

This is the author's version of the work. It is posted here by permission of the AAAS for personal use, not for redistribution. The definitive version was published in Science [Vol 341, 2 Aug 2013] doi: 10.1126/science.1238677: <http://www.sciencemag.org/content/341/6145/526.short>

**Title: The evolution of social monogamy in mammals**

**Authors:** D. Lukas<sup>1\*</sup>, T. H. Clutton-Brock<sup>1</sup>

**Affiliations:**

5 <sup>1</sup>Department of Zoology  
University of Cambridge  
Downing Street  
Cambridge CB2 3EJ  
U.K.

10

\*Correspondence to: [dl384@cam.ac.uk](mailto:dl384@cam.ac.uk)

**Abstract**

15 The evolution of social monogamy has intrigued biologists for over a century. Here, we show that the ancestral condition for all mammalian groups is of solitary individuals and social monogamy is derived almost exclusively from this social system. The evolution of social monogamy does not appear to have been associated with a high risk of male infanticide and paternal care is a consequence rather than a cause of social monogamy. Social monogamy has  
20 evolved in non-human mammals where breeding females are intolerant of each other and female density is low, suggesting that it represents a mating strategy that has developed where males are unable to defend access to multiple females.

25 **One Sentence Summary:** Social monogamy evolved in solitary mammals as a male mating strategy and is not a consequence of selection for paternal care.

## Main Text

Despite extensive interest in the evolution of monogamy stimulated by its prevalence in humans (1–3), the distribution of social monogamy in non-human mammals continues to puzzle evolutionary biologists (4). In contrast to birds, social monogamy in mammals is usually associated with genetic monogamy and the incidence of extra-pair mating is generally low in socially monogamous societies (5). There are two main explanations for its existence. One suggests that it is a consequence of selection for some form of paternal care, such as contributions to carrying or provisioning young or their protection from infanticide by competing males (6). Alternatively, social monogamy may represent a mate guarding strategy and may have evolved where males were unable to defend access to more than one female (7, 8), either because of mutual intolerance between breeding females (9, 10) or because large female home-ranges prevent effective defence by males of territories covering the ranges of more than one female (11).

A recent comparative analysis of primate breeding systems (12) using a Bayesian approach identified six transitions to social monogamy in primates and concluded that social monogamy is derived from an ancestral condition where both sexes are social and live in unstable groups, supporting the suggestion that its evolution may be associated with the risk of male infanticide. However, this seems unlikely to provide a general explanation for the evolution of social monogamy in mammals since groups of breeding females occur much less frequently in other taxonomic groups. Here, we use data for more than 2500 mammals to identify sixty-one independent evolutionary transitions to social monogamy in mammals, assess the characteristics of the species in which transitions occurred and use them to test the predictions of alternative explanations of the evolution of social monogamy.

50 We classified the social systems of all non-human mammalian species for which  
information was available (n=2545) as either solitary (breeding females forage independently in  
individual home-ranges and encounter males only during mating), socially monogamous (a  
single breeding female and a single breeding male share a common range or territory and  
associate with each other for more than one breeding season, with or without nonbreeding  
55 offspring) or group-living (several breeding females share a common range and forage or sleep  
together). Group-living species include those where groups of breeding females are unstable, as  
in the case of ungulate herds or the roosting groups of some bats, as well as species where  
several breeding females associate with each other in stable groups for more than one breeding  
season, whether or not they always forage together (see Supplementary Material and  
60 Supplementary Data). While in some non-human mammalian species smaller social groups  
occasionally merge to form larger unstable groups (as in elephants and gelada baboons),  
associations of socially monogamous pairs, which are common in birds, have not been reported  
except, possibly, in the mara, *Dolichotis patagonum* (13)). Species were classified as showing  
paternal care if males regularly contribute to feeding or carrying offspring (2, 14). After  
65 reconstructing the most parsimonious sequence of transitions across a recently derived  
mammalian supertree (15), all inferences were confirmed using likelihood-based reconstruction  
approaches (16, 17). We first tested for associations between the distribution of social monogamy  
and several social and ecological traits using non-parametric tests, phylogenetic independent  
contrasts (18), and regression models that account for phylogenetic relatedness (19-21). Next, we  
70 assessed the importance of any associated factors in predicting transitions to social monogamy  
by comparing inference models in Bayestraits' Discrete and Multistate (17, 22).

### The distribution of social monogamy

Of the 2545 mammalian species whose social systems could be classified, breeding  
75 females were classified as solitary in 1741 species (68%), as socially monogamous in 229  
species (9%), and as living in social groups in 575 species (23%). The proportion of socially  
monogamous species in our sample is slightly higher than frequently reported earlier estimates  
(3%, (1)), but is still an order of magnitude lower than in birds, where 90% of species are  
considered to be socially monogamous (23). Social monogamy occurs more frequently in some  
80 mammalian Orders, such as Primates (106 of 361 species, 29%) and Carnivora (33 of 201  
species, 16%), and is uncommon in others, such as Artiodactyla (6 of 187 species, 3%), and  
absent in a few, including Cetacea (see Table S1).

### Transitions to social monogamy

85 Our phylogenetic reconstruction shows that, in the common ancestor of all mammalian  
species, females were solitary and males occupied ranges or territories overlapping several  
females. All approaches to reconstructing evolutionary sequences support this inference for the  
2288 species included in the updated mammalian supertree and the likelihood that the common  
ancestor was solitary is 0.99 for all approaches. Solitary living appears to have been the ancestral  
90 condition for the ancestors of all mammalian Orders, with the possible exception of elephant  
shrews (Macroscelidea) and hyraxes (Hyracoidea). Closely related species generally have the  
same breeding system and female sociality has a strong phylogenetic signal: maximum  
likelihood estimate of Pagel's lambda was 0.93 for solitary living, 0.92 for social monogamy, and  
0.86 for group living; all lambda estimates were significantly different from 0 (no phylogenetic  
95 signal) based on likelihood ratio tests. Similarly, the phylogenetic signal for all three social

systems combined using Blomberg's K was significantly different from a chance distribution of sociality across species (0.20,  $Z=-10.99$ ,  $p=0.001$ ).

Parsimonious reconstructions suggest that 61 independent transitions to social monogamy from solitary ancestors are necessary to explain the distribution of social monogamy among current species. In all but one case, socially monogamous species in our dataset appear to have been derived from an ancestor where females were solitary and lived in individual home-ranges and males ranged independently: the only potential transition to social monogamy from an ancestor that is likely to have lived in groups occurs in the primate genus *Eulemur*. The results of Bayestrans' Discrete and Multistate analyses performed for each Order in which socially monogamous species occur confirmed that social monogamy is almost exclusively derived from ancestors where females are solitary. The most likely models suggest that no transitions to social monogamy from group-living occurred except in the one instance in the primates. Models in which transition rates to social monogamy were forced to occur equally from group-living ancestors and solitary ancestors performed significantly worse than models in which all socially monogamous species are derived from a solitary ancestor (Likelihood ratio test (lrt) all  $p<0.005$ ; Table S2). Group-living sister taxa of socially monogamous species occur in some groups (e.g. banded mongooses, *Mungos mungo*; Goeldii's monkey, *Callimico goeldii*; sifakas, *Propithecus spp.*), and probably represent secondary transitions to group living from socially monogamous ancestors.

115

#### Social monogamy and male care

While it is often difficult to exclude the possibility of any form of male contribution to the care of young, detailed field studies have found no evidence of any form of male contribution

in 94 of 229 (41%) socially monogamous species. For example, in dik dik, where males are both  
120 genetically and socially monogamous and are closely associated with their mates, they provide  
no contributions to guarding, carrying, feeding or teaching young or to any other obvious form of  
paternal care (24). The distribution of paternal care in contemporary socially monogamous  
species is closely associated with the form and distribution of maternal care: where females carry  
and/or provision offspring, males commonly contribute to the same activities. Regular  
125 provisioning or carrying of young by males has been recorded in 135 (59%) of the 229 socially  
monogamous mammals, whereas it is found only in three non-monogamous species, two of  
which appear to be derived from a socially monogamous ancestor (*Mungos mungo* (25) and  
*Callimico goeldii* (26); the third species is *Hapalemur griseus* (27)).

Comparisons suggest that paternal care probably contributes to the fitness of both sexes:  
130 females in socially monogamous species with bi-parental care produce more litters per year  
(median 2, range 0.9-9, n=48 species) than in socially monogamous species without bi-parental  
care (median 1, range 0.2-7, n=37 species;  $F=4.43$ ,  $p=0.04$ , phylogenetic gls (phy):  $\lambda=0.92$ ,  
 $t=-2.6$ ,  $p=0.01$ ) or than in solitary species (median 1.1, range 0.2-7, n=242 species;  $F=7.56$ ,  
 $p=0.006$ , phy:  $\lambda=0.97$ ,  $t=2.1$ ,  $p=0.03$ ). Increases in the reproductive rate of females  
135 probably have benefits to males, who sire offspring in more breeding cycles in socially  
monogamous species with paternal care (median 6 breeding seasons, range 4.5-8 breeding  
seasons, n=11 species) than in socially monogamous species where males do not provide care  
(median 3 breeding seasons, range 2-8 breeding seasons, n=8 species;  $F=4.98$ ,  $p=0.04$ ; phy:  
 $\lambda=0.78$ ,  $t=2.0$ ,  $p=0.06$ ), even though there are no differences in male tenure length (with  
140 paternal care median 47 months, without median 45 months;  $F=2.10$ ,  $p=0.17$ , phy:  $\lambda=0.53$ ,  
 $t=-1.1$ ,  $p=0.31$ ).

Although paternal care and social monogamy are associated, analysis of transitions suggests that male care is probably a consequence rather than a cause of the evolution of social monogamy. Approximately half of all independent transitions to paternal care have occurred in  
145 instances where social monogamy was already established while, in the other cases, the evolution of paternal care occurred on the same branch as a transition to social monogamy. Inferences from Bayestraits models indicate that paternal care is a secondary adaptation, as transitions to social monogamy are inferred to occur first on branches where both traits evolved separately (lrt p=0.002; Table S2).

150

#### Social monogamy and male infanticide

An alternative suggestion is that social monogamy allows males to protect their offspring from attacks by infanticidal competitors and has evolved for this reason (28). However, the available evidence suggests that male infanticide is unlikely to be the principal mechanism for  
155 the evolution of social monogamy in mammals. Male infanticide is typically found in species where the duration of lactation exceeds the duration of gestation (6, 28): this is the case in few socially monogamous species (20 of 75 species, 27%) compared to species where females are solitary (148 of 335 species, 44%; W=11733, p=0.34; phylogenetic independent contrasts (pic) t=-1.63, p=0.10) and Bayestraits models also provide no evidence of an association between the  
160 evolution of social monogamy and lactation durations that exceed gestation (lrt p>0.40, Table S2). Although the prevalence of male infanticide is lower among socially monogamous species (4 of 47 species, 9%) than among solitary species (24 of 88 species, 27%; W=1542.5, p=0.01), this difference does not appear to be a consequence of a direct association between social monogamy and male infanticide, as analysis of phylogenetic independent contrasts (t=-0.402,

165  $p=0.69$ ) and Bayestraits models suggest an independent evolution of the two traits (Irt  $p>0.90$ ,  
Table S2).

### Social monogamy and the ecological defensibility of females

The main alternative explanation of the distribution of social monogamy in mammals is  
170 that it has evolved where females are solitary and males are unable to defend access to more than  
one female at a time (7). Evidence that socially monogamous species are derived from ancestors  
where females are solitary (see above) supports this suggestion. Moreover, unlike previous  
analyses (2, 4), our data show that socially monogamous mammals live at significantly lower  
densities (median 15 individuals per square kilometre,  $n=89$  species) than solitary species  
175 (median 156 individuals per square kilometre,  $n=411$  species;  $W=10746.5$ ,  $p<0.001$ ;  
phylogenetically controlled binomial GLM in MCMCglmm (pMCMC)  $p=0.007$ )(Figure 1).  
Socially monogamous species have, on average, higher individual body mass (median 873grams)  
compared to solitary species (median 308grams;  $W=40733$ ,  $p=0.001$ ;  $pMCMC=0.34$ ), which  
may contribute to their low density. However, the residuals of a phylogenetically controlled  
180 regression of population density on body mass are significantly lower for socially monogamous  
species than for solitary species ( $W=10421$ ,  $p<0.001$ ;  $pMCMC<0.001$ ), indicating that size  
differences alone do not account for the low density of socially monogamous species.

Despite the association between social monogamy and low population density, there is no  
significant difference in female home-range size between socially monogamous (median 0.21  
185 square kilometres,  $n=71$  species) and solitary species (median 0.53 square kilometres,  $n=185$   
species;  $W=5553$ ,  $p=0.06$ ;  $pMCMC=0.11$ ), even when differences in body mass are controlled  
for ( $W=6100$ ,  $p=0.70$ ;  $pMCMC=0.08$ ). This suggests that there may be greater overlap of home



ranges between females in solitary species than in socially monogamous ones and comparative data for primates (the only taxonomic group for which comparative data are available) supports  
190 this conclusion: in a sample of 26 socially monogamous primates, home-ranges overlap on average by 21% (median 17%), whereas, in species where females are solitary, the ranges of females overlap on average by 49% (median 58%,  $n=5$  species;  $F=7.08$ ,  $p=0.01$ ; phy:  $\lambda=0.0$ ,  $t=-2.4$ ,  $p=0.02$ ).

The high incidence of social monogamy in Primates and Carnivora compared to more  
195 herbivorous Orders (including Rodentia and Ungulates) suggests that the evolution of low range overlap in females and social monogamy may be a consequence of a reliance on resources of high nutritional quality but low abundance. Comparisons show that a similar association between social monogamy and low density resources occurs within Orders. For example, in 91% (81 of 89) of socially monogamous primates, fruit constitute the main part of the diet, whereas fruit is  
200 the single most important food for only 28% (13 of 46) of solitary primate species ( $W=762.5$ ,  $p<0.001$ ;  $\text{pic } t=3.12$ ,  $p=0.002$ ). In contrast, foods of low nutritional value (gum, bark, fungi) are included in the diet of significantly more solitary (43 of 46, 93%) than socially monogamous primate species (35 of 89, 39%;  $W=3155.5$ ,  $p<0.001$ ;  $\text{pic } t=-4.18$ ,  $p<0.001$ ).

Analyses of patterns of sexual dimorphism also suggest that competition between females  
205 may be more intense in socially monogamous species than in solitary. While males are heavier than females in 134 of 170 species (79%) where females are solitary, male-biased sexual dimorphism is found in only 21 of 44 socially monogamous species (48%;  $W=2736.5$ ,  $p<0.001$ ;  $\text{pic } t=1.53$ ,  $p=0.13$ ). This difference does not appear to be a consequence of a reduction in dimorphism after the transition to social monogamy, for the sequence of transitions (as inferred  
210 by the most likely Bayestrains models) suggests that social monogamy only evolved in species in

which females are at least as large as males (lrt  $p < 0.05$ ; Table S2), and that in some socially monogamous species changes in evolutionary conditions appear to have led to subsequent increases in sexual dimorphism, preceding the loss of social monogamy.

## 215 Discussion

Like previous analyses (2,12) our results suggest that the evolution of social monogamy has been restricted to particular ancestral states. However, our conclusion that social monogamy is derived from an ancestral state in which females are solitary and male ranges overlap those of several females contrasts with recent suggestions that, in primates, it is derived from ancestors in  
220 which females and males live in unstable groups (12). This difference is unlikely to be a consequence of contrasts between primates and other mammals, for five of the six transitions to social monogamy among primates in our dataset were also from ancestors where females were solitary. Instead, it is likely to be a consequence of a contrast in the classification of breeding systems: Shultz et al. classify socially monogamous species that are accompanied by non-  
225 breeding offspring as group-living and do not distinguish between breeding systems of this kind and plural breeders, where groups include several breeding females. As a result, some species that we classify as socially monogamous were classified by Shultz et al. as group-living. This difference in classification highlights the extent to which the way in which breeding systems are classified can influence the interpretation of species differences.

230 The association between social monogamy and low population density also differs from previous analyses, which found no significant difference in population density between socially monogamous species and those where females live in separate home ranges (2, 4). In this case, it seems likely that the contrast is a result of differences in sample size between our analyses and

previous analyses, where sample size was less than 90 species (2, 4). Our larger sample size also  
235 allowed us to assess whether changes in population density preceded transitions to social  
monogamy, whereas comparing average population density between solitary and socially  
monogamous species may fail to detect a difference as changes to low population density in  
social species might not necessarily lead to the evolution of social monogamy (14).

Our results suggest that social monogamy evolved in mammals where feeding  
240 competition between females was intense, breeding females were intolerant of each other and  
population density was low (Figure 2). Under these conditions, guarding individual females may  
represent the most efficient breeding strategy for males (7). The evolution of paternal care  
appears to have succeeded the evolution of social monogamy, suggesting that unlikely to be a  
precondition for its evolution. Transitions to singular cooperative breeding occurred in a small  
245 number of socially monogamous species (29), and occasionally plural breeding by several  
females whose offspring are raised by all group members evolved from such an ancestor (e.g.  
banded mongooses, (25)). This suggests that there are at least two independent routes to female  
sociality in mammals (Figure 2).

As all the African apes are polygynous and group-living, it is likely that the common  
250 ancestor of hominids was also polygynous, and this is supported by evidence of substantial  
sexual size dimorphism in early hominids (30) as well as by sex differences in rates of aging in  
modern humans (31). The rarity of transitions to social monogamy from group-living,  
polygynous species in non-human mammals could suggest that the shift to monogamy in humans  
was the result of a change in dietary patterns that reduced female density and limited the  
255 potential for males to guard more than one female (32). Alternatively, the evolution of human  
monogamy could have been a consequence of the need for extended paternal investment (3).

## References and Notes:

1. D. Kleiman, Monogamy in mammals, *Q. Rev. Biol.* 39-69 (1977).
- 260 2. P. Brotherton, P. Komers, in *Monogamy: mating strategies and partnerships in birds, humans and other mammals*. Eds. C. Boesch, U. Reichard (Cambridge Univ. Press, Cambridge, 2003) pp. 42-58.
3. S. Gavrillets, S. (2012). Human origins and the transition from promiscuity to pair-bonding. *Proc. Natl. Acad. Sci. U.S.A* **109**, 9923-9928 (2012).
- 265 4. F. S. Dobson, B. M. Way, C. Baudoin, Spatial dynamics and the evolution of social monogamy in mammals, *Behav. Ecol.* **21**, 747–752 (2010).
5. T. H. Clutton-Brock, K. Isvaran, Paternity loss in contrasting mammalian societies, *Biol. Lett.* **2**, 513–6 (2006).
6. C. P. van Schaik in *Primate males: causes and consequences of variation in group composition*. ed. P. Kappeler (Cambridge Univ. Press, Cambridge, 2000) pp. 61-71.
- 270 7. S. Emlen, L. Oring, Ecology, Sexual Selection, and the Evolution of Mating Systems, *Science* **197**, 215–224 (1977).
8. S. Shuster, M. Wade, *Mating systems and mating strategies*. (Princeton Univ. Press, Princeton, 2003).
- 275 9. J. Wittenberger, R. Tilson, The evolution of monogamy: hypotheses and evidence, *Annu. Rev. Ecol. Syst.*, 197-232 (1980).
10. U. Reichard, in *Monogamy: mating strategies and partnerships in birds, humans and other mammals*. eds. C. Boesch, U. Reichard (Cambridge Univ. Press, Cambridge, 2003)
11. G. Orians, On the evolution of mating systems in birds and mammals, *Am. Nat.* **103**, 589-603

25

280 (1969)

12. S. Shultz, C. Opie, Q. D. Atkinson, Stepwise evolution of stable sociality in primates, *Nature* **479**, 219–222 (2011).
13. A. B. Taber, D. W. Macdonald, Spatial organization and monogamy in the mara *Dolichotis patagonum*. *J. Zool.* **227**, 417–438 (1992).
- 285 14. C. Van Schaik, P. Kappeler, in *Monogamy: mating strategies and partnerships in birds, humans and other mammals*. eds. C. Boesch, U. Reichard (Cambridge Univ. Press, Cambridge, 2003).
15. S. A. Fritz, O. R. P. Bininda-Emonds, A. Purvis, Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics, *Ecol. Letters* **12**, 538–49  
290 (2009).
16. D. Schluter, T. Price, A. Mooers, D. Ludwig, Likelihood of ancestor states in adaptive radiation, *Evolution* **51**, 1699–1711 (1997).
17. M. Pagel, Inferring the historical patterns of biological evolution, *Nature* **401**, 877–84 (1999).
- 295 18. J. Felsenstein, Phylogenies and the comparative method, *Am. Nat.* **125**, 1–15 (1985).
19. C. D. L. Orme, R. P. Freckleton, G. H. Thomas, T. Petzoldt, S. A. Fritz, N. J. Isaac, N. J. B. caper: Comparative Analyses of Phylogenetics and Evolution in R, *Methods Ecol. Evol.* **3**, 145–151 (2012).
20. J. D. Hadfield, S. Nakagawa, General quantitative genetic methods for comparative biology:  
300 phylogenies, taxonomies and multi-trait models for continuous and categorical characters, *J. Evol. Biol.* **23**, 494–508 (2010).
21. More detailed information on materials and methods is available on Science Online.

22. M. Pagel, A. Meade, Bayesian analysis of correlated evolution of discrete characters by reversible-jump Markov chain Monte Carlo, *Am. Nat.* **167**, 808–825 (2006).
- 305 23. A. Cockburn, Prevalence of different modes of parental care in birds, *Proc. R. Soc. London Ser. B* **273**, 1375-1383 (2006).
24. P. Brotherton, M. Manser, Female dispersion and the evolution of monogamy in the dik-dik, *Anim. Behav.* **54**, 1413-1424 (1997)
25. M. Cant, Patterns of helping effort in co-operatively breeding banded mongooses (Mungos mungo), *J. Zool.* **259**, 115-121 (2003).
- 310 26. L. M. Porter, Social organization, reproduction and rearing strategies of *Callimico goeldii*: new clues from the wild. *Folia Primat.* **72**, 69-79 (2001).
27. P. C. Wright, Patterns of paternal care in primates. *Int. J. Primatol.* **11**, 89-102 (1990).
28. C. Van Schaik, R. Dunbar, The evolution of monogamy in large primates: a new hypothesis and some crucial tests, *Behaviour* **115**, 30-62 (1990).
- 315 29. D. Lukas, T. Clutton-Brock, Cooperative breeding and monogamy in mammalian societies, *Proc. R. Soc. London Ser. B* **259**, 2171-2176 (2012).
30. J. M. Plavcan, Sexual Size Dimorphism, Canine Dimorphism, and Male-Male Competition in Primates. *Human Nature* **23**, 45-67 (2012).
- 320 31. L. Mealy, *Sex differences: developmental and evolutionary strategies*. (Academic Press, San Diego, 2000).
32. K. E. Langergraber, J. C Mitani, D. P. Watts, L. Vigilant, Male–female socio-spatial relationships and reproduction in wild chimpanzees. *Behav. Ecol. Sociobiol.* **67**, 861-873 (2013).
- 325 33. D. E. Wilson, D. M. Reeder, *Mammal species of the world: a taxonomic and geographic*

reference (Johns Hopkins, Boston, 2005).

34. R. N. Nowak, *Walker's mammals of the world*. (John Hopkins, Baltimore, 1999).
35. Nievergelt, C. M., Mutschler, T., Feistner, A. T., & Woodruff, D. S Social system of the  
Alaotran gentle lemur (*Hapalemur griseus alaotrensis*): genetic characterization of group  
330 composition and mating system. *American Journal of Primatology*, 57(4), 157-176 (2002).
36. M. van Noordwijk, C. Van Schaik, in *Infanticide by males and its implications*, C. van  
Schaik, C. H. Janson, Eds. (Cambridge University Press, Cambridge, 2000), pp. 322–360.
37. D. T. Blumstein, in *Infanticide by males and its implications* eds. C. van Schaik, C. Janson,  
(Cambridge Univ. Press, Cambridge, 2000) pp. 178-197.
- 335 38. S. K. M. Ernest, Life history characteristics of placental nonvolant mammals, *Ecology* **84**,  
3402 (2003).
39. K. E. Jones et al., PanTHERIA: a species-level database of life history, ecology, and  
geography of extant and recently extinct mammals, *Ecology* **90**, 2648–2648 (2009).
40. J. P. de Magalhães, J. Costa, A database of vertebrate longevity records and their relation to  
340 other life-history traits. *J. Evol. Biol.* **22**, 1770–4 (2009).
41. F. Pearce, C. Carbone, G. Cowlshaw, N. J. Isaac, N. J. Space-use scaling and home range  
overlap in primates. *Proc. R. Soc. London Ser. B* **280**, 1751 (2013).
42. J.M. Gómez, M. Verdú, Mutualism with plants drives primate diversification. *Syst. Biol.* **61**,  
567-577 (2012).
- 345 43. D. Lukas, T. H. Clutton-Brock, Group structure, kinship, inbreeding risk and habitual female  
dispersal in plural-breeding mammals. *J. Evol. Biol.* **24**, 2624-2630 (2011).
44. P. Jarman, Mating system and sexual dimorphism in large terrestrial, mammalian herbivores.  
*Biol. Rev.* **58**, 485-520 (1983).

45. A. Loison, J. M. Gaillard, C. Pelabon, N. G. Yoccoz, What factors shape sexual size  
350 dimorphism in ungulates? *Evol. Ecol. Res.* **1**, 611-633 (1999).
46. R. J. Smith, J. M. Cheverud, Scaling of sexual dimorphism in body mass: a phylogenetic  
analysis of Rensch's rule in primates. *Int. J. Primatol.* **23**, 1095-1135 (2002).
47. N. J. Isaac, K. E. Jones, J. L. Gittleman, A. Purvis, Correlates of species richness in  
mammals: body size, life history, and ecology. *Amer. Natural.* **165**, 600-607 (2005).
- 355 48. E. Paradis, J. Claude, K. Strimmer, APE: analyses of phylogenetics and evolution in R  
language. *Bioinf.* **20**, 289-290 (2004).
49. R Development Core Team, *R: A Language and Environment for Statistical Computing*. (R  
Foundation for Statistical Computing, Vienna, 2010).
50. W. P. Maddison, D.R. Maddison, *Mesquite: a modular system for evolutionary analysis*.  
360 Version 2.75 <http://mesquiteproject.org> (2011).
51. L. J. Harmon, J. T. Weir, C. D. Brock, R. E. Glor, W. Challenger, W. GEIGER: investigating  
evolutionary radiations. *Bioinf.* **24**, 129-131 (2008).
52. S. P. Blomberg, T. Garland, A. R. Ives, Testing for phylogenetic signal in comparative data:  
behavioral traits are more labile. *Evolution* **57**, 717-745 (2003).
- 365 53. S. W. Kembel, P. D. Cowan, M. R. Helmus, W. K. Cornwell, H. Morlon, D. D. Ackerly, S. P.  
Blomberg, C. O. Webb, Picante: R tools for integrating phylogenies and ecology. *Bioinf.* **26**,  
1463-1464 (2010).
54. A. Grafen, The phylogenetic regression. *Phil. Trans. Royal Soc. B: Biol. Sciences* **326**, 119–  
157 (1989).
- 370 55. J. Hadfield, MCMCglmm: *Markov chain Monte Carlo methods for Generalised Linear  
Mixed Models*. Retrieved from:



cran.uvigo.es/web/packages/MCMCglmm/vignettes/Tutorial.pdf (2010).

56. M. Plummer, N. Best, K. Cowles, K. Vines, Convergence Diagnosis and Output Analysis for MCMC. *R News*, **6**, 7-11 (2006).

375 57. A. Gelman, D. Rubin, D. Inference from iterative simulation using multiple sequences. *Stat. Science*, **7**, 457-511 (1992).

380

385

**Acknowledgments:**

390 We thank D. Blumstein, S. Dobson, P. Kappeler and N. Solomon for detailed comments and critical feedback on the classification of species, and B. Dantzer, E. Huchard, C. Logan and everyone in the Large Animal Research Group in Cambridge for helpful discussions. Data are available as Supplementary Material. The Leverhulme Trust, the Isaac Newton Trust, and the European Research Council provided the funding for this study.

395

**Figure legends:**

**Fig. 1.** Fitted values of the probability that a species is socially monogamous given a population density obtained by a binomial GLM (dashed line).

The blue dots are the observed values for solitary species (n=411), the red crosses the observed values for socially monogamous species (n=89, 18% of all species), values can overlap (e.g. there are four socially monogamous species with a log population density of -2). Population density (logarithm of the number of individuals per km<sup>2</sup>) has a significant influence on the probability of that a species is socially monogamous or solitary. At the highest population densities, there is only a 6% probability that a species will be socially monogamous, whereas the probability rises to 44% at the lowest population densities. Several of the socially monogamous species showing high population densities are cooperative breeders, where many of the adult individuals do not breed.

**Fig. 2.** Evolutionary pathway to monogamy and singular cooperative breeding in mammals

In mammals, social monogamy derives from ancestral social systems in which females are solitary and male ranges overlap those of several females. Social monogamy appears to have evolved in species where females rely on high quality, low density diets and breeding females are intolerant of each other and female density is low, preventing breeding males from guarding more than one breeding female. In some monogamous lineages where females are polytocous and habitats are unpredictable, systems where one female monopolizes breeding and her young are raised by other group members have evolved (29).

All pictures under Creative Commons Attribution License:

[http://en.wikipedia.org/wiki/File:Eichhörnchen\\_Düsseldorf\\_Hofgarten\\_Crisco\\_edit.jpg](http://en.wikipedia.org/wiki/File:Eichhörnchen_Düsseldorf_Hofgarten_Crisco_edit.jpg)

[http://en.wikipedia.org/wiki/File:Nine-banded\\_Armadillo.jpg](http://en.wikipedia.org/wiki/File:Nine-banded_Armadillo.jpg)

420 [http://en.wikipedia.org/wiki/File:Cheetah\\_Feb09\\_02.jpg](http://en.wikipedia.org/wiki/File:Cheetah_Feb09_02.jpg)

<http://en.wikipedia.org/wiki/File:Numbat.jpg>

[https://commons.wikimedia.org/wiki/File:Dik-dik\\_%28male%29\\_-Tarangire\\_National\\_Park\\_-Tanzania.jpg](https://commons.wikimedia.org/wiki/File:Dik-dik_%28male%29_-Tarangire_National_Park_-Tanzania.jpg)

[https://commons.wikimedia.org/wiki/File:Panamanian\\_Night\\_Monkeys2.jpg](https://commons.wikimedia.org/wiki/File:Panamanian_Night_Monkeys2.jpg)

[https://commons.wikimedia.org/wiki/File:Rhynchocyon\\_petersi\\_from\\_side.jpg](https://commons.wikimedia.org/wiki/File:Rhynchocyon_petersi_from_side.jpg)

425 [https://commons.wikimedia.org/wiki/File:Aonyx\\_cinera\\_in\\_Zoo-002.jpg](https://commons.wikimedia.org/wiki/File:Aonyx_cinera_in_Zoo-002.jpg)

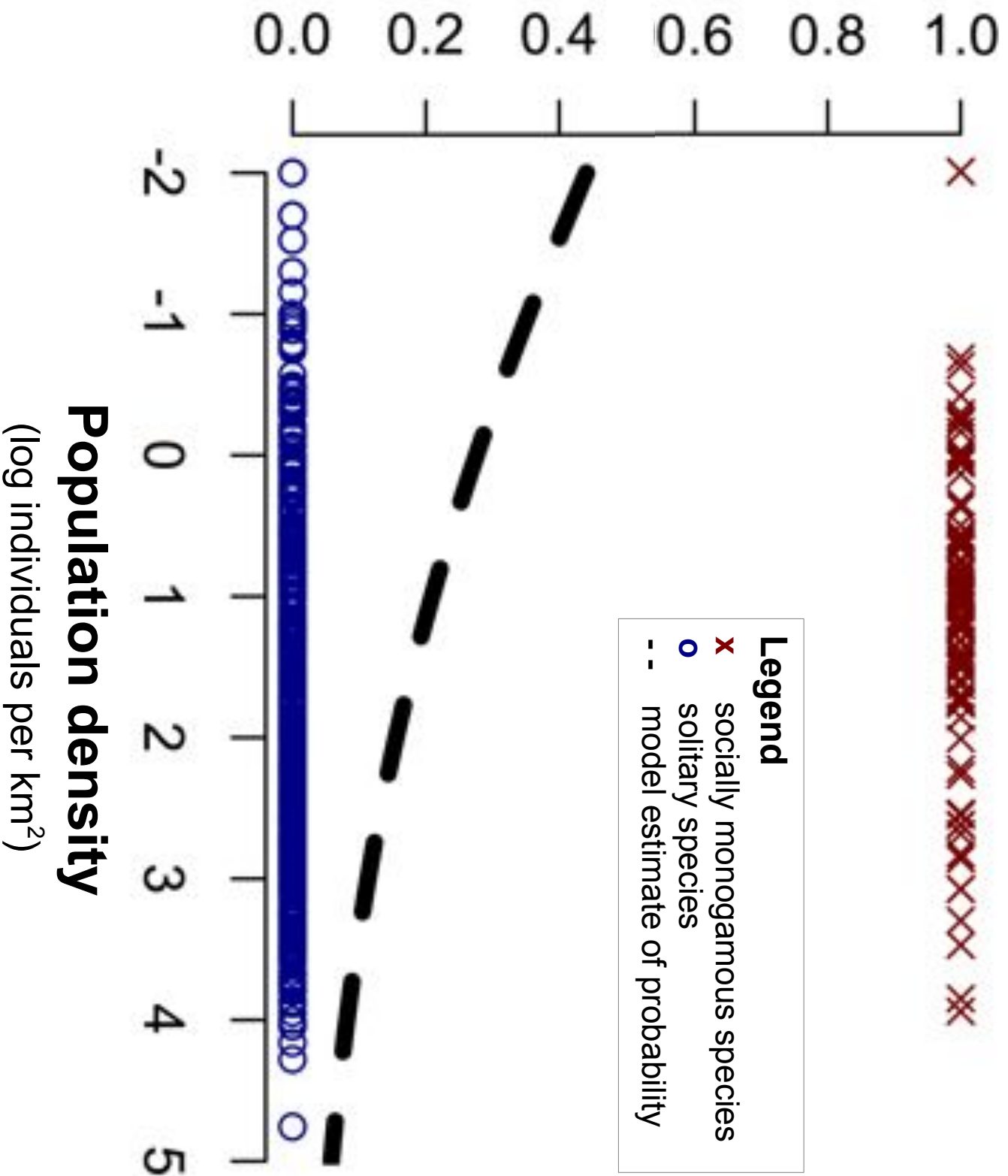
<http://www.flickr.com/photos/bobowen/4252523174/>

<http://www.flickr.com/photos/finchlake/5460526644/in/photostream/>

<http://www.flickr.com/photos/digitalart/2267158454/>

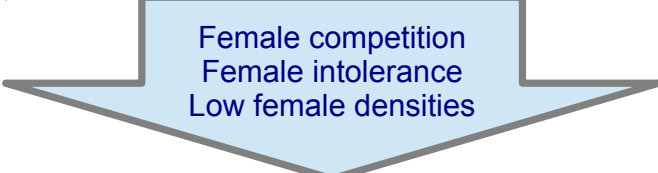
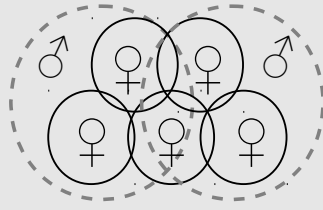
<http://www.flickr.com/photos/jeremyweber/7744688998/sizes/z/in/photostream/>

# Estimated probability of social monogamy





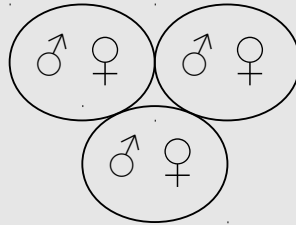
**Ancestral condition:**  
Solitary females,  
roaming males



Female competition  
Female intolerance  
Low female densities



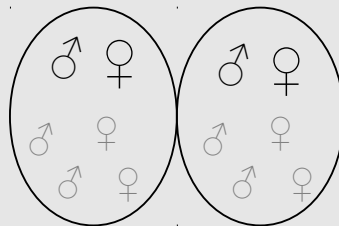
**Social monogamy**



Unpredictable environments  
Production of litters  
Reproductive suppression  
Helping



**Singular cooperative breeders**



## Lukas & Clutton-Brock: The evolution of social monogamy in mammals

### Supplementary Materials:

435 Materials and Methods

Figure S1

Tables S1-S3

References (33-57)

Dataset

440

### Material and Methods

445

#### Classification of social system

Information on the social system and the occurrence of paternal care was collected during a systematic literature review where we searched for information on every non-human mammalian species (following the nomenclature of (33)), collecting information from the primary literature, by searching for each species latin name on Google Scholar, from encyclopedias (34), and from published reviews (including 1, 4). Our classification of species focused on the social organization, the distribution of breeding adults in the population. We classified a species as socially monogamous if the majority of breeding females (>50%) share a home-range for more than one year with one male, but no other conspecific breeders. Our focus on breeding females means that species such as *Hapalemur griseus*, where 60% of groups contain only one breeding female, were classified as social, since the majority of breeding females reside with at least one other breeding female (35). Singular cooperative breeders, where

40

non-breeding offspring provide support to the dominant pair, were classified as socially monogamous (29). We excluded species in which males guard individual females during their  
460 receptive period, but might guard several females during a breeding season/year. Species were classified as solitary if breeding females occupy independent home-ranges, even though they may share foraging grounds or sleeping places. Social interactions in solitary species are restricted to mating and interactions between mothers and offspring. Species were classified as group-living if two or more breeding females associate with each other within the same home-  
465 range or at the same breeding site and females tolerate the presence of other females, sharing all parts of their home-ranges. Species were classified as showing paternal care if males regularly contribute to feeding or carrying offspring. Like previous authors (2, 14), we restricted paternal care to only include behaviour that is clearly adapted to benefit offspring, and excluded behaviour that might have benefits for the individual itself or all other group members (such as  
470 alarm-calling). We provide all data as supplement; please contact D. L. for a spreadsheet copy. While the supplement provides a single reference for each species for further information, classification of most species was based on information from several sources. Information on the occurrence of infanticide was compiled from previous reviews (36, 37).

475 Data on ecological and life-history parameters

We compiled information on the potential correlates of social monogamy from the following reviews and databases: body mass, litters per year, and length of gestation and lactation (38–40); population density and home-range size (39); home-range overlap (41); diet (42); male tenure length (43); and sexual dimorphism (44–47). We provide links to all external  
480 databases in Supplementary Table S3. All continuous variables were log-transformed before analyses.

The updated mammalian supertree (15) was used as the basis for the phylogenetic analyses. The tree was truncated to match the species in the dataset using functions of the package 'ape' (48) in the statistical software R (49), leading to the exclusion of 255 species  
485 during the phylogenetic reconstruction. The distribution of social monogamy in mammals according to this phylogeny is illustrated in Supplementary Figure 1. We resolved polytomies randomly for all analyses that require bifurcating trees, and repeated each analysis with three independent resolutions, which in all cases gave consistent results.

A variety of approaches were used to reconstruct ancestral states for all mammalian  
490 species and for each mammalian Order. We inferred ancestral states using the multistate reconstruction in Bayestraits' Discrete and the maximum likelihood approach for discrete characters implemented in the package 'ape' in R and in Mesquite (50). The reconstructed states were used to determine the ancestral social system before transitions to social monogamy. We estimated Pagel's lambda as a measure of phylogenetic signal for each social system using  
495 functions in the R-package 'geiger' (51), and calculated Blomberg's K (52) for all three social systems combined (socially monogamous: 0, solitary: 1, group living: 2) using functions in the



R-package 'picante' (53).

We subsequently tested whether transitions to social monogamy were constrained to solitary species using the modules "Discrete" (24) and "Multistate" from the program "Bayestraits" (20). In all "Bayestraits" analyses, likelihoods models of trait evolution were estimated based on the dated phylogeny, an ultrametric phylogeny, where all tips have the same distance to the root and branch lengths are proportional to the number of descendants (54), and a phylogeny with all branch lengths set to equal one. Analyses based on trees in which all branch length were set to be equal to one produced the best likelihoods, and we present their results below. We allowed the traits to vary their rate of evolution across the tree, and run each analysis for 50 maximum likelihood estimations. In "Discrete", we assessed significance between dependent and independent models by comparing the likelihood ratio statistic against a chi-squared distribution with four degrees of freedom (24). If results suggested that transition in one of the variables depended on the state of the other variable (e.g. transition to social monogamy only occurring from solitary ancestors), we repeated the analysis constraining the rate of transition in the dependent variable to be equal for both states of the other variable. Unconstrained models were considered to explain the data significantly better if the likelihood ratio statistic exceeded a chi-squared distribution with one degree of freedom. In "Multistate", we compared the likelihood of an unconstrained model the to likelihood of a model that forced the transitions to social monogamy to occur equally likely from solitary and from group-living ancestors, and to a model in which we forced transitions to social monogamy to only occur from group-living ancestors.

We performed a series of different statistical analyses to investigate potential correlates of social monogamy, depending on the hypotheses and the type of data. When assessing the

520 relationship between social monogamy and other binary traits, such as paternal care, we first compared the occurrence of the trait between solitary and socially monogamous species using Wilcoxon-tests and we regressed phylogenetic independent contrasts. Next, we assessed whether the two traits evolved independently through model comparisons in Bayestraits' Discrete. For tests where we predicted that social monogamy or paternal care might influence a continuous  
525 response variable, such as the number of litters per year, we used Anova and phylogenetic Anova in the R-package 'geiger', and phylogenetic generalized least squares regressions (pgls). In the pgls analyses, we estimated the degree of phylogenetic signal by performing a maximum-likelihood estimate of Pagel's lambda. In cases where we predicted that a continuous variable, such as population density, might influence the occurrence of social monogamy, we performed  
530 Wilcoxon-tests and binomial GLMMs. Binomial regressions were performed using MCMCglmm (21), including the phylogenetic relationship between species as covariance matrix. In MCMCglmm, terms were considered statistically significant when the calculated pMCMC values were less than 0.05. We ran analyses initially with two different priors, either fixing the variances at 1 and covariances at 0, or using a very informative prior (55). The two different  
535 priors led to highly similar estimates for the fixed terms, and we report the values from the fixed prior. Each analysis was repeated three times, and was checked for convergence using the Gelman-Rubin statistic to compare within- and between- chain variance in the R-package 'coda' (56). In all cases the potential scale reduction factor was less than 1.1 (57). We additionally checked the associations between the distribution of social monogamy and population density,  
540 home range size, and life history for any potential confounding effects of body mass (4), even though body mass did not differ significantly between socially monogamous and solitary species in phylogenetically controlled regressions. We performed phylogenetic generalized linear

squares regressions of population density and of home range size on body mass using the package 'caper' in R (60) to assess the effect of the residuals from these regressions on the  
545 distribution of social monogamy. In addition, we included body mass and social monogamy or paternal care as explanatory factors in regression models explaining variation in population density, home range size, and life history. None of this changed any of the results.

**Supplementary Table S1: Overview of the distribution of social monogamy across**

550 **mammalian Orders**

<b>Order</b>	<b>Species classified</b>	<b>Species with social monogamy</b>	<b>Proportion of socially monogamous species</b>
AFROSORICIDA	11		0%
ARTIODACTYLA	187	6	3%
CARNIVORA	202	32	16%
CETACEA	54		0%
CHIROPTERA	174	10	6%
CINGULATA	14		0%
DASYUROMORPHIA	14		0%
DIDELPHIMORPHIA	13		0%
DIPROTODONTIA	15	2	13%
ERINACEOMORPHA	15		0%
HYRACOIDEA	3		0%
LAGOMORPHA	72	1	1%
MACROSCELIDEA	15	14	93%
MONOTREMATA	5		0%
NOTORYCTEMORPHIA	2		0%
PERAMELEMORPHIA	5		0%
PERISSODACTYLA	16		0%
PHOLIDOTA	8		0%
PILOSA	10		0%
PRIMATES	361	106	29%
PROBOSCIDEA	3		0%
RODENTIA	941	57	6%
SCANDENTIA	16		0%
SIRENIA	1		0%
SORICOMORPHA	384	1	0%
TUBULIDENTATA	1		0%
<b>Total</b>	<b>2545</b>	<b>229</b>	<b>9%</b>

**Supplementary Table S2: Likelihood comparisons of different Bayestrats' Discrete models**

555

We first compared models assuming a dependent evolution between the two traits under analysis to models assuming an independent evolution. If a model of dependent evolution had a significantly better likelihood, we constructed dependent models that constrained the relevant transition rate (e.g. from solitary ancestors to social monogamy). Because models investigating the evolution of social monogamy from solitary ancestors that included all species did not converge, we run separate analyses for each of the Orders which contain more than 10 socially monogamous species and more than 10 solitary species. In all instances where the best model assumes a dependent evolution, the transition rate to social monogamy from an ancestor that is not solitary is estimated to be zero.

565

570

575

580

## Supplementary Table 3: References to external databases

585

36. van Noordwijk & van Schaik 2000 and Blumstein 2000: Infanticide: [http://books.google.co.uk/books?id=CKrtWt4rtf-](http://books.google.co.uk/books?id=CKrtWt4rtf-UC&printsec=frontcover#v=onepage&q&f=false)

[UC&printsec=frontcover#v=onepage&q&f=false](http://books.google.co.uk/books?id=CKrtWt4rtf-UC&printsec=frontcover#v=onepage&q&f=false)

38. Ernest 2003: Mammalian life history: <http://www.esapubs.org/archive/ecol/E084/093/>

39. Jones et al. 2009: Panthera: <http://esapubs.org/archive/ecol/E090/184/default.htm>

590

40. de Magalhaes & Costa 2009: Anage: <http://genomics.senescence.info/species/>

41. Pearce et al. 2013: Home range overlap: <http://rspsb.royalsocietypublishing.org/content/280/1751/20122122/suppl/DC1>

42. Gomes & Verdu 2012: Diet: <http://www.datadryad.org/handle/10255/dryad.36943?show=full>

43. Lukas & Clutton-Brock 2011: Male tenure length: <http://datadryad.org/resource/doi:10.5061/dryad.0r0p6>

44. Jarman 1983: Sexual dimorphism: <http://onlinelibrary.wiley.com/doi/10.1111/j.1469-185X.1983.tb00398.x/abstract>

595

45. Loison et al. 1999: Sexual dimorphism: <http://www.evolutionary-ecology.com/issues/v01n05/jiar1019.pdf>

46. Smith & Cheverud 2002: Sexual dimorphism: <http://link.springer.com/article/10.1023/A%3A1019654100876>

47. Isaac et al. 2005: Sexual dimorphism: <http://www.jstor.org/stable/10.1086/429148>