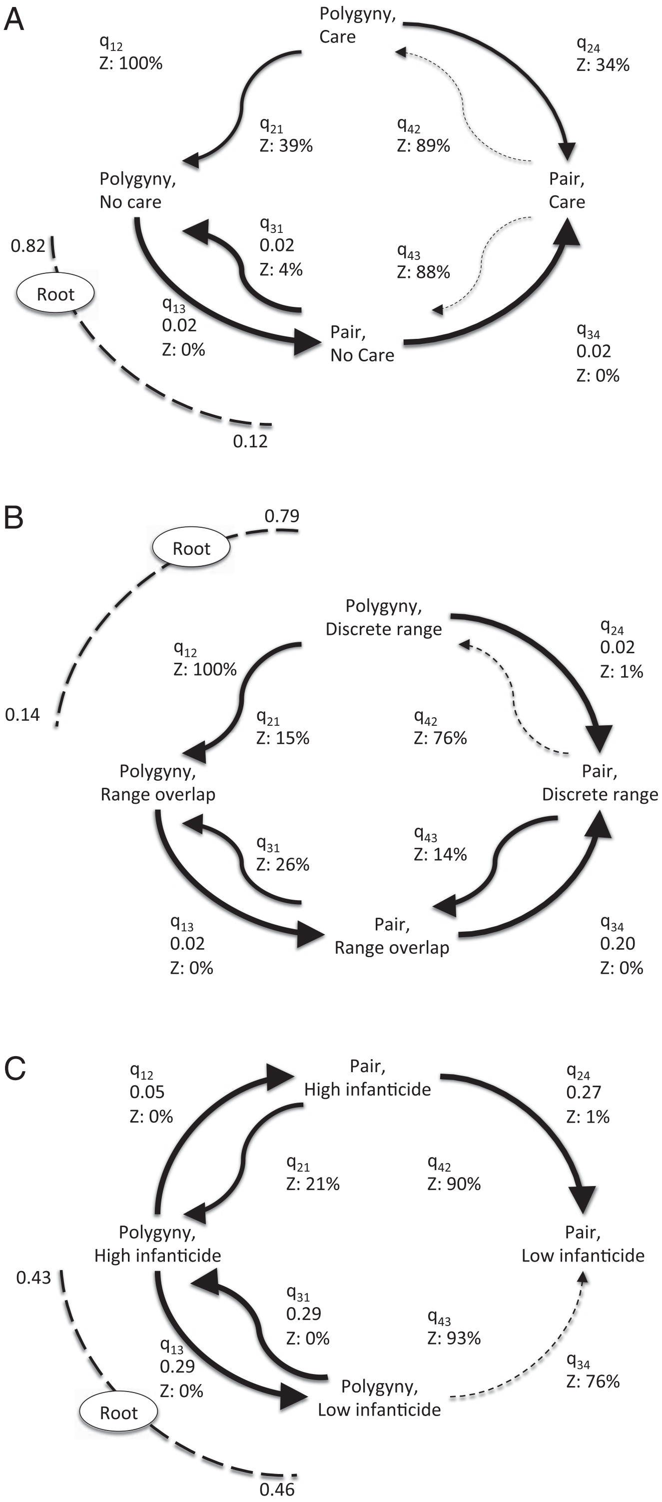

Fig. 1. Coevolution between primate mating system and: (*A*) paternal care, (*B*) discrete female ranges, and (*C*) reported infanticide. The ancestral state reconstruction is depicted by dashed lines, which includes the proportion of the posterior distribution for alternative states. Z denotes visits assigned to zero as a proportion of the posterior probability distribution. Thickness of arrows reflects proportion of time transition rate is not assigned to zero, with dashed line >50% zeros and no line ≥90% zeros. Number below rate name (qij) is the mean transition rate where rate distribution has zero or very low *z* value.

Table 2. Phylogenetic *t* test of mating system and weaning proportion and paternal care and weaning proportion using MCMC methods in BayesTraits

Model	β	SE β	*P* value
Weaning proportion and mating system	0.01	0.00	0.044
Weaning proportion and paternal care	0.16	0.05	<0.001

Nevertheless, these results could explain why social monogamy is more prevalent among primates than in other mammalian orders. Complex sociality in primates is associated with large brains (32), which in turn is associated with altricial young and long development and lactation periods (25, 33). This extended dependency period increases the time unweaned infants are vulnerable to male infanticide (34). However, social monogamy can help overcome the gray ceiling imposed by the high metabolic and developmental costs of large brains through male care (24), and allow for slow reproductive rates (35) without increased infanticide risk. Encephalization in great apes (and especially humans) has led to very long lactation periods and heightened risk of infanticide (as measured by the weaning proportion). Chimpanzees deal with the infanticide risk imposed by this extended dependency period with a polygynandrous mating system: males defend females and infants within their territory (36), and females ensure paternity confusion through multiple mating with community males (37). Promiscuous mating in orangutans has also been suggested as an anti-infanticide strategy (38). For gorillas, although polygyny ensures paternity certainty for the group male, it also results in the highest infanticide rates seen among apes (37). Human pair bonds may also be a response to the pressure that long infant dependency places on females to find effective protection for their young (39). Indeed, a recent reconstruction of ancestral mating/marriage systems in humans suggests that Australopithecines (40, 41) and early modern humans (42) may have been (at least facultatively) monogamous. The transition to social monogamy in humans has been proposed to depend on females choosing to stay faithful to males, even when of lower quality (43). Once in place these pair-bonds would facilitate paternal care in the form of male protection and provisioning (44, 45). Male infanticide could thus have been the pressure that drove females as well as males to stay in long-term consortships or bonds (35).

Methods

Primate Phylogeny. Analyses were conducted on a Bayesian posterior distribution of 10,000 phylogenies based on mitochondrial and autosomal genes for 230 primate species [version 2 of the 10kTrees Project (46)]. A large posterior sample allowed us to infer the evolutionary history of traits while accounting for phylogenetic uncertainty (46). To display ancestral character traits, we inferred a maximum-clade credibility tree from the complete 10kTrees sample (46) using TreeAnnotator (47) with nodes dated using median molecular branch lengths and six known fossil calibration points.

Primate Trait Data. Primate trait data were extracted from the literature and from primary sources (*SI Appendix* and Dataset S1). Levels of allocare vary widely across primate species; we define paternal care as occurring only where males provide care for at least 30% of infant time (48). We use two indices of infanticide pressure. First, we collated data on actual cases of infanticide for wild populations; we only included cases where the infanticide was substantiated either by direct observation or by the exclusion of other possibilities. It may be that infanticide is affected by sampling effort, such that it is more likely to have been observed in well-studies species, and may have been missed in less well-studied ones. For example, it is only after extensive fieldwork that infanticide has been suggested to take place following male absence in *Hylobates lar* (49). We accounted for possible sampling issues in several ways. First, we only included species that had at least 20 publications. Second, we classified infanticide rates as low or high, so as to allow for the possibility that low levels of infanticide are occurring in species where it has not been documented. Third, we demonstrate that systematic sampling biases could not account for the observed patterns (*SI Appendix*). Fourth, we used an independent index of infanticide risk that is not open to such bias (the proportion of the breeding cycle, defined as Gestation + Lactation, devoted to lactation) (17). To avoid the issues of nonnormally distributed data associated with ratios, we converted these data to a measure of the proportion of the breeding cycle taken up by lactation, hereafter termed "weaning proportion" [L/(L+G)], which was arc sine-transformed for analysis. Seasonal breeders with a reproductive "time-out" period were excluded, as a weaning proportion value above 50% would falsely suggest that infanticide would bring a female back into oestrus sooner, and thereby improve mating opportunities for males.

Analyses. ***Modeling trait evolution.*** We used a likelihood framework and Bayesian inference to model the evolution of traits along the branches of the primate phylogeny. Following Shultz, Opie, and Atkinson (20), analyses were carried out in BayesTraits (50, 51) using an MCMC (52) sampling algorithm together with a reversible jump (RJ) procedure. Rather than fitting a model in which all changes are possible, the RJ procedure searches the posterior distribution of possible models by linking (setting to equal) or removing (setting to zero) transition-rate parameters. Models are then sampled in proportion to their likelihood, accounting for variation in the number of parameters. This process allows us to explore the space of possible models and derive a Bayesian posterior distribution of model log-likelihoods, rate parameters, and inferred ancestral states on the primate phylogeny.

Maximum-likelihood analysis of the data, which gives point estimates of model parameters, indicated a small number of changes per unit of branch length such that the prior distribution on rates could be described by an exponential probability distribution. The prior was seeded from an exponential hyperprior with a mean and variance in the range of 0–2 (50). 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 15% and 40% (50). Convergence was checked visually by evaluating changes in the log-likelihood in Tracer (53). Each MCMC chain was run five 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 postconvergence portion of each run are reported.

Ancestral states. We used an RJ MCMC approach within the Multistate procedure in BayesTraits (50, 51) to infer states at ancestral nodes for each trait (*SI Appendix* and Figs. S4–S7). Although these results 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 node of the tree (the colored pies in *SI Appendix* and Figs. S4–S7) are the combined posterior probability of each state at that node with the posterior probability that the node itself exists.

Correlated evolution between social monogamy and other traits. The Discrete option in BayesTraits can be used to test for the correlated evolution of two binary traits over a phylogeny. We coded mating system as a binary variable-polygyny (0) (including both uni-male/multifemale and multimale/multifemale systems) versus social monogamy (1), and tested for evidence of correlated evolution with the other binary traits (Table 1). Evidence for correlated evolution was measured using a Bayes factor (54) comparing model fit between a model in which the traits are allowed to evolve independently (the independent model) to one in which rates of change in one trait are dependent on rates in the other (the dependent model). The independent model can be rejected if there is support for the dependent model, indicating correlated evolution between the mating system and the chosen trait. For comparisons between models we calculated the $\log_{10}$ Bayes factor, generated with Tracer (53). The $\log_{10}$ Bayes factor 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) (54). We also tested the relative timing of the evolution of the traits by comparing the transition rates between states (Fig. 1), and the switches inferred from the ancestral state reconstructions (*SI Appendix* and Figs. S4–S7).

A random-walk MCMC procedure in BayesTraits Continuous (50, 55) was used to infer the ancestral states of the continuous trait weaning proportion (representing infanticide risk) across the primate phylogeny, which was then plotted onto the maximum-clade probability primate tree (*SI Appendix* and Fig. S8). Phylogenetic *t* tests were run using Continuous to test for correlated evolution between the binary mating system trait and weaning proportion, and paternal care and weaning proportion, in a Bayesian framework using MCMC methods, where the percentage of the posterior of the regression coefficient that crosses zero indicates the *P* value (55).

ACKNOWLEDGMENTS. This work was supported in part by a European Research Council Advanced grant (to C.O.); a Rutherford Discovery Fellowship (to Q.D.A.); a European Research Council Advanced grant (to R.I.M.D.); and a Royal Society University Research Fellowship (to S.S.).

1. Lack D (1968) *Ecological Adaptations for Breeding in Birds* (Methuen & Co, London).
2. Kleiman DG (1977) Monogamy in mammals. *Q Rev Biol* 52(1):39–69.
3. Orians GH (1969) On the evolution of mating systems in birds and mammals. *Am Nat* 103(934):589.
4. Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. *Anim Behav* 28(4):1140–1162.
5. Dobson FS (1982) Competition for mates and predominant juvenile male dispersal in mammals. *Anim Behav* 30(4):1183–1192.
6. Brotherton PNM, Komers PE (2003) Mate guarding and the evolution of social monogamy in mammals. *Monogamy: Mating Strategies and Partnerships in Birds, Humans and Other Mammals*, eds Reichard UH, Boesch C (Cambridge Univ Press, Cambridge, UK), pp 42–58.
7. Clutton-Brock TH, Harvey PH (1977) Primate ecology and social organization. *J Zool* 183(1):1–39.
8. Wynne-Edwards KE, Lisk RD (1989) Differential effects of paternal presence on pup survival in two species of dwarf hamster (*Phodopus sungorus* and *Phodopus campbelli*). *Physiol Behav* 45(3):465–469.
9. Ribble D (2003) The evolution of social and reproductive monogamy in *Peromyscus*: Evidence from *Peromyscus californicus* (the California mouse). *Monogamy: Mating Strategies and Partnerships in Birds, Humans, and Other Mammals*, eds Reichard UH, Boesch C (Cambridge Univ Press, Cambridge, UK), pp 161–166.
10. Clutton-Brock TH (1989) Mammalian mating systems. *Proc R Soc Lond B Biol Sci* 236(1285):339–372.
11. Komers PE, Brotherton PNM (1997) Female space use is the best predictor of monogamy in mammals. *Proc Biol Sci* 264(1386):1261–1270.
12. Brotherton PNM, Manser MB (1997) Female dispersion and the evolution of monogamy in the dik-dik. *Anim Behav* 54(6):1413–1424.
13. van Schaik CP, Dunbar RIM (1990) The evolution of monogamy in large primates: A new hypothesis and some crucial tests. *Behaviour* 115(1-2):30–61.
14. van Schaik CP, Kappeler PM (1997) Infanticide risk and the evolution of male-female association in primates. *Proc Biol Sci* 264(1388):1687–1694.
15. Dunbar RIM (1995) The mating system of callitrichid primates: I. Conditions for the coevolution of pair bonding and twinning. *Anim Behav* 50(4):1057–1070.
16. Palombit RA (1999) Infanticide and the evolution of pair bonds in nonhuman primates. *Evol Anthropol* 7(4):117–129.
17. van Schaik CP (2000) Social counterstrategies against infanticide by males in primates and other mammals. *Primate Males: Causes and Consequences of Variation in Group Composition*, ed Kappeler P (Cambridge Univ Press, Cambridge, UK), pp 34–52.
18. van Schaik CP, Kappeler PM (2003) The evolution of social monogamy in primates. *Monogamy: Mating Strategies and Partnerships in Birds, Humans and Other Mammals*, eds Reichard UH, Boesch C (Cambridge Univ Press, Cambridge, UK), pp 59–80.
19. Opie C, Atkinson QD, Shultz S (2012) The evolutionary history of primate mating systems. *Commun Integr Biol* 5(5):458–461.
20. Shultz S, Opie C, Atkinson QD (2011) Stepwise evolution of stable sociality in primates. *Nature* 479(7372):219–222.
21. Huelsenbeck JP, Ronquist F, Nielsen R, Bollback JP (2001) Bayesian inference of phylogeny and its impact on evolutionary biology. *Science* 294(5550):2310–2314.
22. Dunbar RIM (1995) The mating system of callitrichid primates: II. The impact of helpers. *Anim Behav* 50(4):1071–1089.
23. Shultz S, Dunbar RIM (2010) Social bonds in birds are associated with brain size and contingent on the correlated evolution of life-history and increased parental investment. *Biol J Linn Soc Lond* 100(1):111–123.
24. Isler K, Van Schaik CP (2009) Why are there so few smart mammals (but so many smart birds)? *Biol Lett* 5(1):125–129.
25. Lee PC (1999) Comparative ecology of postnatal growth and weaning among haplorhine primates. *Comparative Primate Socioecology*, ed Lee PC (Cambridge Univ Press, Cambridge, UK), pp 111–139.
26. Sommer V (1994) Infanticide among the langurs of Jodhpur: Testing the sexual selection hypothesis with a long-term record. *Infanticide and Parental Care*, eds Parmigiani S, vom Saal F (Harwood, Reading, UK), pp 155–198.
27. Watts DP (1989) Infanticide in mountain gorillas: New cases and a reconsideration of the evidence. *Ethology* 81(1):1–18.
28. Shultz S, Noë R, McGraw WS, Dunbar RIM (2004) A community-level evaluation of the impact of prey behavioural and ecological characteristics on predator diet composition. *Proc Biol Sci* 271(1540):725–732.
29. van Schaik CP (1983) Why are diurnal primates living in groups? *Behaviour* 87(1-2):120–144.
30. Isbell LA (1991) Contest and scramble competition: Patterns of female aggression and ranging behavior among primates. *Behav Ecol* 2(2):143–155.
31. Sterck EHM, Watts DP, van Schaik CP (1997) The evolution of female social relationships in nonhuman primates. *Behav Ecol Sociobiol* 41(5):291–309.

32. Shultz S, Dunbar RIM (2007) The evolution of the social brain: Anthropoid primates contrast with other vertebrates. *Proc Biol Sci* 274(1624):2429–2436.
33. Charnov EL, Berrigan D (1993) Why do female primates have such long lifespans and so few babies? Or life in the slow lane. *Evol Anthropol* 1(6):191–194.
34. van Schaik CP (2000) Vulnerability to infanticide by males: Patterns among mammals. *Infanticide by Males and its Implications*, eds van Schaik CP, Janson CH (Cambridge Univ Press, Cambridge, UK).
35. Dunbar RIM, Shultz S (2007) Understanding primate brain evolution. *Philos Trans R Soc Lond B Biol Sci* 362(1480):649–658.
36. Williams JM, Oehlert GW, Carlis JV, Pusey AE (2004) Why do male chimpanzees defend a group range? *Anim Behav* 68(3):523–532.
37. Harcourt AH, Greenberg J (2001) Do gorilla females join males to avoid infanticide? A quantitative model. *Anim Behav* 62(5):905–915.
38. Knott CD, Emery Thompson M, Stumpf RM, McIntyre MH (2010) Female reproductive strategies in orangutans, evidence for female choice and counterstrategies to infanticide in a species with frequent sexual coercion. *Proc Biol Sci* 277(1678): 105–113.
39. Dunbar RIM (2009) The social brain hypothesis and its implications for social evolution. *Ann Hum Biol* 36(5):562–572.
40. Nelson E, Rolian C, Cashmore L, Shultz S (2011) Digit ratios predict polygyny in early apes, Ardipithecus, Neanderthals and early modern humans but not in *Australopithecus*. *Proc Biol Sci* 278(1711):1556–1563.
41. Reno PL, Meindl RS, McCollum MA, Lovejoy CO (2003) Sexual dimorphism in *Australopithecus afarensis* was similar to that of modern humans. *Proc Natl Acad Sci USA* 100(16):9404–9409.
42. Walker RS, Hill KR, Flinn MV, Ellsworth RM (2011) Evolutionary history of hunter-gatherer marriage practices. *PLoS ONE* 6(4):e19066.
43. Gavrilets S (2012) Human origins and the transition from promiscuity to pair-bonding. *Proc Natl Acad Sci USA* 109(25):9923–9928.
44. Lovejoy CO (2009) Reexamining human origins in light of *Ardipithecus ramidus*. *Science* 326(5949):e1–e8.
45. Lovejoy CO (1981) The origin of man. *Science* 211(4480):341–350.
46. Arnold C, Matthews LJ, Nunn CL (2010) The 10kTrees website: A new online resource for primate phylogeny. *Evol Anthropol* 19(3):114–118.
47. Drummond AJ, Rambaut A (2007) BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evol Biol* 7(1):214.
48. Ross C, MacLarnon A (2000) The evolution of non-maternal care in anthropoid primates: A test of the hypotheses. *Folia Primatol (Basel)* 71(1-2):93–113.
49. Borries C, Savini T, Koenig A (2011) Social monogamy and the threat of infanticide in larger mammals. *Behav Ecol Sociobiol* 65(4):685–693.
50. Pagel MD, Meade A, Barker D (2004) Bayesian estimation of ancestral character states on phylogenies. *Syst Biol* 53(5):673–684.
51. Pagel MD, Meade A (2006) Bayesian analysis of correlated evolution of discrete characters by reversible-jump Markov chain Monte Carlo. *Am Nat* 167(6):808–825.
52. Metropolis N, Rosenbluth AW, Rosenbluth MN, Teller AH, Teller E (1953) Equation of state calculations by fast computing machines. *J Chem Phys* 21(6):1087.
53. Rambaut A, Drummond A (2007) Tracer v1.4. Available from http://beast.bio.ed.ac.uk/Tracer. Accessed July 25, 2012.
54. Kass RE, Raftery AE (1995) Bayes factors. *J Am Stat Assoc* 90(430):773–795.
55. Organ CL, Shedlock AM, Meade A, Pagel M, Edwards SV (2007) Origin of avian genome size and structure in non-avian dinosaurs. *Nature* 446(7132):180–184.

Supplementary Appendix

Data

The sample sizes and distribution of traits used in the analyses are summarised in Table S1. Primate trait data were extracted from the literature and from primary sources (Dataset S1).

Table S1. Coding for binary traits and number by coding (Dataset S1).

Binary trait	**Coding**				
	State (0)	N	State (1)	N	Polymorphic (01)
Mating system	Polygyny	152	Pair living	34	28
Paternal care	No care	192	Care	27	-
Female ranging patterns	Discrete ranges	49	Overlapping ranges	164	-
Infanticide	Low infanticide	120	High infanticide	56	-

Paternal care

Ross and MacLarnon (1) use a four point scale: 1 (no or very low care, 0 – 5% of infant time), 2 (low care, 5-30% of infant time), 3 (medium care 30-55% of infant time), and 4 (high care, > 55% of infant time) for allocare (by all carers) in anthropoid primates, including feeding, carrying, playing and grooming. They suggest that category 3 (30 - 55% of infant time) and above represents significant allocare. We have redefined this scheme to focus on paternal care across the primate order, defining significant care as adult males providing care for at least 30% of infant time (Dataset S1).

Female Ranging Patterns

Female ranges are designated as either discrete or overlapping. Discrete female ranges are defined as overlapping by less than 5% (following Komers and Brotherton (2)). Data were collected from the literature (Dataset S1).

Infanticide

Reports of infanticide were taken from the literature and were included where infanticide was observed in wild populations (Dataset S1). Furthermore, because of the rarity of infanticide, it is not possible to be certain that a lack of reporting of infanticide, even in well-studied species, confirms that infanticide does not take place in that species. This issue has been highlighted by a recent study using long-term data (spanning 29 years) on *Hylobates lar (3)*. Although this well-studied species (726 publications - Dataset S1) was presumed to have no infanticide, by using the full data set Borries and colleagues (3) were able to show that male infanticide did take place, even if very rarely. We have therefore categorised species as “high infanticide”, where infanticide has be widely documented, and “low infanticide” where infanticide has not been reported or is thought to be rare. We classified species as ‘low rates of infanticide’ in order to reflect the possibility that there is some low-level of infanticide pressure even in species where it is unreported. Species with less than 20 publications have been excluded from these analyses on the grounds that they have not been sufficiently studied to determine the level of infanticide that takes place in the species.

Since infanticide is a rare event, even in those populations where infanticide is a significant cause of infant death, the reporting of infanticide for species may be influenced by the intensity of study. In particular, it may be that polygynous species have been more intensely studied than monogamous species, since they are more likely to occupy open habitats, and therefore infanticide is more likely to have been seen in those species. We therefore performed a literature search for the number of publications for each primate species using Web of Science (http://apps.webofknowledge.com).

Those species with >100 publications were deemed well studied. There was no association between being well studied and being polygynous (Table S2, $X^2 = 0.87$, df = 1, p = 0.35). Moreover, there was no significant difference in the mean $\log_{10}$ number of publications for monogamous versus polygynous species (two tailed t=0.22, p = 0.82, Figure S1).

Table S2. Study intensity of primate species by mating system.

Study Intensity	**Polygynous**	**Monogamous**
Limited study	97	36
Well studied	66	17

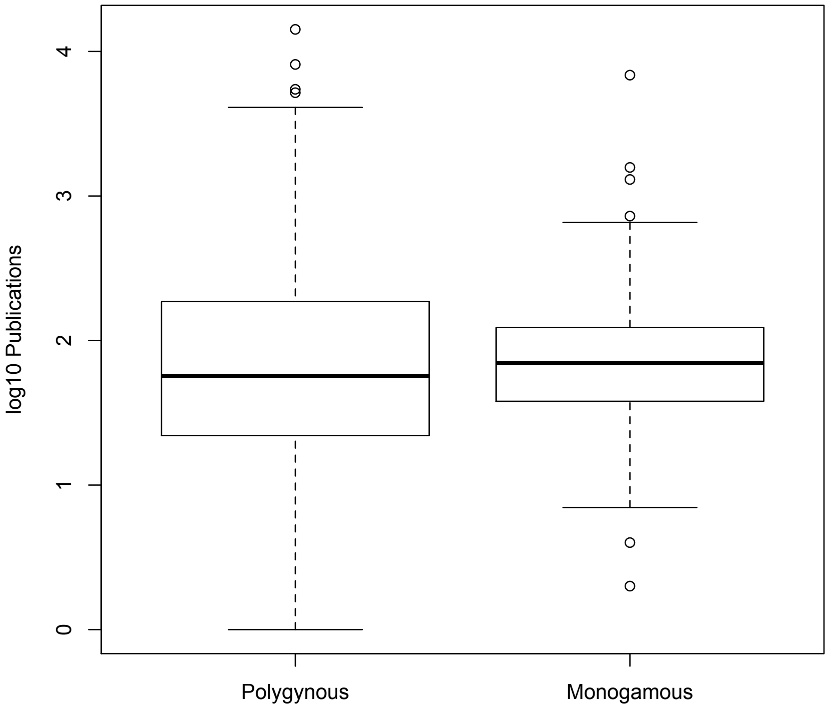

Figure S1. Plot of number of publications for individual primate species by mating system.

The main text shows a clear association between low infanticide and monogamous mating. In order to test whether this association was influenced by intensity of study we also subset the data to well-studied species. The association between low infanticide and monogamy still holds when the data was subset to well-studied species. Correlated evolution is strong between infanticide and mating system ($\log_{10}$ Bayes Factor 2.98) and there is a clear association between low infanticide and monogamy, with low transition rates out of the derived state of monogamy with low infanticide (Figure S2).

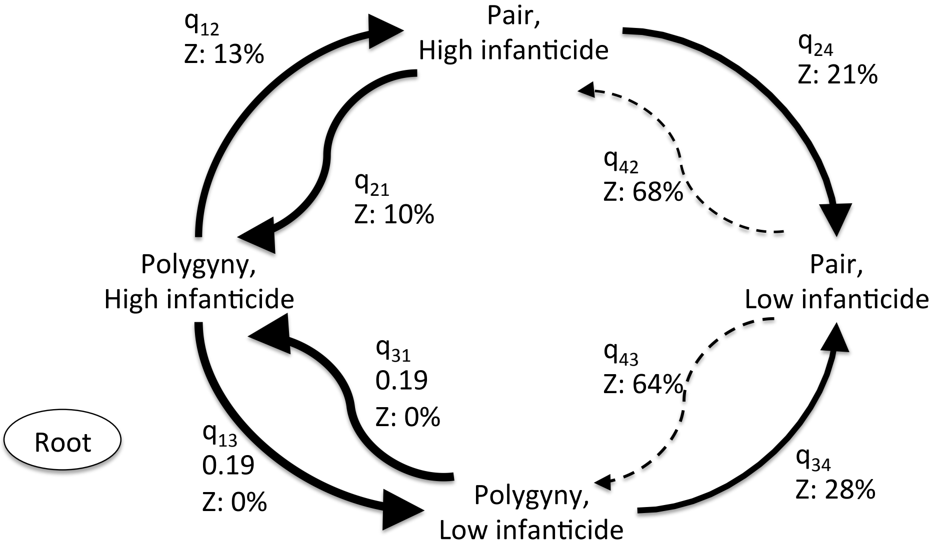

Figure S2. Correlated evolution between primate mating system and male infanticide in well-studied species. Z denotes visits assigned to zero as a proportion of the posterior probability distribution. Thickness of arrows reflects proportion of time transition rate is not assigned to zero, with dashed line > 50% zeros. Number below rate name (q_{ij}) is the mean transition rate where rate distribution has zero or very low Z value.

Weaning proportion

Data for gestation length (G) and lactation length (L) were collected from the literature (Dataset S1). The weaning proportion (L/(L+G)) shows the relative length of lactation to the inter-birth interval and indicates infanticide risk (Figure S3). Data were Arc Sine transformed.

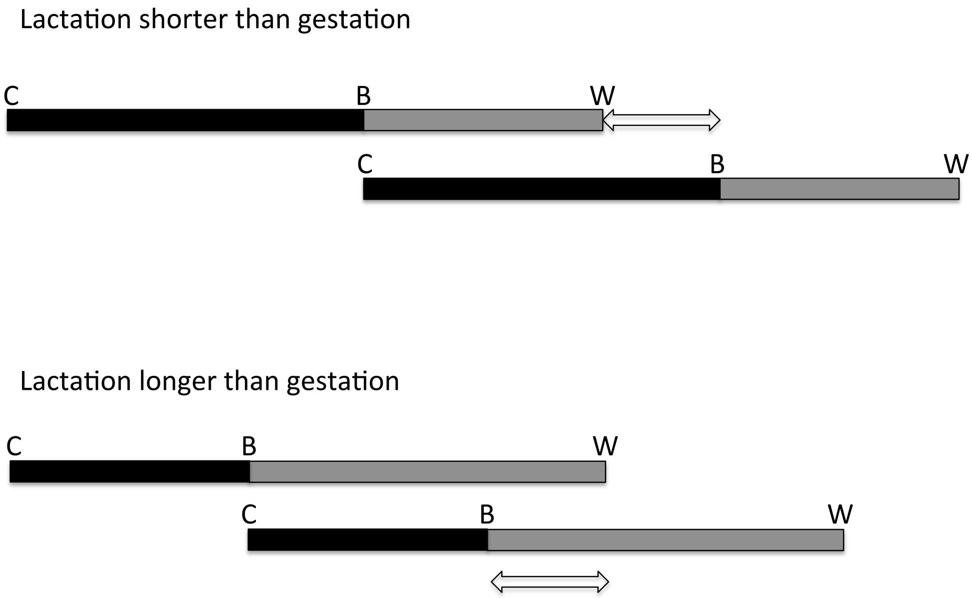

Figure S3. The relative length of lactation and gestation affects the occurrence of two lactating offspring of different ages in non-seasonal breeding primates indicating infanticide risk (following van Schaik (4)). (C=conception, B=birth, and W=weaning). Where lactation is short relative to gestation (top) conception can occur soon after the birth of the previous offspring without lactation periods overlapping (as shown by open arrow). Male infanticide would have no effect on birth timing of the subsequent offspring and is therefore predicted to be low. Where lactation is long relative to gestation (bottom) post-partum conception would lead to two lactating offspring for a period (as shown by the open arrow), and therefore conception is delayed. However, this delay then enables a male to hasten a return to oestrus in a female by killing her lactating infant.

For seasonal breeding species with a single reproductive event each year followed by a 'timeout period', lactation longer than gestation would falsely suggest that there was infanticide risk, but the killing of her infant would not speed a female's return to oestrus. Seasonal breeders (with a timeout period) are identified in the Dataset S1, and these species were removed from this analysis (following van Schaik (4)).

Phylogenetic Signal

Phylogenetic signal was tested in discrete traits (Table S3) by calculating D using the function *phylo.d* (5) in the *Caper* package (6) in *R* (7). A D value significantly different from random indicates that related species are more similar in a particular trait than would be expected by chance (5). For the continuous trait the *Continuous* procedure in BayesTraits (8) was used to test for phylogenetic signal by calculating Pagel's λ (9, 10). A λ value of 1 indicates the probability of shared inheritance is proportional to relatedness, while a λ value of 0 suggests evolution is independent of the phylogenetic tree.

Each of the discrete traits tested have a phylogenetic structure that has a zero probability of being generated from a random distribution (no phylogenetic structure) (Table S3), while the continuous trait has a λ value close to 1 (Table S4). These results suggest that for the traits used here phylogenetic ancestry is a significant factor in their distribution across extant taxa.

Table S3. D statistic for phylogenetic structure of binary traits.

Trait Data	Est. D	Probability of Est. D resulting from:	
		No phylogenetic structure (random)	Brownian motion
Mating system	-0.11	0.000	0.722
Paternal care	-0.55	0.000	0.994
Female ranging patterns	-0.17	0.000	0.807
Infanticide	0.54	0.000	0.001

Table S4. Bayesian analyses of traits with results for root values and phylogenetic signal (λ)

Analysis	Lh	Harmonic mean	Alpha (Root)	Lambda (λ)
Weaning Proportion	74.95	73.56	0.54	0.92

Transition Rates

Transition rates between states can be used to determine the relative timing of changes between states where there is correlated evolution between two binary traits (Figure 1, Table S5).

Table S5. The posterior probability of transition rate being zero for correlated evolution analyses between mating system and other traits. 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 correlated evolution Figure 1.

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	99.7	0.0	39.5	34.5	3.8	0.0	89.5	87.5
Female ranging patterns	99.6	0.0	14.5	1.4	26.4	0.0	76.5	14.1
Infanticide	0.0	75.8	0.0	0.12	93.2	90.1	20.7	0.8

Evolutionary Models

As outlined in the methods section, analyses were carried out in BayesTraits (8, 11) using a Markov Chain Monte Carlo (MCMC) (12) sampling algorithm together with a reversible jump (RJ) procedure. The RJ procedure searches the posterior distribution of possible models by linking (setting to equal) or removing (setting to zero (Z)) transition rate parameters. Models were sampled in proportion to their posterior probability, accounting for variation in the number of parameters (Tables S6-S8).

Table S6. Top ten and fiftieth model of mating system and paternal care with their posterior probabilities. (Note: Z = transition rate assigned to zero. 0, 1 and 2 are non-zero rates.) 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 87 visits are expected by chance (following Pagel and Meade (11)).

Model	Transition Rates								Frequency	Probability (%)	Cumulative probability (%)
	q_{12}	q_{13}	q_{21}	q_{24}	q_{31}	q_{34}	q_{42}	q_{43}			
1	Z	0	0	0	0	0	Z	Z	11025	22.1	22.1
2	Z	0	Z	0	0	0	Z	Z	10678	21.4	43.4
3	Z	0	0	Z	0	0	Z	Z	8561	17.1	60.5
4	Z	0	Z	Z	0	0	Z	Z	5773	11.5	72.1
5	Z	0	0	0	0	0	Z	0	1884	3.8	75.8
6	Z	0	0	0	0	0	0	Z	1163	2.3	78.2
7	Z	1	0	1	1	1	1	Z	625	1.3	79.4
8	Z	0	Z	Z	0	0	0	Z	623	1.2	80.7
9	Z	0	Z	0	Z	0	Z	0	572	1.1	81.8
10	Z	0	Z	Z	Z	0	Z	0	538	1.1	82.9
50	Z	1	Z	1	0	1	Z	Z	45	0.1	91.9

Table S7. Top ten and fiftieth model of mating system and female ranging patterns with their posterior probabilities. (Note: Z = transition rate assigned to zero. 0, 1 and 2 are non-zero rates.) 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 95 visits are expected by chance (following Pagel and Meade (11)).

Model	Transition Rates								Frequency	Probability (%)	Cumulative Probability (%)
	q_{12}	q_{13}	q_{21}	q_{24}	q_{31}	q_{34}	q_{42}	q_{43}			
1	Z	1	1	1	0	0	Z	1	10082	20.2	20.2
2	Z	1	1	1	1	0	Z	1	6253	12.5	32.7
3	Z	1	1	1	Z	0	Z	1	6050	12.1	44.8
4	Z	0	0	0	1	1	Z	0	4215	8.4	53.2
5	Z	1	1	1	Z	0	Z	Z	2299	4.6	57.8
6	Z	0	0	0	Z	1	Z	0	1926	3.9	61.7
7	Z	0	0	0	0	1	Z	0	1837	3.7	65.3
8	Z	1	Z	1	1	0	1	1	1503	3.0	68.3
9	Z	1	1	1	1	0	Z	Z	1489	3.0	71.3
10	Z	1	1	1	0	0	1	1	1291	2.6	73.9
50	Z	1	Z	2	0	0	1	2	39	0.1	94.9

Table S8. Top ten and fiftieth model of mating system and infanticide with their posterior probabilities. (Note: Z = transition rate assigned to zero. 0, 1 and 2 are non-zero rates.) 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 124 visits are expected by chance (following Pagel and Meade (11)).

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	Z	1	0	Z	Z	1	1	11364	22.7	22.7
2	1	Z	1	0	Z	Z	0	1	8880	17.8	40.5
3	1	Z	1	0	Z	Z	Z	0	5737	11.5	52.0
4	1	Z	1	1	Z	Z	0	1	2524	5.0	57.0
5	1	0	1	0	Z	Z	0	1	2186	4.4	61.4
6	1	0	1	0	Z	Z	Z	1	2050	4.1	65.5
7	0	Z	0	1	Z	Z	0	0	1594	3.2	68.7
8	1	0	1	0	Z	Z	1	1	1444	2.9	71.6
9	1	Z	1	0	Z	0	0	1	932	1.9	73.4
10	0	Z	0	1	Z	Z	1	0	911	1.8	75.2
50	2	Z	2	0	Z	Z	2	1	71	0.1	94.8

Ancestral States

We used an RJ MCMC approach within the Multistate procedure in BayesTraits (8, 11) to infer states at ancestral nodes for each binary trait (Figures S4-S7). For the continuous trait we also used an MCMC approach in the Continuous procedure in BayesTraits (8, 11) to infer states at ancestral nodes (Figure S8).

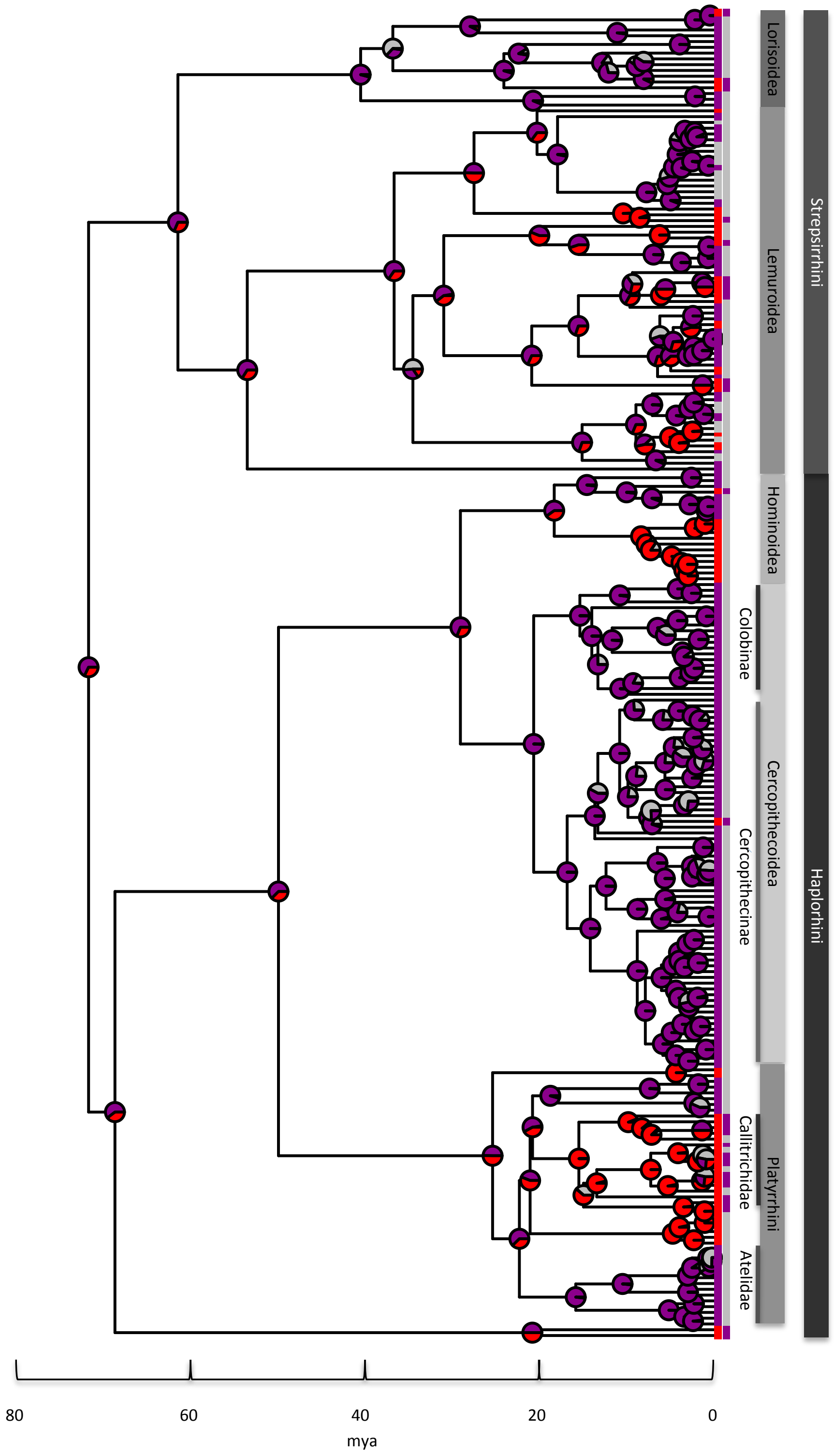

Figure S4. Ancestral node reconstructions for primate mating systems from MCMC analysis plotted on the maximum clade credibility tree derived from the full posterior sample of trees. The pies at ancestral nodes are the combined posterior probability of each state at that node with the posterior probability that the node itself exists. Red shading indicates probability of monogamy at each node and tip; purple indicates probability of polygyny. Two columns used at tips for polymorphic species. Grey represents missing data or monomorphic species (if in 2nd column) at tips, and node uncertainty derived from the full phylogeny.

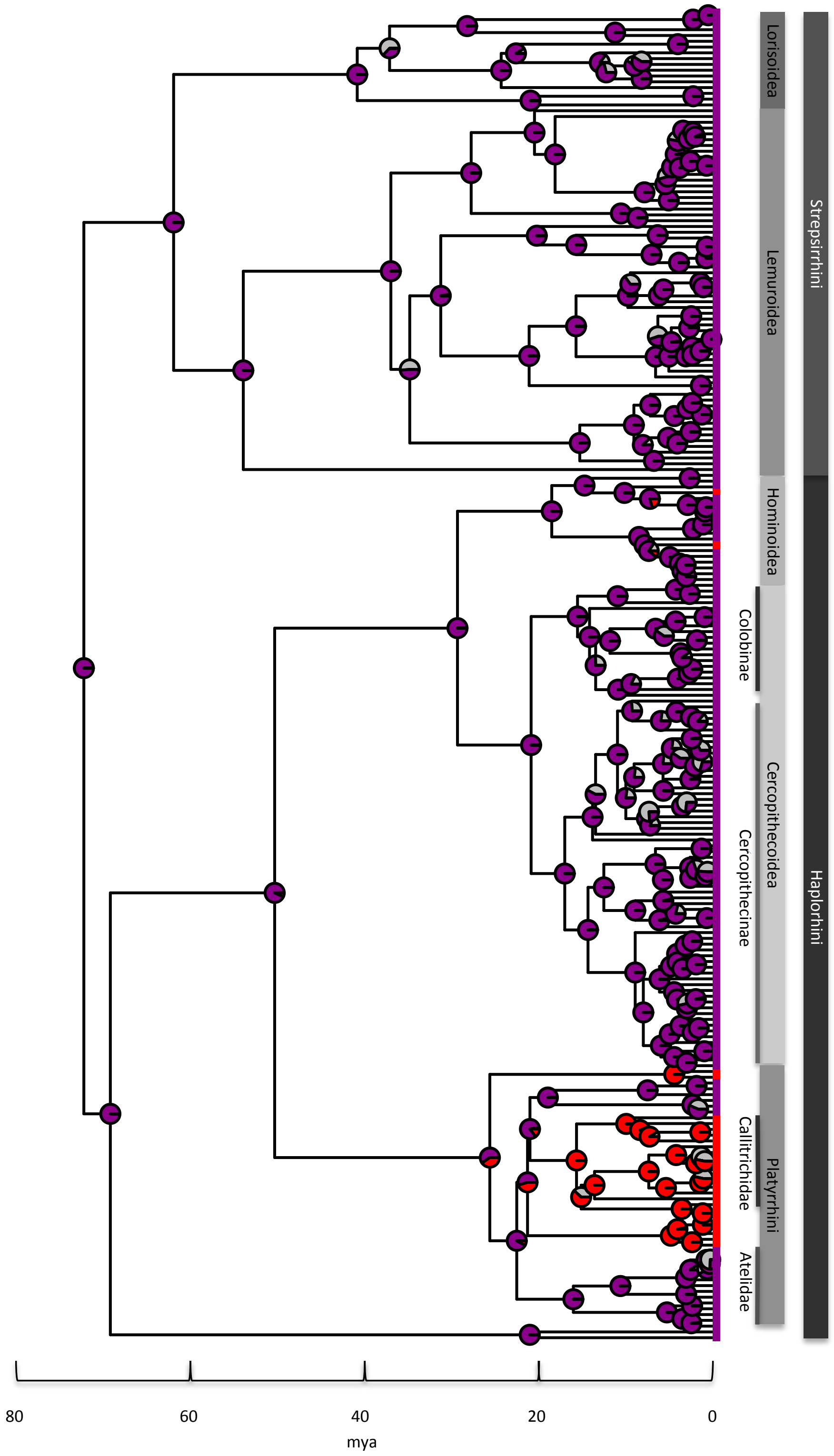

Figure S5. Ancestral node reconstructions for paternal care from MCMC analysis plotted on the maximum clade credibility tree derived from the full posterior sample of trees. Red shading indicates probability of paternal care at each node and tip; purple indicates probability of no care. Grey represents node uncertainty derived from the full phylogeny.

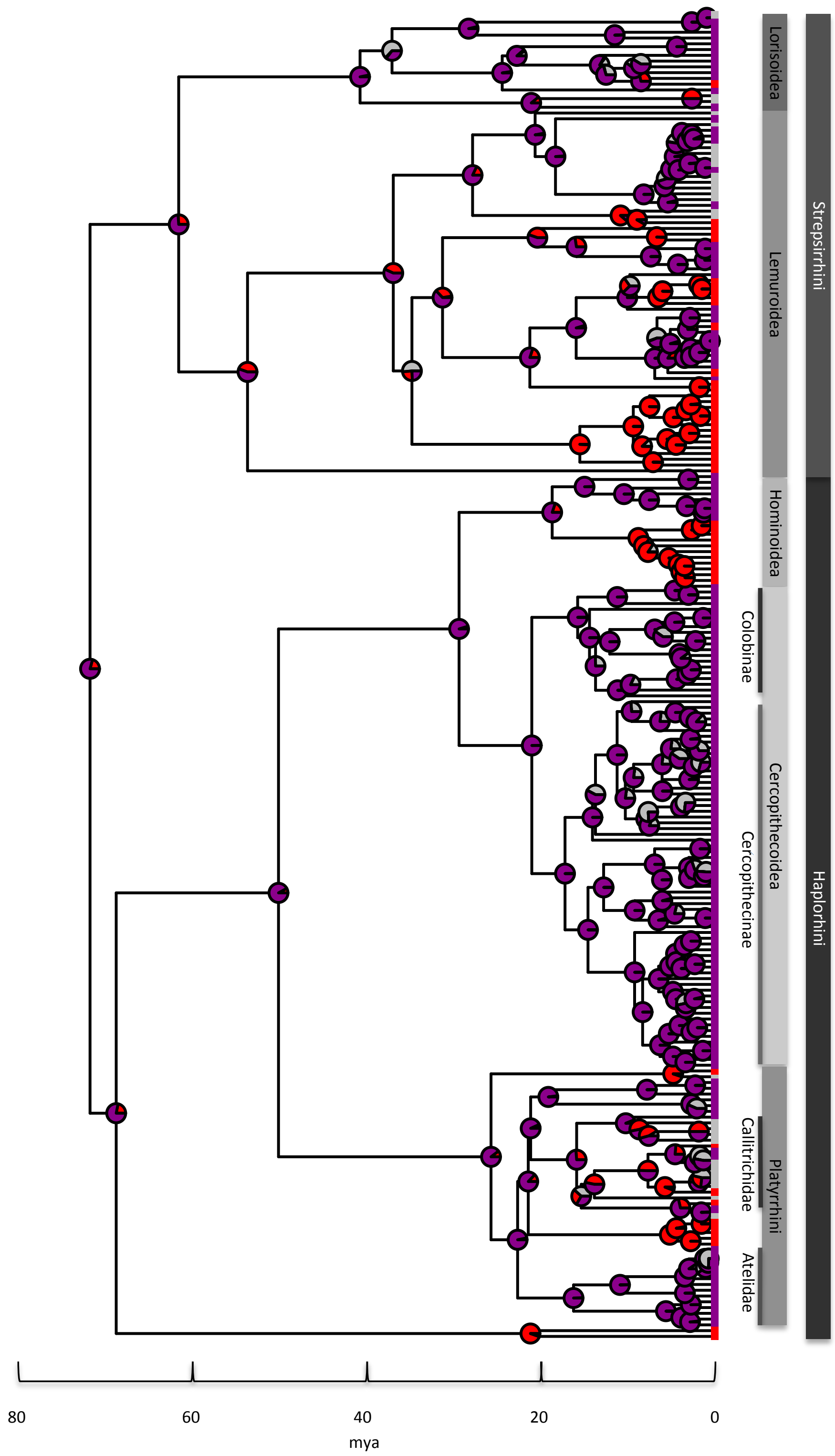

Figure S6. Ancestral node reconstructions for female ranging patterns from MCMC analysis plotted on the maximum clade credibility tree derived from the full posterior sample of trees. Purple shading indicates probability of overlapping female ranges at each node and tip; red indicates probability of discrete female ranges. Grey represents missing data at tips and node uncertainty derived from the full phylogeny.

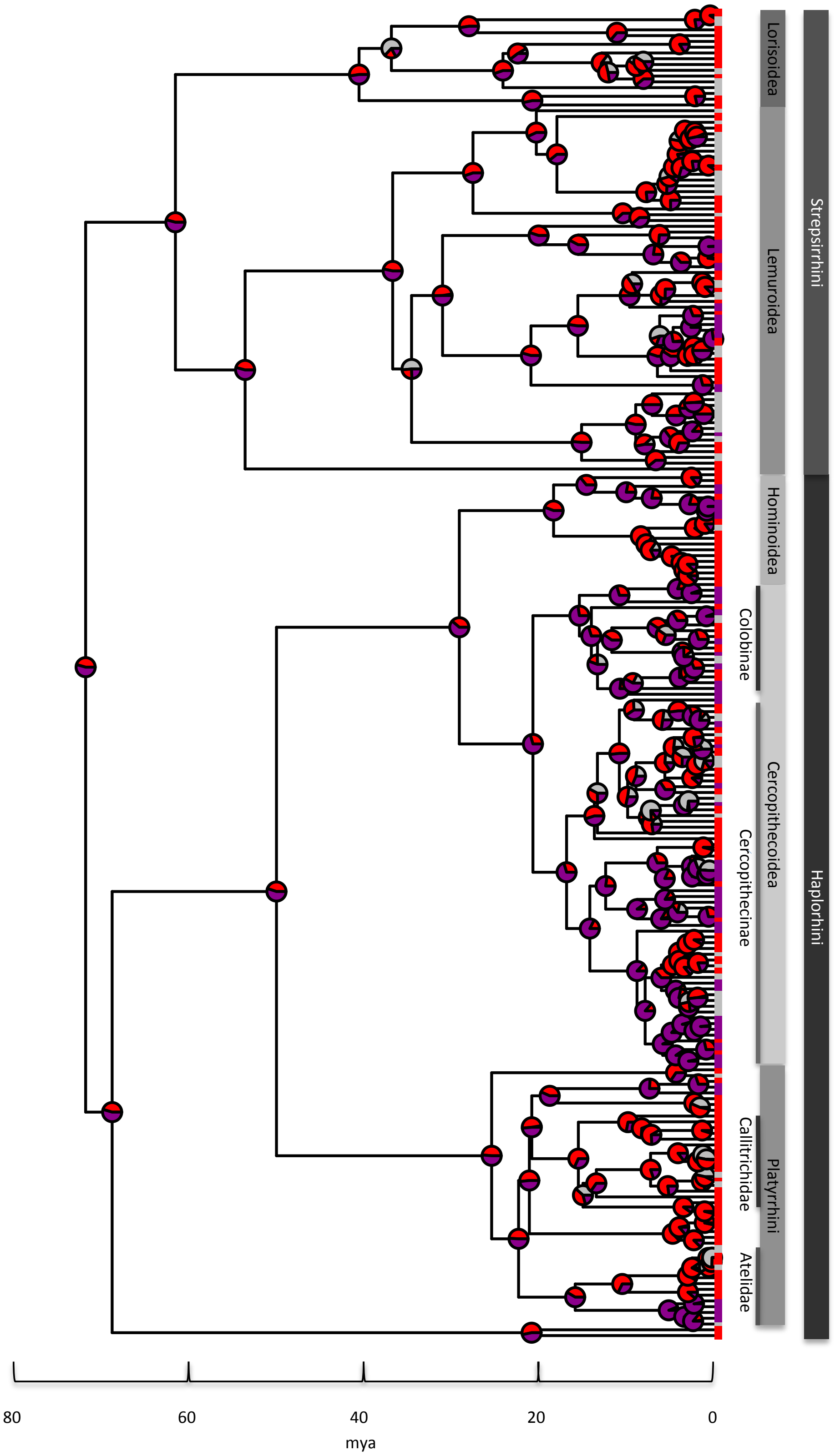

Figure S7. Ancestral node reconstructions for infanticide from MCMC analysis plotted on the maximum clade credibility tree derived from the full posterior sample of trees. Purple shading indicates probability of high infanticide at each node and tip; red indicates probability of low infanticide. Grey represents missing data at tips and node uncertainty derived from the full phylogeny.

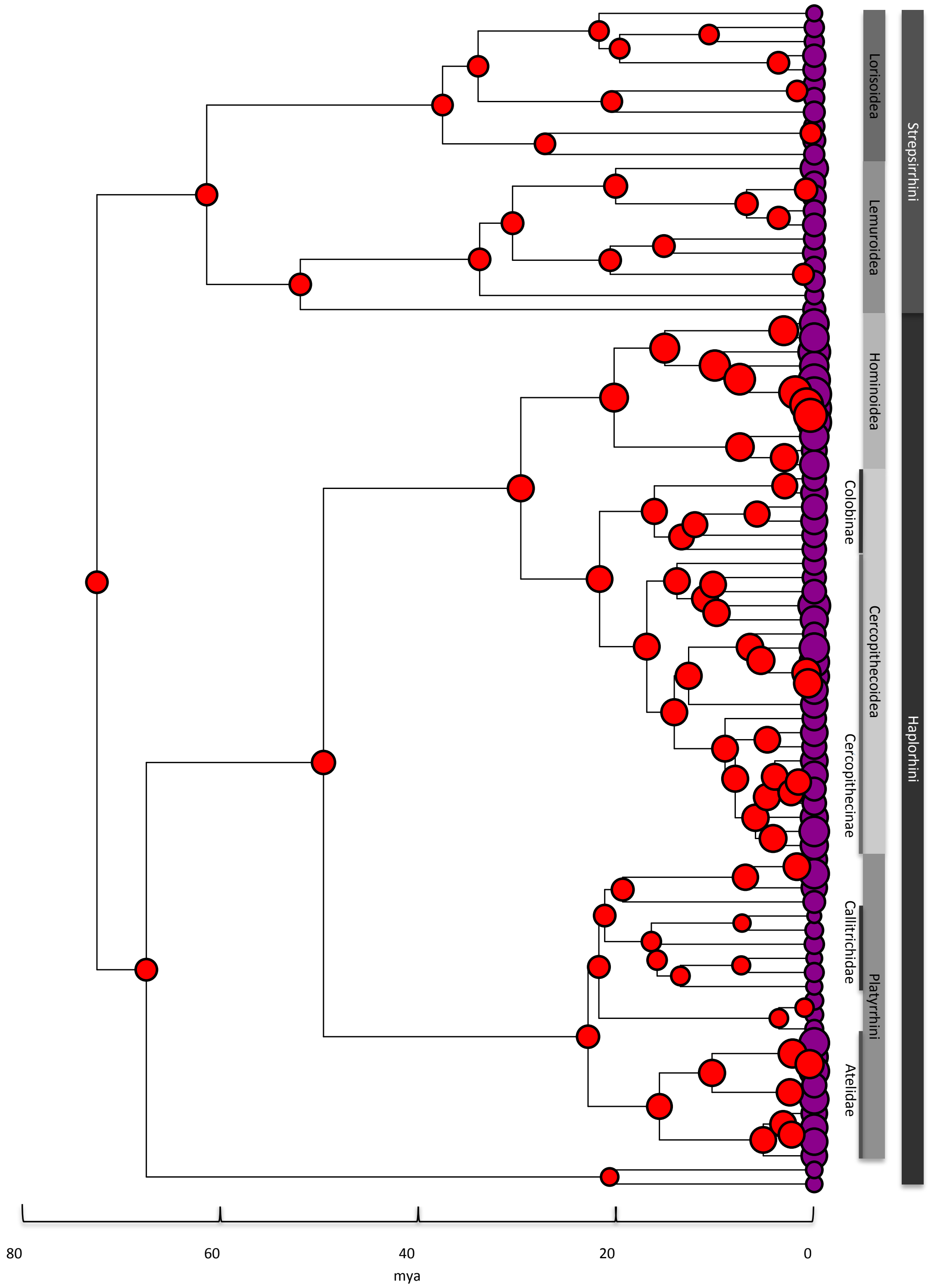

Figure S8. Inferred proportion of the breeding cycle dedicated to lactation at ancestral nodes of the primate phylogeny from MCMC analysis plotted on the maximum clade credibility tree derived from the full posterior sample of trees. Size of circle at nodes is proportional to value. Red denotes ancestral node; purple denotes extant taxa.

Supplementary References

1. Ross C & MacLarnon A (2000) The Evolution of non-maternal care in anthropoid primates: a test of the hypotheses. *Folia Primatologica* 71(1-2):93-113.
2. Komers PE & Brotherton PNM (1997) Female space use is the best predictor of monogamy in mammals. *Proceedings of the Royal Society B-Biological Sciences* 264(1386):1261-1270.
3. Borries C, Savini T, & Koenig A (2011) Social monogamy and the threat of infanticide in larger mammals. *Behavioral Ecology and Sociobiology* 65(4):685-693.
4. van Schaik CP (2000) Social counterstrategies against infanticide by males in primates and other mammals. *Primate Males: Causes and Consequences of Variation in Group Composition*, ed Kappeler P (Cambridge University Press, Cambridge), pp 34–52.
5. Fritz SA & Purvis A (2010) Selectivity in Mammalian Extinction Risk and Threat Types: a New Measure of Phylogenetic Signal Strength in Binary Traits. *Conservation Biology* 24(4):1042-1051.
6. Orme C*, et al.* (2011) caper: Comparative Analyses of Phylogenetics and Evolution in R. *URL:* http://cran.r-project.org/web/packages/caper/index.html.
7. R Development Core Team (2008) R: A language and environment for statistical computing (R Foundation for Statistical Computing, Vienna, Austria).
8. Pagel MD, Meade A, & Barker D (2004) Bayesian estimation of ancestral character states on phylogenies. *Systematic Biology* 53(5):673-684.
9. Pagel MD (1994) 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(1342):37-45.
10. Pagel MD (1999) Inferring the historical patterns of biological evolution. *Nature* 401(6756):877-884.
11. Pagel MD & Meade A (2006) Bayesian analysis of correlated evolution of discrete characters by reversible-jump Markov chain Monte Carlo. *American Naturalist* 167(6):808-825.
12. Metropolis N, Rosenbluth AW, Rosenbluth MN, Teller AH, & Teller E (1953) Equation of state calculations by fast computing machines. *Journal of Chemical Physics* 21(6):1087.

Supplementary Data Table

Family	**Species (10k Tree version 2)**	**Common Name**	**Mating System**
			Sources
			1,7,8,11,13,29,34
Lemuriformes	Allocebus_trichotis	Hairy-eared dwarf lemu	Monogamous
	Avahi_laniger	Eastern Woolly lemur	Monogamous
	Avahi_occidentalis	Western Woolly Lemur	Monogamous
	Cheirogaleus_crossleyi	Furry-eared Dwarf Lem	Monogamous
	Cheirogaleus_major	Greater dwarf lemur	Monogamous
	Cheirogaleus_medius	Fat-tailed dwarf lemur	lygynous/Monogam
	Daubentonia_madagascariensis	Aye-aye	Polygynandrous
	Eulemur_coronatus	Crowned lemur	Polygynandrous
	Eulemur_fulvus_albifrons	white-fronted Brown le	Polygynandrous
	Eulemur_fulvus_albocollaris	White-collared lemur	Polygynandrous
	Eulemur_fulvus_collaris	Red-collared lemur	Polygynandrous
	Eulemur_fulvus_fulvus	common Brown lemur	Polygynandrous
	Eulemur_fulvus_mayottensis	Brown lemur of Mayott	Polygynandrous
	Eulemur_fulvus_rufus	Red-fronted lemur	Polygynandrous
	Eulemur_fulvus_sanfordi	Sanford's lemur	Polygynandrous
	Eulemur_macaco_flavifrons	blue-eyed black lemur	Polygynandrous
	Eulemur_macaco_macaco	Black lemur	Polygynandrous
	Eulemur_mongoz	Mongoose lemur	Monogamous
	Eulemur_rubriventer	Red-bellied lemur	Monogamous
	Hapalemur_aureus	Golden bamboo lemur	Monogamous
	Hapalemur_griseus_alaotrensis	Lac Alaotra bamboo Le	lygynous/Monogam
	Hapalemur_griseus_griseus	Eastern grey bamboo le	lygynous/Monogam
	Hapalemur_griseus_meridionali	Grey gentle lemur	lygynous/Monogam
	Hapalemur_griseus_occidentalis	Western gentle lemur	lygynous/Monogam
	Hapalemur_simus	Broad-nosed gentle le	Polygynandrous
	Indri_indri	Indri	Monogamous
	Lemur_catta	Ring-tailed lemur	Polygynandrous
	Lepilemur_aeeclis	Red-shouldered Sportiv	DD
	Lepilemur_ankaranensis	Ankarana Sportive Lem	DD
	Lepilemur_dorsalis	gray-backed sportive le	Polygynous
	Lepilemur_edwardsi	Milne-Edwards's sportiv	Monogamous
	Lepilemur_leucopus	white-footed sportive l	Polygynous
	Lepilemur_microdon	Small-toothed sportive	Polygynous
	Lepilemur_mitsinjoensis	Mitsinjo sportive lemur	DD
	Lepilemur_mustelinus	Weasel lemur, Sportive	Polygynous
	Lepilemur_randrianasoli	Randrianasoli's sportive	DD
	Lepilemur_ruficaudatus	red-tailed sportive lem	Monogamous
	Lepilemur_sahamalazensis	Sahamalaza sportive le	DD
	Lepilemur_seali	Seal's sportive lemur	DD
	Lepilemur_septentrionalis	northern sportive lemu	Polygynous
	Microcebus_berthae	Madame Berthe's mous	Polygynandrous
	Microcebus_bongolavensis	Bongolava mouse lemu	DD
	Microcebus_danfossi	Danfoss' mouse lemur	DD
	Microcebus_griseorufus	reddish-gray mouse le	DD
	Microcebus_jollyae	Jolly's mouse lemur	DD

	Microcebus_lehilahytsara	Goodman's mouse lemu	DD
	Microcebus_lokobensis	Lokobe mouse lemur	DD
	Microcebus_mittermeieri	Mittermeier's mouse le	DD
	Microcebus_murinus	gray mouse lemur	Polygynandrous
	Microcebus_myoxinus	Pygmy mouse lemur	Polygynandrous
	Microcebus_ravelobensis	golden-brown mouse le	Polygynandrous
	Microcebus_rufus	Brown mouse lemur	Polygynandrous
	Microcebus_sambiranensis	Sambirano mouse lemu	DD
	Microcebus_simmonsi	Simmons' mouse lemur	DD
	Microcebus_tavaratra	Northern Rufous mouse	DD
	Mirza_coquereli	Coquerel's dwarf lemur	Polygynandrous
	Propithecus_coquereli	Coquerel's sifaka	Polygynandrous
	Propithecus_diadema	Diadem sifaka	ynandrous/Monoga
	Propithecus_edwardsi	Milne-Edwards sifaka	Polygynandrous
	Propithecus_tattersalli	Golden-crowned sifaka	Polygynandrous
	Propithecus_verreauxi_verreaux	Verreaux's sifaka	Polygynandrous
	Varecia_rubra	Red ruffed lemur	ynandrous/Monoga
	Varecia_variegata_variegata	Ruffed lemur	ynandrous/Monoga
Loridae	Arctocebus_aureus	Golden Potto/angwanti	Polygynous
	Arctocebus_calabarensis	Angwantibo, Calabar P	Polygynous
	Loris_lydekkerianus_malabaricu	Malabar gray slender lo	Polygynandrous
	Loris_tardigradus	Slender loris	ynandrous/Monoga
	Loris_tardigradus_nordicus	Slender loris	Polygynandrous
	Nycticebus_coucang	Slow loris	Polygynous
	Nycticebus_pygmaeus	Pygmy slow loris	Polygynous
	Perodicticus_potto	Western Potto	Polygynous
Galagonidae	Euoticus_elegantulus	Western needle-clawed	Polygynandrous
	Galago_alleni	Allen's bushbaby	Polygynous
	Galago_gallarum	Somali galago	Polygynandrous
	Galago_moholi	Southern lesser bushba	Polygynandrous
	Galago_senegalensis	Northern lesser bushba	Polygynandrous
	Galagoides_demidoff	Demidoff's galago	lygynous/Monogam
	Galagoides_zanzibaricus	Zanibar bushbaby	lygynous/Monogam
	Otolemur_crassicaudatus	thick-tailed bush baby	Polygynandrous
	Otolemur_garnettii	small-eared galago	Polygynandrous
Tarsiidae	Tarsius_bancanus	Western tarsier	lygynous/Monogam
	Tarsius_syrichta	Philippine tarsier	lygynous/Monogam
Pitheciidae	Callicebus_donacophilus	White-eared/ Bolivian T	Monogamous
	Callicebus_moloch	Dusky titi	Monogamous
Cebidae	Aotus_azarai	Southern night monkey	Monogamous
	Aotus_infulatus	Kuhl's Owl Monkey	Monogamous
	Aotus_lemurinus_griseimembra	Lemurine Owl Monkey	Monogamous
	Aotus_nancymaae	Peruvian Red-necked O	Monogamous
	Aotus_trivirgatus	Northern night monkey	Monogamous
	Callimico_goeldii	Goeldi's marmoset	lygynous/Monogam
	Callithrix_argentata	Silvery bare-ear marmo	lygynous/Monogam
	Callithrix_aurita	Buffy-tufted-ear marm	lygynous/Monogam
	Callithrix_emiliae	Snethlage's Marmoset	lygynous/Monogam
	Callithrix_geoffroyi	Geoffroy's tufted-ear m	yandrous/Monogam
	Callithrix_humeralifera	Tassel-ear marmoset	lygynous/Monogam

	Callithrix_jacchus	Common marmoset	yandrous/Monogam
	Callithrix_kuhli	Wied's black-tufted-ear	lygynous/Monogamo
	Callithrix_penicillata	Black-tufted-ear marmo	lygynous/Monogamo
	Callithrix_pygmaea	Pygmy marmoset	Monogamous
	Cebus_albifrons	Brown pale-fronted cap	Polygynandrous
	Cebus_apella	Black-capped capuchin	Polygynandrous
	Cebus_capucinus	White-throated capuchi	Polygynandrous
	Leontopithecus_chrysomelas	Golden-headed lion tan	lygynous/Monogamo
	Leontopithecus_chrysopygus	Golden-rumped lion tar	Monogamous
	Leontopithecus_rosalia	Golden lion tamarin	lygynous/Monogamo
	Saguinus_fuscicollis	brown-headed tamarin	ıs/Polyandrous/Mon
	Saguinus_geoffroyi	Geoffroy's tamarin	lygynous/Monogamo
	Saguinus_imperator	tamarin	ıs/Polyandrous/Mon
	Saguinus_midas	Red-handed tamarin	Monogamous
	Saguinus_oedipus	Cotton-top tamarin	ynandrous/Monoga
	Saimiri_boliviensis_boliviensis	Bolivian squirrel monke	Polygynandrous
	Saimiri_oerstedii	Red backed squirrel mo	Polygynandrous
	Saimiri_sciureus	Common squirrel monk	Polygynandrous
Atelidae	Alouatta_caraya	Black howler	gynous/Polygynand
	Alouatta_palliata	Mantled howler	gynous/Polygynand
	Alouatta_pigra	Guatemalan howler	gynous/Polygynand
	Alouatta_sara	Bolivian red Howler	gynous/Polygynand
	Alouatta_seniculus	Red howler	gynous/Polygynand
	Ateles_belzebuth	Long-haired spider mon	Polygynandrous
	Ateles_fusciceps	Brown spider monkey	Polygynandrous
	Ateles_geoffroyi	Black-handed spider mo	Polygynandrous
	Ateles_geoffroyi_panamensis	Panama spider monkey	Polygynandrous
	Ateles_geoffroyi_vellerosus	Mexican spider monkey	Polygynandrous
	Ateles_geoffroyi_yucatanensis	Yucatan spider monkey	Polygynandrous
	Ateles_paniscus	Black spider monkey	Polygynandrous
	Brachyteles_arachnoides	Southern muriqui/wool	Polygynandrous
	Lagothrix_lagotricha	Common woolly monke	Polygynandrous
Cercopithecini	Allenopithecus_nigroviridis	Allen's swamp monkey	Polygynandrous
	Cercopithecus_ascanius	Schmidt's guenon or re	Polygynous
	Cercopithecus_campbelli_lowei	Campbell's monkey	Polygynous
	Cercopithecus_cephus	moustached guenon	Polygynous
	Cercopithecus_cephus_cephus	moustached guenon	Polygynous
	Cercopithecus_cephus_ngottoei	Ngotto guenon	Polygynous
	Cercopithecus_diana	Diana monkey	Polygynous
	Cercopithecus_erythrogaster_er	Red bellied monkey	Polygynous
	Cercopithecus_erythrotis	red-eared guenon	Polygynous
	Cercopithecus_hamlyni	Owl-faced monkey	Polygynous
	Cercopithecus_lhoesti	L'Hoest's monkey	Polygynous
	Cercopithecus_mitis	Blue monkey	Polygynous
	Cercopithecus_mona	Mona monkey	Polygynous
	Cercopithecus_neglectus	De Brazza's Monkey	lygynous/Monogamo
	Cercopithecus_nictitans	Greater white-nosed m	Polygynous
	Cercopithecus_petaurista	Lesser white-nosed mo	Polygynous
	Cercopithecus_preussi	Preuss's monkey	Polygynous
	Cercopithecus_solatus	Sun-tailed monkey	Polygynous

	Cercopithecus_wolfi	Wolf's monkey	Polygynous
	Chlorocebus_aethiops	African green monkey	Polygynandrous
	Chlorocebus_pygerythrus	Vervet monkey	Polygynandrous
	Chlorocebus_sabaeus	green monkey	Polygynandrous
	Chlorocebus_tantalus	Tantalus monkey	Polygynandrous
	Erythrocebus_patas	Patas monkey	Polygynous
	Miopithecus_talapoin	Talapoin	Polygynandrous
Papionini	Cercocebus_agilis	Agile mangabey	Polygynandrous
	Cercocebus_galeritus	Tana river mangabey	Polygynandrous
	Cercocebus_torquatus	Red-capped/White-coll	Polygynandrous
	Cercocebus_torquatus_atys	Sooty mangabey	Polygynandrous
	Lophocebus_albigena	White-cheeked mangab	gynous/Polygynand
	Lophocebus_aterrimus	black mangabey	gynous/Polygynand
	Macaca_arctoides	Stump-tailed macaque	Polygynandrous
	Macaca_assamensis	Assam macaque	Polygynandrous
	Macaca_brunnescens	Muna-Buton Macaque	Polygynandrous
	Macaca_cyclopis	Taiwanese macaque	Polygynandrous
	Macaca_fascicularis	Crab-eating macaque	Polygynandrous
	Macaca_fuscata	Japanese macaque	Polygynandrous
	Macaca_hecki	Heck's Macaque	Polygynandrous
	Macaca_leonina	Northern pig-tailed mac	Polygynandrous
	Macaca_maura	Moor macaque	Polygynandrous
	Macaca_mulatta	Rhesus macaque	Polygynandrous
	Macaca_nemestrina	Pig-tailed macaque	Polygynandrous
	Macaca_nemestrina_leonina	Northern pig-tailed mac	Polygynandrous
	Macaca_nemestrina_nemestrin	Southern pig-tailed mac	Polygynandrous
	Macaca_nemestrina_siberu	Siberut/pig-tailed maca	Polygynandrous
	Macaca_nigra	Celebes crested macaq	Polygynandrous
	Macaca_nigrescens	Gorontalo macaque/Du	Polygynandrous
	Macaca_ochreata	Booted macaque	Polygynandrous
	Macaca_pagensis	Mentawai macaque	Polygynandrous
	Macaca_radiata	Bonnet macaque	Polygynandrous
	Macaca_silenus	Liontail macaque	Polygynandrous
	Macaca_sinica	Toque macaque	Polygynandrous
	Macaca_sylvanus	Barbary macaque	Polygynandrous
	Macaca_thibetana	Tibetan stump-tailed m	Polygynandrous
	Macaca_tonkeana	Tonkean macaque	Polygynandrous
	Mandrillus_leucophaeus	Drill	Polygynandrous
	Mandrillus_sphinx	Mandrill	Polygynandrous
	Papio_anubis	Olive baboon	Polygynandrous
	Papio_cynocephalus	Yellow baboon	Polygynandrous
	Papio_hamadryas	Hamadryas baboon	Polygynous
	Papio_papio	Guinea baboon	Polygynandrous
	Papio_ursinus	Chacma baboon	Polygynandrous
	Rungwecebus_kipunji	Kipunji	Polygynandrous
	Theropithecus_gelada	Gelada baboon	Polygynous
Colobinae	Colobus_angolensis	Angolan colobus	Polygynandrous
	Colobus_guereza	Guereza (Eastern black	Polygynous
	Colobus_polykomos	Kings colobus (Western	Polygynandrous
	Nasalis_larvatus	Proboscis monkey	Polygynous

	Piliocolobus_badius	Red colobus	Polygynandrous
	Presbytis_melalophos	Banded leaf monkey	ygynous/Polygynand
	Pygathrix_nemaeus	Douc langur	ygynous/Polygynand
	Rhinopithecus_avunculus	Tonkin snub-nosed mo	Polygynous
	Rhinopithecus_bieti	Black snub-nosed monk	Polygynous
	Rhinopithecus_brelichi	Gray snub-nosed monk	Polygynous
	Rhinopithecus_roxellana	Golden-snub nosed mo	Polygynous
	Semnopithecus_entellus	Hanuman Langur	ygynous/Polygynand
	Trachypithecus_auratus	Javan langur	Polygynous
	Trachypithecus_cristatus	Silvered leaf monkey	Polygynous
	Trachypithecus_francoisi	Francois leaf monkey	Polygynous
	Trachypithecus_johnii	Nilgiri langur	Polygynous
	Trachypithecus_obscurus	Dusky leaf monkey	Polygynous
	Trachypithecus_phayrei	Phayre's leaf monkey	Polygynous
	Trachypithecus_pileatus	Capped leaf monkey	Polygynous
	Trachypithecus_poliocephalus	white-headed langur	Polygynous
Hominoidea	Bunopithecus_hoolock	Hoolock gibbon	Monogamous
	Gorilla_gorilla_gorilla	Western lowland Gorill	Polygynous
	Homo_sapiens	Human	lygynous/Monogam
	Hylobates_agilis	Agile gibbon	Monogamous
	Hylobates_klossii	Kloss's gibbon	Monogamous
	Hylobates_lar	Common/white-hande	Monogamous
	Hylobates_moloch	Javan gibbon	Monogamous
	Hylobates_muelleri	Muller's gibbon	Monogamous
	Hylobates_pileatus	Pileated gibbon	Monogamous
	Nomascus_concolor	Black Crested Gibbon	Monogamous
	Nomascus_gabriellae	Yellow-cheeked Gibbon	Monogamous
	Nomascus_leucogenys	Northern White-cheeke	Monogamous
	Pan_paniscus	Bonobo	Polygynandrous
	Pan_troglodytes_schweinfurthii	Eastern Chimpanzee	Polygynandrous
	Pan_troglodytes_troglodytes	Central Chimpanzee	Polygynandrous
	Pan_troglodytes_verus	Western Chimpanzee	Polygynandrous
	Pongo_abelii	Sumatran Orang-utan	Polygynandrous
	Pongo_pygmaeus_pygmaeus	West Bornean Orang-ut	Polygynandrous
	Symphalangus_syndactylus	Siamang	Monogamous

Note: DD is data deficient. For infanticide <20 publications defined as DD.

Sources

1 B. Sillen-Tullberg, A. P. Møller, The relationship between concealed ovul
2 P. E. Komers, P. N. M. Brotherton, Female space use is the best predicto
3 C. Fimbel, A. Vedder, E. Dierenfeld, F. Mulindahabi, An ecological basis f
4 A. Korstjens, Utrecht (2001).
5 F. B. Bercovitch, N. Harvey, in *Macaque Societies: A model for the study*
6 C. J. Jolly, *Lemur Behaviour* . (University of Chicago Press, Chicago, 1966
7 C. J. Campbell, A. Fuentes, K. C. MacKinnon, M. Panger, S. K. Bearder, Ed
8 A. F. Dixson, *Primate Sexuality: Comparative Studies of the Prosimians,*
9 D. Maestripieri, J. R. Roney, Primate copulation calls and postcopulatory
10 C. L. Nunn, The evolution of exaggerated sexual swellings in primates an
11 C. M. Nievergelt, T. Mutschler, A. T. C. Feistner, D. S. Woodruff, Social sy

12 T. Q. Bartlett, R. W. Sussman, J. M. Cheverud, Infant Killing in Primates:

13 B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham, T. Struhsaker, Eds., *Prim*

14 A. E. Müller, U. Thalmann, Origin and evolution of primate social organis

15 W. G. Kinzey, in *New World Primates: Ecology, Evolution, and Behavior,*

16 P. Charles-Dominique, in *Prosimian Biology,* R. D. Martin, G. A. Doyle, A.

17 C. S. Harcourt, Ecology and Behavior of Avahi-laniger. *International Jour*

18 P. M. Kappeler, C. P. van Schaik, Evolution of primate social systems. *Int*

19 C. van Schaik, in *Infanticide by males and its implications,* C. van Schaik,

20 P. M. Kappeler, M. Pereira, Eds., *Primate Life Histories and Socioecology*

21 I. Fürtbauer, O. Schülke, M. Heistermann, J. Ostner, Reproductive and Li

22 S. B. Hrdy, P. L. Whitter, in *Primate Societies,* B. Smuts, D. Cheney, R. Se

23 C. P. van Schaik, M. A. van Noordwijk, C. L. Nunn, in *Comparative Primat*

24 C. Ross, A. MacLarnon, The Evolution of non-maternal care in anthropoi

25 S. Gursky, K. A. I. Nekaris. (2003), vol. 74, pp. 241-245.

26 M. Bastian, D. Brockman, Paternal Care in Propithecus verreauxi coquer

27 R. Hilgartner, D. Zinner, P. M. Kappeler, Life history traits and parental c

28 G. Solanki, A. Kumar, B. Sharma, Reproductive Strategies of Trachypithe

29 P. M. Kappeler, Determinants Of Primate Social Organization: Comparati

30 J. Fleagle, *Primate Adaptation and Evolution.* , (Academic Press, New Yo

31 P. C. Wright, L. M. Toyama, E. L. Simons, Courtship and Copulation in Ta

32 P. C. Wright, D. Haring, E. L. Simons, P. Andau, Tarsiers: A conservation p

33 N. Shelmidine, C. Borries, A. Koenig, Genital swellings in silvered langurs

34 A. Fuentes, Patterns and Trends in Primate Pair Bonds. *Journal Internati*

35 P. C. Wright, Patterns of paternal care in primates. *International Journal*

36 R. Kummerli, R. D. Martin, Patterns of infant handling and relatedness in

37 Z. F. Xiang, K. Sayers, C. C. Grueter, Direct paternal care in black-and-whi

38 J. Fietz *et al.* , High Rates of Extra-Pair Young in the Pair-Living Fat-Tailed

39 T. Mutschler, C. Tan, in *The Natural History of Madagascar. SM Goodma*

40 C. L. Tan, Group Composition, Home Range Size, and Diet of Three Symp

41 K. Gupta, *Socioecology and conservation of the slender loris(Loris tardigr*

42 P. Lindenfors, Sexually antagonistic selection on primate size. *Journal of*

43 L. M. Porter, A. Christen, Fungus and Callimico goeldii: New insights into

44 C. Veracini, in *The Smallest Anthropoids,* S. M. Ford, L. M. Porter, L. C. D

45 L. Digby, W. Saltzman, in *The Smallest Anthropoids,* S. M. Ford, L. M. Po

46 L. Digby, Infant Care, Infanticide, and Female Reproductive Strategies in

47 C. Nievergelt, L. Digby, U. Ramakrishnan, D. Woodruff, Genetic Analysis

48 M. Arruda *et al.* , Two breeding females within free-living groups may n

49 M. Passamani, A. B. Rylands, Feeding behavior of Geoffroy's marmoset (

50 J. M. Dietz, A. J. Baker, D. Miglioretti, Seasonal variation in reproduction,

51 J. Terborgh, G. Ann Wilson, On the Mating System of the Cooperatively

52 P. A. Garber, A. Estrada, M. S. Pavelka, in *New perspectives in the study*

53 C. T. Snowdon, in *Advances in the Study of Behavior,* S. R. Jay, T. S. Charl

54 A. Savage, L. H. Giraldo, L. H. Soto, C. T. Snowdon, Demography, group c

55 M. E. Pereira, M. L. Weiss, Female Mate Choice, Male Migration, and the

56 S. Rasoloharijaona, B. Rakotosamimanana, E. Zimmermann, Infanticide

57 J. A. Rehg, *Ranging patterns of Callimico goeldii (callimico) in a mixed sp*

58 M. Barros, C. Alencar, C. Tomaz, Differences in aerial and terrestrial visu

59 B. E. Raboy, J. M. Dietz, Diet, foraging, and use of space in wild golden-h

60 R. W. Sussman, W. G. Kinzey, The ecological role of the callitrichidae: A

61 R. T. Day, R. W. Elwood, Sleeping Site Selection by the Golden-handed T

62 K. L. Enstam, L. A. Isbell, Comparison of responses to alarm calls by pata

63 M. Singh, B. A. Krishna, M. Singh, Dominance hierarchy and social groom

64 C. M. Berman, C. Ionica, J. Li, Supportive and Tolerant Relationships amo

65 J. M. Setchell, E. J. Wickings, L. A. Knapp, Life history in male mandrills (

66 P. Sicotte, J. Teichroeb, T. Saj, Aspects of Male Competition in Colobus v

67 A. Korstjens, E. Nijssen, R. Noë, Intergroup Relationships in Western Blac

68 G. Agoramoorthy, M. J. Hsu, Occurrence of Infanticide among Wild Prob

69 Z.-f. Xiang, C. C. Grueter, First direct evidence of infanticide and cannibal

70 S. Zhang, B. Liang, L. Wang, Infanticide within Captive Groups of Sichuan

71 Q.-H. Zhou, B. Luo, C.-M. Huang, Attacks on adult females with infants b

72 Q. Zhao, C. Borries, W. Pan, Male takeover, infanticide, and female coun

Paternal Care	Female Ranging Patterns	Gestation Length (G) (days)	Weaning Age (L) (days)
Sources	*Sources*	*Sources*	*Sources*
7,24,35	2,7,13	7,13,20	7,13,20
Absent	DD		
Absent	Discrete	136.15	150
Absent	Discrete		
Absent	DD	70	45
Absent	DD	71	70
Absent	Discrete	62	61
Absent	Discrete	164	170
Absent	Overlap	125	
Absent	Overlap	120	135
Absent	Overlap	120	135
Absent	Overlap	120	135
Absent	Overlap	120	135
Absent	Overlap	120	135
Absent	Overlap	120	135
Absent	Overlap	120	135
Absent	Overlap	126	
Absent	Overlap	129	135
Absent	Discrete	129	152
Absent	Discrete		
Absent	Discrete	138	140
Absent	Discrete	138	
Absent	Discrete	140	120
DD	DD	140	
DD	DD	140	
Absent	Overlap	149	
Absent	Discrete	159	363
Absent	Overlap	141	120
Absent	Discrete		
Absent	Discrete		
Absent	Discrete		
Absent	Discrete		
Absent	Discrete	130	121.66
Absent	Discrete		
Absent	Discrete		
Absent	Discrete	135	75
Absent	Discrete		
Absent	Discrete	150	119
Absent	Discrete		
Absent	Discrete		
Absent	Discrete	134	120.97
Absent	Overlap		
DD	DD		
DD	DD		
Absent	Overlap		
DD	DD		

DD	DD		
DD	DD		
DD	DD		
Absent	Overlap	60	40
Absent	Overlap	59	
Absent	Overlap		
Absent	Overlap	57	40
DD	DD		
DD	DD		
DD	DD		
Absent	Overlap	87	136
Absent	Overlap		
Absent	Overlap	178	183
Absent	Overlap	179	210
Absent	Overlap	170	153
Absent	Overlap	162	180
Absent	Discrete	102	89
Absent	Discrete	102	89
Absent	DD	134	115
Absent	Discrete	135	105
Absent	Overlap	167	135
Absent	Overlap	166	170
Absent	Overlap		
Absent	Overlap	170	135
Absent	Overlap	185	
Absent	Overlap	170	150
Absent	Overlap		
Absent	Overlap	135	
Absent	Overlap		
Absent	Overlap	123	84
Absent	Overlap	142	98
Absent	Overlap	110	45
Absent	Discrete	126	59
Absent	Overlap	135	135
Absent	Overlap	132	140
Absent	Discrete	178	79
Absent	Discrete	180	82
Present	Discrete		
Present	Discrete	164	60
Present	Discrete		
Present	Discrete		
Present	Discrete	133	75
Present	Discrete	131	75
Present	Discrete	133	75
Present	Overlap	151	65
Present	Overlap		
Present	Discrete	140	
Present	DD		
Present	DD		
Present	DD		

Present	Overlap	148	60
Present	Overlap	143	
Present	Overlap		
Present	Discrete	137	90
Absent	Overlap	155	269
Absent	Overlap	154	261
Absent	Overlap	162	510
Present	Overlap	125	
Present	DD		
Present	Overlap	129	90
Present	Overlap	150	90
Present	Overlap	145	55
Present	Overlap		
Present	Overlap	127	70
Present	Overlap	168	50
Absent	Overlap		
Absent	Overlap		
Absent	Overlap	170	168
Absent	Overlap	187	325
Absent	Overlap	186	325
Absent	Overlap		
Absent	Overlap	191	371
Absent	Overlap	191	372
Absent	Overlap		
Absent	Overlap	226	486
Absent	Overlap	225	750
Absent	Overlap		
Absent	Overlap		
Absent	Overlap		
Absent	Overlap	230	760
Absent	Overlap	233	638
Absent	Overlap	223	315
Absent	Overlap		
Absent	Overlap	172	146
Absent	Overlap	180	362
Absent	Overlap	170	362
Absent	Overlap		
Absent	Overlap		
Absent	Overlap		362
Absent	Overlap		180
Absent	Overlap		
Absent	Overlap		
Absent	Overlap		
Absent	Overlap	140	692
Absent	Overlap		
Absent	Overlap	165	365
Absent	Overlap	170	
Absent	Overlap		
Absent	Overlap		
Absent	Overlap		

Absent	Overlap		
Absent	Overlap		217
Absent	Overlap	163	201
Absent	Overlap		
Absent	Overlap		
Absent	Overlap	167	213
Absent	Overlap	162	180
Absent	Overlap		
Absent	Overlap	171	
Absent	Overlap	171	
Absent	Overlap	167	
Absent	Overlap	186	210
Absent	Overlap		
Absent	Overlap	178	393
Absent	Overlap	164	
Absent	Overlap		
Absent	Overlap	162	206
Absent	Overlap	160	330
Absent	Overlap	173	365
Absent	Overlap		
Absent	Overlap		
Absent	Overlap	163	
Absent	Overlap	165	192
Absent	Overlap	167	234
Absent	Overlap		
Absent	Overlap		
Absent	Overlap		
Absent	Overlap	170	
Absent	Overlap		
Absent	Overlap		
Absent	Overlap		
Absent	Overlap	162	365
Absent	Overlap	180	365
Absent	Overlap	168	
Absent	Overlap	165	210
Absent	Overlap	170	561
Absent	Overlap	176	
Absent	Overlap	173	
Absent	Overlap	175	348
Absent	Overlap	180	584
Absent	Overlap	173	365
Absent	Overlap	170	561
Absent	Overlap	187	
Absent	Overlap	187	
Absent	Overlap		
Absent	Overlap	170	540
Absent	Overlap		
Absent	Overlap	170	330
Absent	Overlap	170	215
Absent	Overlap	166	210

Absent	Overlap		
Absent	Overlap		300
Absent	Overlap	165	
Absent	Overlap		
Absent	Overlap	204	
Absent	Overlap		
Absent	Overlap	195	
Absent	Overlap	184	249
Absent	Overlap		
Absent	Overlap	195	365
Absent	Overlap		394
Absent	Overlap		330
Absent	Overlap		365
Absent	Overlap	205	305
Absent	Overlap	200	
Absent	Overlap		
Absent	Discrete		700
Absent	Overlap	260	1278
Present	Overlap	267	730
Absent	Discrete		
Absent	Discrete	210	330
Absent	Discrete	205	548
Absent	Discrete		
Absent	Discrete	195	
Absent	Discrete		
Absent	Discrete		
Absent	Discrete		
Absent	Discrete	202	
Absent	Overlap	240	1080
Absent	Overlap	235	1680
Absent	Overlap	235	1680
Absent	Overlap	235	1680
Absent	Overlap	250	720
Absent	Overlap	250	720
Present	Discrete	232	639

ulation and mating systems in anthropoid primates: a phylogenetic analysis *American Natura*
or of monogamy in mammals *Proceedings of the Royal Society B-Biological Sciences* **264**, 12
for large group size in *Colobus angolensis* in the Nyungwe Forest, Rwanda. *African Journal of*

of social organisatio B. Thierry, M. Singh, W. Kaumanns, Eds. (Cambridge University Press,
6
ds. *Primates in Perspective* , (Oxford University Press, Oxford, 2007).
Monkeys, Apes, and Human Being. (Oxford University Press, Oxford, 1998).
y female choice *Behav. Ecol.* **16**, 106 (2005).
nd the graded-signal hypothesis *Animal Behaviour* **58**, 229 (1999).
system of the Alaotran gentle lemur (Hapalemur griseus alaotrensis): genetic characterizatio

: A Review of Observed Cases with Specific Reference to the Sexual Selection Hypothesis*Am*
ate Societies , (University of Chicago Press, Chicago, 1987).
isation: a reconstruction*Biological Reviews* **75**, 405 (2000).
W. G. Kinzey, Ed. (Aldine de Gruyter, New York, 1997).
A. C. Walker, Eds. (University of Pittsburgh Press, Pittsburgh, 1974
rnal of Primatolog **8**, 501 (Oct, 1987).
ernational Journal of Primatology **23**, 707 (2002).
, C. Janson, Eds. (Cambridge University Press, Cambridge, 2000), pp. 27–6
, (University of Chicago Press, Chicago, 2002).
Life History Parameters of Wild Female Macaca assamensis*International Journal of Primatol*
eyfarth, R. Wrangham, T. Struhsaker, Eds. (University of Chicago Press, Chicago, 1987), pp.
ate Socioecolog P. C. Lee, Ed. (Cambridge University Press, Cambridge, 1999), pp. 204-240.
oid primates: a test of the hypotheses*Folia Primatologica* **71**, 93 (2000).

reli*International Journal of Primatology* **28**, 305 (2007).
care in Lepilemur ruficaudatus*American Journal of Primatology* **70**, 2 (2008).
ecus pileatus in Arunachal Pradesh, India*International Journal of Primatology* **28**, 1075 (200
ative Evidence And New Insights From Malagasy Lemurs*Biological Reviews* **72**, 111 (1997).
ork, 1988), pp. 22
arsius bancanus*Folia Primatologica* **46**, 142 (1986).
perspective*Primate Conservation* **8**, 51 (1987).
s: what do they indicate*American Journal of Primatology* **69**, 519 (2007).
tional Journal of Primatolog **23**, 953 (2002).
al of Primatolog **11**, 89 (1990).
in Barbary macaques (Macaca sylvanus) on Gibraltar*Primates* **49**, 271 (Oct, 2008).
hite snub-nosed monkeys*Journal of Zoology* **278**, 157 (Jun, 2009).
d Dwarf Lemur, Cheirogaleus medius*Behavioral Ecology and Sociobiology* **49**, 8 (2000).
an and JP Benstead (eds . (2003), pp. 1324.
patric Bamboo Lemur Species (Genus Hapalemur) in Ranomafana National Park, Madagasc
gradus) in southern Indi . (2007), vol. 68.
Evolutionary Biology **15**, 595 (2002).
o Callimico goeldii behavior and ecology*Evolutionary Anthropology: Issues, News, and Revie*
Davis, Eds. (Springer US, 2009), pp. 221-24
orter, L. C. Davis, Eds. (Springer US, 2009), pp. 135-15
n Polygynous Groups of Common Marmosets (Callithrix jacchus)*Behavioral Ecology and Soci*
of Group Composition and Breeding System in a Wild Common Marmoset (Callithrix jacch
not always indicate polygyny: alternative subordinate female strategies in common marmos
(Callithrix geoffroyi) in an Atlantic forest fragment of South-eastern Brazil*Primates* **41**, 27
n, juvenile growth, and adult body mass in golden lion tamarins (Leontopithecus rosalia)*Am*
Breeding Saddle-Backed Tamarin (Saguinus fuscicollis)*Behavioral Ecology and Sociobiology*
of Mesoamerican primat . (Springer, 2006), pp. 563-584.
rles, Eds. (Academic Press, 1996), vol. Volume 25, pp. 643-68
composition, and dispersal in wild cotton-top tamarin (Saguinus oedipus) groups*American J*
ne Threat of Infanticide in Ringtailed Lemurs*Behavioral Ecology and Sociobiology* **28**, 141 (1
by a Male Milne-Edwards' Sportive Lemur (Lepilemur edwardsi) in Ampijoroa, NW-Madaga
pecies grou . (Springer, 2009).
ual scanning in captive black tufted-ear marmosets (Callithrix penicillata) exposed to a nove
headed lion tamarins*American Journal of Primatology* **63**, 1 (2004).
review*American Journal of Physical Anthropology* **64**, 419 (1984).
Tamarin Saguinus midas midas: The Role of Predation Risk, Proximity to Feeding Sites, and

as (Erythrocebus patas) and vervet (Cercopithecus aethiops) monkeys in relation to habitat
ming in female lion- tailed macaques (Macaca silenus) in the Western Ghats, India*J Biosci* **3**
ıong Male Tibetan Macaques at Huangshan, China*Behaviour* **144**, 631 (2007).
(Mandrillus sphinx): Physical development, dominance rank, and group association*American*
vellerosus: Preliminary Data on Male and Female Loud Calling, and Infant Deaths After a Ta
ack-and-White Colobus, Colobus polykomos polykomos*International Journal of Primatology*
boscis Monkeys (Nasalis larvatus) in Sabah, Northern Borneo*Folia Primatologica* **76**, 177 (2
alism in wild snub-nosed monkeys (Rhinopithecus bieti)*American Journal of Primatology* **69**
n Golden Snub-Nosed Monkeys <i>(Rhinopithecus roxellana)</i>*Folia Primatologica* **70**, 27
by no-resident males in the François langur. *Zoological Research* **34**, (2013).
ıntertactics in white-headed leaf monkeys (Trachypithecus leucocephalus)*Behavioral Ecolog*

Weaning Proportion	**Seasonal Breeders (with time out**	**Infanticide**	**Total Publications**
(L/(G+L))	*Sources*	*Sources*	*(Web of Science)*
	7,13,23	12,19,23	
		DD	17
0.52	Yes	Low	71
	Yes	Low	34
0.39		DD	10
0.50	Yes	Low	68
0.50	Yes	Low	181
0.51	No	Low	172
	Yes	Low	65
0.53	Yes	Low	41
0.53	Yes	DD	17
0.53	Yes	Low	22
0.53	No	High	34
0.53	Yes	Low	27
0.53	No	High	199
0.53	Yes	DD	13
	Yes	Low	38
0.51	Yes	High	52
0.54	Yes	High	86
	Yes	Low	111
0.50	Yes	Low	41
	No	Low	41
0.46	Yes	Low	41
	Yes	DD	4
	Yes	DD	10
	No	Low	56
0.70	Yes	Low	86
0.46	Yes	High	979
		DD	0
		DD	4
		DD	11
	Yes	High	46
0.48	Yes	Low	31
		DD	10
		DD	0
0.36		Low	33
		DD	1
0.44	Yes	Low	38
		DD	2
		DD	1
0.47		DD	19
	No	DD	12
		DD	0
		DD	0
		Low	26
		DD	2

		DD	4
		DD	0
		DD	3
0.40	Yes	Low	786
		DD	18
	Yes	Low	46
0.41		Low	85
		DD	1
		DD	4
		DD	3
0.61	Yes	Low	37
		Low	25
0.51	No	High	200
0.54	No	High	68
0.47	No	Low	33
0.53	No	High	92
0.47	Yes	Low	39
0.47	Yes	High	110
0.46	No	DD	2
0.44	No	Low	27
0.45	No	DD	4
0.51	No	Low	183
	No	DD	3
0.44	No	Low	361
		Low	97
0.47	No	Low	147
	No	Low	23
	Yes	Low	36
		DD	5
0.41	No	Low	81
0.41	No	Low	518
0.29		DD	17
0.32		DD	10
0.50	Yes	Low	105
0.51	Yes	Low	179
0.31	No	Low	118
0.31	No	Low	105
		DD	20
0.27	Yes	Low	192
	Yes	Low	76
		Low	22
0.36	No	Low	69
0.36	No	Low	128
0.36	No	Low	1576
0.30	No	Low	245
		Low	63
		Low	38
		DD	16
		Low	110
		DD	2

0.29	No	Low	6858
		Low	46
		Low	210
0.40	No	Low	31
0.63	No	Low	377
0.63	No	High	4101
0.76	No	High	649
	No	Low	122
		Low	56
0.41	No	Low	376
0.38	No	Low	656
0.28		Low	82
		Low	70
0.36		Low	123
0.23	No	Low	1301
	Yes	Low	49
	Yes	Low	44
0.50	No	Low	5472
0.63	No	High	290
0.64	No	High	682
	No	High	240
0.66	No	DD	9
0.66	No	High	400
	No	Low	155
0.68		Low	71
0.77	No	Low	610
		DD	9
		DD	11
		Low	24
0.77	No	Low	173
0.73	No	Low	242
0.59	No	Low	187
		Low	31
0.46	No	High	195
0.67	No	High	100
0.68		Low	103
		DD	3
		DD	1
	No	Low	146
		DD	6
		Low	29
	No	DD	20
	No	Low	61
0.83	No	High	138
		Low	126
0.69	No	Low	123
	No	Low	148
		Low	47
		Low	27
		Low	25

		DD	17
		High	1181
0.55	No	Low	858
		Low	57
		DD	16
0.56	No	High	942
0.53	No	Low	101
		Low	28
		High	110
	No	High	278
		High	53
0.53	No	Low	132
	No	Low	21
0.69	No	Low	1182
	No	Low	171
		DD	16
0.56	No	High	76
0.67	No	High	5184
0.68	No	High	1302
		DD	19
		DD	11
	No	Low	55
0.54	No	High	8132
0.58	No	High	1276
	No	DD	15
	No	DD	18
	No	DD	0
	No	Low	208
		Low	26
		Low	26
		DD	9
0.69	No	High	512
0.67	No	High	111
	No	High	40
0.56	No	High	305
0.77	No	High	84
	No	Low	118
	No	High	47
0.67	No	High	207
0.76	No	High	1080
0.68	No	High	896
0.77	No	High	723
		Low	150
	No	High	561
		Low	26
0.76	No	High	106
	No	Low	35
0.66	No	High	169
0.56	No	High	34
0.56	No	High	74

	No	High	40
	No	Low	67
		High	105
		Low	36
		High	171
		Low	42
		High	186
0.58	No	High	144
		Low	30
0.65	No	High	46
		High	64
		DD	18
	No	Low	37
0.60		Low	82
	No	Low	27
		DD	7
	No	Low	95
0.83	No	High	1188
0.73	No	High	14214
	No	Low	161
0.61	No	Low	64
0.73	No	Low	726
	No	Low	91
	No	Low	74
	No	Low	84
	No	Low	52
	No	DD	19
	No	Low	78
0.82	No	Low	1586
0.88	No	High	438
0.88	No	High	227
0.88	No	High	367
0.74	No	Low	182
0.74	No	Low	130
0.73	No	Low	167

ralis **141**, 1 (1993).
61 (1997).
of Ecolog **39**, 83 (2001).

s, Cambridge, 2004), pp. 61-8

on of group composition and mating system*American Journal of Primatology* **57**, 157 (2002).

erican Anthropologist **95**, 958 (1993).

log **31**, 501 (2010).
370-384

7).

ar*International Journal of Primatology* **20**, 547 (1999/08/01, 1999).

ew **11**, 87 (2002).

ciobiolog **37**, 51 (1995).
us) Population*International Journal of Primatology* **21**, 1 (2000/02/01, 2000).
ets (Callithrix jacchus)*Folia Primatologica* **76**, 10 (2005)
2000/01/01, 2000).
erican Journal of Primatology **34**, 115 (1994).
16, 293 (1985).

ournal of Primatology **38**, 85 (1996).
991).
scar*International Journal of Primatology* **21**, 41 (2000/02/01, 2000).

l environment*Folia Primatologica* **75**, 85 (2004).

erritorial Defence*Ethology* **105**, 1035 (1999).

structure*American Journal of Physical Anthropology* **119**, 3 (2002).
1, 369 (2006/09/01, 2006).

Journal of Physical Anthropology **131**, 498 (2006).
keover*International Journal of Primatology* **28**, 627 (2007/06/01, 2007).
26, 1267 (2005/12/01, 2005).
05).
, 249 (2007).
4 (1999).

gy and Sociobiolog **65**, 1535 (2011/08/01, 2011).

Additional Sources
17
17
18,25, 38
55
7,29
17
11, 39
29, 40
40
40
6
30
18, 56
30
30
18,27
30

19
26

16
16

41

16

42
18

19,31
32
15

15
15
15
15
15
43,57
44
45

46, 47, 48

58

24

49, 59

50
51
52, 60
60
61
53, 54, 60

15
15,24
15,24
15
15
15
15

24

10
10

10, 62

24,30
30
5,24
21
5,9,10
5,9,10
5,9,10,24
5,9,10
5,9,10
5,9,10
5,9,10
5,9,10

5
5

5
63

24,36
9, 64
5,10
10
10, 65
9
24

9,10
9

3,10

4,10, 66, 67
68

10
10

37, 69

70

33
71

33
28
72