Biological Journal of the Linnean Society (1998), *64:* 413–447. With 9 figures
Article ID: bj980237

Phylogenetic analyses of primate size evolution: the consequences of sexual selection

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Received 19 November 1997; accepted for publication 16 March 1998

We have analysed the relationship between primate mating system, size and size dimorphism by utilizing several phylogenetically based methods. An independent contrast analysis of male and female size (log weight) showed that these are tightly correlated and that size dimorphism is not a simple allometric function of size. We found no relationship between mating system and sexual dimorphism in strepsirhines but a strong relationship in haplorhines. By matched-pairs analysis, where sister groups were matched according to whether the mating system predicted higher or lower intrasexual selection for male size, haplorhine species in more polygynous clades (with a predicted higher sexual selection) were significantly more dimorphic, had larger males, and also, but to a lesser degree, larger females. Both independent contrast and matched-pairs analyses are non-directional and correlational. By using a directional test we investigated how a transition in mating system affects size and dimorphism. Here, each observation is the sum of changes in dimorphism or size in a clade that is defined by a common origin of a mating system. Generally, dimorphism, as well as male and female size, increased after an expected increase in sexual selection, and decreased after an expected decrease in sexual selection. The pattern was, however, not significant for all of the alternative character reconstructions. In clades with an expected increase in sexual selection, male size increased more than female size. This pattern was significant for all character reconstructions. The directional investigation indicates that the magnitude of change in haplorhine dimorphism is larger after an increase in sexual selection than after a decrease, and, for some reconstructions, that the magnitude of size increase is larger than the magnitude of size decrease for both sexes. Possible reasons for these patterns are discussed, as well as their implications as being one possible mechanism behind Cope's rule, i.e. general size increase in many phylogenetic lineages.

ADDITIONAL KEY WORDS:—dimorphism – body size – common origins – Rensch's rule – Cope's rule.

CONTENTS

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INTRODUCTION

Hypotheses on the evolution of size and size dimorphism

Many primate species are sexually dimorphic in size, males most often being larger. For example, some baboons (*Papio* spp.) have males who are twice as big as the females. Other species, for example many callitrichids, have no such dimorphism or even reversed size dimorphism. The common state in the animal kingdom is that females are the larger sex (Andersson, 1994), which is most often explained by fecundity selection on females (Darwin, 1871). Egg production increases with body size and more space is required for keeping eggs than keeping sperm. Females also need to use much energy for the eggs and may therefore need to build a larger energy storage. In mammals and birds, however, males are commonly the larger sex. In spite of this, there is still a high positive correlation between maternal body mass and mean mass of both individual progeny and the entire litter (Cabana *et al.*, 1982, and references cited therein). This does not mean that life-time reproductive success for larger females necessarily is higher than that of smaller females since growth to larger size takes time and energy (Shine, 1988). Small size may instead be favoured in these groups by energy reallocation from investment in body mass to investment in litter mass as well as earlier breeding opportunities. Females could also be constrained to a comparatively smaller size by the added energetic needs for pregnancies and lactation (Willner & Martin, 1985; Martin, Willner & Dettling, 1994; Pickford, 1986). Energy reallocation in females is thus a potential cause of the variation in primate sexual size dimorphism.

Darwin (1871) noted that species with high male intrasexual competition over females, and thus high degree of polygyny, exhibit more sexual size dimorphism since larger males presumably have an advantage over smaller males in direct competition. In particular, males who provide little or no parental investment can increase their reproductive success by competing for matings (Trivers, 1972, 1985). This reasoning depends mainly on three assumptions: (1) that there is more variation in reproductive success of males in polygynous species, (2) that this larger variation

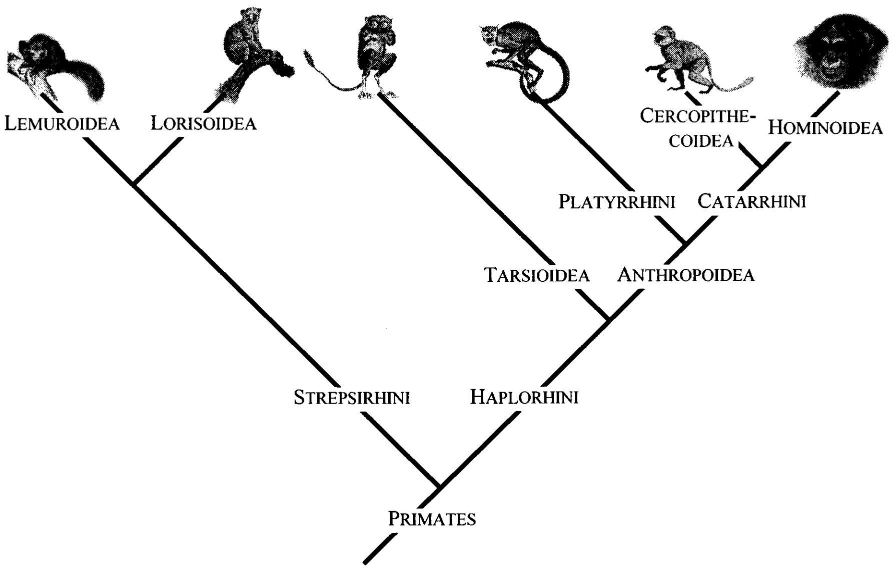

Figure 1. An outline of the primate phylogeny. Tarsiers were formerly grouped together with strepsirhines in prosimians. The other primates were then known collectively as simians.

is associated with an increase in competition between males, and (3) that this increased competition selects for characters in males which increase success in such competition (Clutton-Brock, 1985). This predicts changes in male size and size dimorphism after changes in mating system. There is no expected effect of mating system on female size, and females should therefore generally be expected to have a size more 'optimal' for the species in question (Gaulin & Sailer, 1985).

Available size data on different primate species show some general patterns concerning their dimorphism. Dimorphism is typically lacking in monogamous species and present in many polygynous species, with some important exceptions: it is almost non-existent in strepsirhine (lemurs and lorises) species, uncommon in platyrrhine (New World monkeys) primates and clearly present only among catarrhine (Old World monkeys and apes) primates (Martin, 1980) (see Fig. 1 for an outline of the primate phylogeny). The observation that size dimorphism is connected to mating system in haplorhines (tarsiers, platyrrhines and catarrhines), and thereby hypothetically to intensity in sexual selection, suggests that it may be a sexually selected character. This has also been the explanation of choice of many authors (e.g. Alexander *et al.*, 1979; Clutton-Brock & Harvey, 1977; Gaulin & Sailer, 1984; Harvey & Harcourt, 1984; Mitani, Gros-Louis & Richards, 1996). Thus, size dimorphism in primates seems to be a typically sexually selected character.

There are, however, several other competing explanations. Terrestrial primate species, for example, tend to be more dimorphic than arboreal species. This could be due to an increased need in terrestrial species for males to defend the flock against predators (Leutenegger & Kelly, 1977; Rowell & Chism, 1986), but also because arboreal species might be constrained in size by the need to venture out on thin branches when they forage (Harvey, Martin & Clutton-Brock, 1987). Large size has been shown to be correlated to large dimorphism across many animal taxa to the degree that it has been regarded as one of the rules of ecology: Rensch's rule

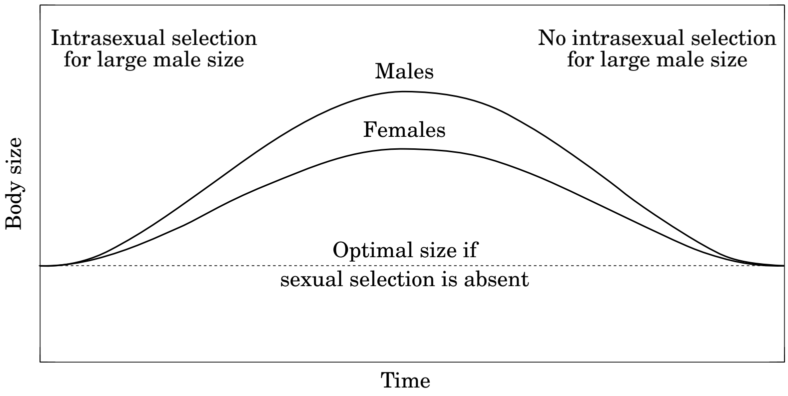

Figure 2. The hypothetical path to and from sexual size dimorphism if it is caused by sexual selection for male size. Due to genetic correlation between the sexes, both male and female size increase over the optimal species value until the costs and benefits of the new, larger size, are equal. Because of a difference in benefits for the sexes, where benefits are smaller or non-existent for females, size dimorphism originates and is maintained. A change in mating system where sexual selection for size decreases, reduces size dimorphism as well as male and female size.

(Rensch, 1950, 1959). Several analyses (e.g. Abouheif & Fairbairn, 1997; Clutton-Brock, Harvey & Rudder, 1977; Leutenegger, 1978) confirm that primates conform to this rule. This correlation could be a consequence of sexual selection, as selection for large size in males would, through correlation between the sexes concerning size-controlling genes, make the average size for both sexes increase over time (Lande, 1980, 1987; Lande & Arnold, 1983; Clutton-Brock *et al.*, 1977; Leutenegger, 1978). Such a response to sexual selection would indeed result in larger species being more dimorphic, making sexual selection a driving force not only for size dimorphism but for size as such (Fig. 2).

Some researchers have attempted to show that primate dimorphism is a non-adaptive by-product of size increase alone (Leutenegger & Cheverud, 1982, 1985), while others have remarked that their conclusion is a consequence of a size dependent measure of dimorphism, and, as a consequence, there is lack of evidence supporting this hypothesis (Gaulin & Sailer, 1984). Overall size might, however, determine whether dimorphism will be expressed as size dimorphism or take some other form (Gaulin & Sailer, 1984; Clutton-Brock, 1985; Martin *et al.*, 1994), body size itself in turn being the result of, for example, feeding adaptations and habitat (Ford, 1994; Gaulin & Sailer, 1985). Dimorphism has also been proposed to be the consequence of phylogenetic inertia, a genetically constrained character retained from an ancestor which was dimorphic (Cheverud, Dow & Leutenegger, 1985, 1986). Other authors have noted methodological problems in these studies which invalidate this conclusion (Ely & Kurland, 1989). It could be argued that phylogenetic lag is a valid explanation in specific cases, for example in the primate *Cercopithecus neglectus* Schlegel, which is reportedly mainly monogamous, exhibits extreme size dimorphism, and whose closest relatives are dimorphic but polygynous (Leutenegger & Lubach, 1987). However, as a general rule, phylogenetic inertia is invalid as an explanation simply because it leaves wanting an ultimate cause of the origin of size dimorphism. Finally, there is a possibility that many, if not all, of these factors are important for the evolution of size dimorphism (Gaulin & Sailer, 1984; Ely & Kurland, 1989). Thus, size dimorphism might be the consequence of many different selection pressures, and to study the effect of one particular cause, one needs to isolate it from the others. There are inherent difficulties with this since many proposed characters vary together (Fleagle, 1985). However, in this study we attempt to isolate the effect of sexual selection by observing the change in direction and magnitude of size evolution when selection pressures potentially working only on male size are strong or weak.

The scaling of the brain in anthropoid primates has been suggested to indicate that sexual size dimorphism evolved through body size reduction in females rather than through body size increase in males (Willner & Martin, 1985; Martin *et al.*, 1994). Female reduction in size should, however, leave a different historical imprint in the primate phylogeny as compared to male size increase. Examination of this question makes it necessary not only to look at patterns and correlations but to unravel the specific path to dimorphism.

Although sexual dimorphism in body size is found most commonly in polygynous species, not all polygynous species are dimorphic. In particular, strepsirhine primates do not show this correlation (Kappeler 1990, 1991). However, sexual selection may work on alternative features to body size, and even if larger size is selected for this does not necessarily produce dimorphism. Other selection pressures on males can be contradictory, pushing male size downwards, for example in tree-living primates who need to venture out on weak branches (Harvey *et al.*, 1987). Selection pressures on females can also work to pull female size upwards, for example if there is a need to dominate males (Richard, 1987) or other females, or, if females are selected to be large for fecundity reasons (see above), or, by other processes. In spite of these potentially confounding additional selection pressures, some patterns revealing the consequences of sexual selection are likely to be found by using appropriate phylogenetic methods.

Phylogenetic comparative methods

Different phylogenetic methods answer different questions (e.g. Ridley, 1983; Felsenstein, 1985; Huey & Bennet, 1987; Maddison, 1990; Harvey & Pagel, 1991; Brooks & McLennan, 1991; Sillén-Tullberg, 1993; Pagel, 1994). One such difference between methods is whether they focus on evolutionary sequences or correlations, that is, whether the hypotheses to be tested are directional or non-directional (Nylin & Wedell, 1994; Pagel, 1993). Several comparative studies on primate sexual size dimorphism have been made which control for taxonomic dependence when analysing primate sexual size dimorphism. Some of these studies have supported the sexual selection hypothesis (Harvey & Clutton-Brock, 1985; Gaulin & Sailer, 1985; Ford, 1994), while others have attributed the pattern to phylogenetic inertia and size effects (Cheverud *et al.*, 1985, 1986; Leutenegger & Cheverud, 1982, 1985). One phylogenetic comparative study has also been made which supports the sexual selection hypothesis, but then only on 16 polygynous haplorhine species (Mitani *et al.*, 1996). All of these analyses used non-directional approaches, establishing correlations but not causation. In this paper we try to reveal the causal relationships between male intrasexual competition and sexual size dimorphism by investigating how changes in mating system affect the direction and magnitude of changes in male and female body size.

MATERIALS

Data on mating systems and size were collected from different literature sources as summarized in Appendix 1. We chose to use weight data because it has been shown to be a reasonably reliable measure of size (Iskjaer *et al.*, 1989). Strepsirhine weights were predominantly taken from captive animals, while all haplorhine weights, where stated by the authors, were taken from wild caught specimens. Some size data, particularly for Old World primates, were extracted from a data set in Harvey *et al.* (1987) which has uncertainties in it because some weights were estimated instead of measured. These weights were all removed and not used in this analysis. Calculations on weights were done using logarithms, as is the common procedure, since it was the relative size change and not the absolute which was interesting for the analysis.

In the literature, mating systems for primate species are mostly given in discrete form—i.e. uni-male, multi-male and monogamous—a classification also used in this study. We adopted this rather crude classification instead of a more exact and therefore more preferable measurement such as operational sex ratio (see Mitani *et al.*, 1996) to maximize the number of data points and consequentially the accuracy when reconstructing ancestral states. Optimally, we would have used a variable such as variation in reproductive success between males in different mating systems, but this information is not available for most species. For strepsirhines the most complete data set comes from studies by Kappeler (1990, 1991) who preferred not to separately define many of the strepsirhine polygynous species as uni-male and multi-male since the mating systems for this group often are difficult to classify and not well known. These were coded as uni-male *or* multi-male in this study, in contrast to uni-male *and* multi-male which was used for species having both these mating systems. However, there is a difference in kind between polygynous haplorhines and polygynous strepsirhines. Many of the polygynous strepsirhines are solitary and nocturnal and thus have less opportunity for male-male competition than does the gregarious and diurnal polygynous haplorhines. For this reason, and because of the different patterns concerning dimorphism, i.e. the lack of dimorphism for strepsirhines, the two suborders were mainly analysed separately.

The phylogeny used in the analysis was a composite phylogeny by Purvis (1995), shown in Appendix 2, made with a 'super-tree' technique using phylogenies based on both molecular and morphological data (but see Ronquist, 1996 for a critique of this technique).

METHODS

Character reconstructions

Mating systems do not fossilize and data on size and size dimorphism of fossils are scarce, scattered and debated (e.g. Ciochon & Fleagle, 1987). To do the analyses it was therefore necessary to reconstruct ancestral states of mating system as well as size and size dimorphism using data from extant species. We here therefore assume that mating system is a heritable character, most probably not as a directly genetically coded character, but as the product of a set of independently inherited behaviours.

Mating system was considered a 3-state unordered character. Parsimony reconstruction was carried out with the aid of MacClade (Maddison & Maddison, 1992). Equivocal branches were dealt with by considering two extreme resolutions, namely one that maximized the number of transitions to an expected increase in sexual selection, and the other that maximized the number of transitions to an expected decrease in sexual selection. This gave us two separate sets of results.

The most parsimonious reconstruction of mating systems gave the ancestral state of all primates as multi-male. This multi-male reconstruction encompasses a lot, however, and we need to recognize that multi-male in strepsirhines often means multi-male with a small potential male-male competition (e.g. lorises with solitary males having ranges that overlap many females and other males' ranges), and in haplorhines often means aggregated bands with several adult males and consequently large potential male intrasexual competition. This distinction between multi-male strepsirhines and multi-male haplorhines need not concern us here, however, as the sister clades being compared are closely related and the matched-pairs comparisons (see below) investigated are within these groups and not between. When using the common origins test (see below), we investigated only mating systems originating within the primate clade, so the distinction between the different kinds of multi-male primates did not, therefore, introduce any error into this test.

Reconstructing dimorphism in the phylogeny poses some special problems. Due to statistical problems using ratios in calculations (Ranta, Laurila & Elmberg, 1994) and the fact that dimorphism is not a character in itself but a composite of two characters, male and female size, the size evolution of each sex was reconstructed separately. Dimorphism values for the internal nodes were calculated as the ratio between male size and female size using the node values of the two independent reconstructions. For some species, data was available on mating system only, while for others data was available on size only. Since we wanted to use all available information, the reconstructions of size evolution were manually superimposed on the reconstruction of mating systems.

For the size reconstructions, linear parsimony reconstruction (Swofford & Maddison, 1987) was favoured over squared change parsimony reconstruction because the latter 'smears' changes from one part of the tree onto neighbouring branches (Maddison, 1991). The linear parsimony method, however, gives a range instead of a single value for each node (Maddison & Maddison, 1992). In order not to make calculations unnecessarily numerous, the average value of each node was used in the analyses; these average values were also part of the set of most parsimonious reconstructions.

Independent contrasts

Change in dimorphism is a product of sex differences in changes of size. In order to study the evolution of sexual size dimorphism, one therefore first has to take into account the evolution of size itself. If there is an allometric relationship between size and size dimorphism, then the residual dimorphism, after the effect of size has been removed, is the correct variable to use in the analysis. To see whether this is so we analysed the co-variation between male size and female size, two continuous characters. A non-directional correlation method was appropriate and thus the

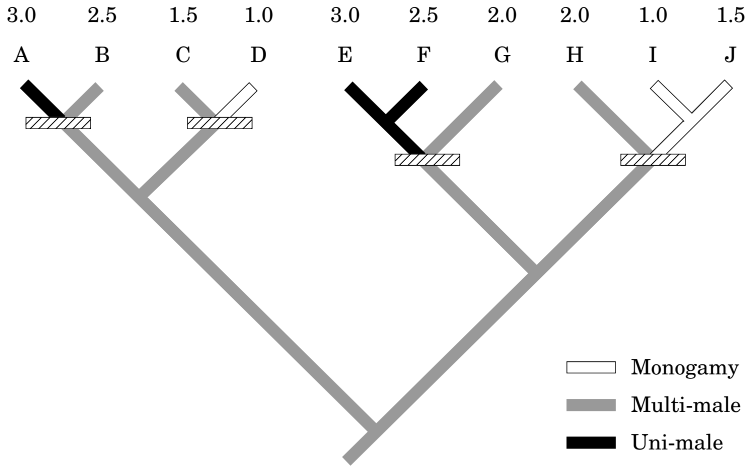

Figure 3. Matched-pairs analysis. Consider a phylogeny of 10 species, A–J, with values of a continuous variable, in this case a variable denoting size, as indicated above each species. Each species also has a discrete value, in this case mating system, which is parsimoniously reconstructed as in the phylogeny above. One matched pair consists of the two most closely related clades which differ in the discrete variable as indicated with a striped crossbar. Thus, in this example we have four such comparisons, A⇔B, C⇔D, E&F⇔G, and H⇔I&J. Where there are more than one species in a clade, the average of all included species is taken as representative for the clade. The comparison A⇔B gives a value 0.5 indicating that in this comparison the more polygynous species is also the larger species. Similarly, C⇔D gives 0.5, E&F⇔G 0.75 and H⇔I&J 0.75. Note that the order when subtracting is important. In this example we thus have four comparisons, all indicating that a higher degree of polygyny is correlated with larger size.

independent contrasts method developed by Felsenstein (1985), as implemented in the computer program Phylip (Felsenstein, 1989), was used. In this test, a contrast between two nodes is considered as one independent data point. All branch lengths were set to equal length, which means we chose the punctuational view of evolution, as compared to a more gradualistic view (Pagel, 1992; Purvis & Rambaut, 1994; Mitani *et al.*, 1996). We believe that this is warranted because size is a character crucial to reproductive success and therefore potentially subject to strong selection from many directions, and a consequential rapid change after speciation (West-Eberhard, 1983). Polytomies were handled by using zero-length branches (Felsenstein, 1985). Independent contrasts for males and females were compared using a paired *t*-test, following the standardizing procedure by Garland, Harvey & Ives (1992) by first giving a positive sign to female contrasts, simultaneously switching the sign if needed of the male contrasts.

Non-directional analysis: matched-pairs comparison

To analyse the possible consequences of sexual selection, mating system was used as a variable indicating the strength of male intrasexual competition. As this is a discrete variable, it becomes necessary to redefine what should be considered an independent observation as compared to the data points previously used in the independent contrasts method. One suggested approach to do this has been to compare closely related species, or species groups, which differ in the character of interest; in this case mating system (Felsenstein, 1985; Møller & Birkhead, 1992; Tullberg & Hunter, 1996). The independent data point then becomes one such matched-pairs comparison (Fig. 3). In this study we have compared unweighted species averages and polytomies therefore did not pose any problem. These matched-pairs comparisons give access to information concerning differences between closely related species with alternative mating systems, and can thus identify the effects different selection pressures have had on lineages with a common starting point.

Certain information is lost, however, by contrasting sister clades. The comparisons reveal nothing of the direction that evolution has taken. If, in order to solve this, we were to make matched-pairs comparisons of average values of inferred changes along branches we would essentially answer the same question as when making comparisons of averaged species values. To see that this is so, picture two sister species with weight values X and Y, and their common ancestor with reconstructed weight value Z. The comparison X-Y will always yield a result identical to the comparison (X-Z)-(Y-Z). When doing matched-pairs comparisons between sister groups including more than one species, the comparisons of branch change data will be identical in sign to the comparisons of species data, although not necessarily in magnitude. If there is a decrease in dimorphism in both sister clades being compared, there might still be a difference in magnitude between them. The difference itself, of course, reveals something about the intensity of the selection pressure being studied, but it would be more revealing if the direction also differed.

Directional analysis: common origins test

For the directional analysis we derived an independent data point from the origin of a mating system and inferred changes thereafter. As this test groups species which have a common origin with regard to a switch in the independent character, in this case mating system, it is henceforth referred to as the ‘common origins test’ (Fig. 4). If, for example, there is a switch from a multi-male mating system to a uni-male mating system, this indicates a likely increase in sexual selection pressure working on males and we should thus expect an increase in male size after this point. On the other hand, if one can see a decrease in male size after a switch to a mating system indicating less sexual selection pressure, this would hint at a cost associated with being of large size. In this study six transitions were possible: monogamous ⇔ multi-male, monogamous ⇔ uni-male and multi-male ⇔ uni-male. All transitions going to the right in this line-up were classified as indications of an expected increased sexual selection pressure, while all transitions going to the left were classified as an expected decreased sexual selection pressure. Thus we get two groups to compare, which we have called ‘expected decrease’ and ‘expected increase’.

The change in the dependent character, in this case size, after a common origin of mating system, could be dealt with in several ways. Here, we have used the sum of all changes inferred along the branches as representing the typical trend in the clade in question (Fig. 4). This sum is influenced by the addition of more branches only when change has taken place along these. If using the common origins test when analysing a continuous variable in which maintenance is important, then the value representing a clade would be better calculated as the average of changes

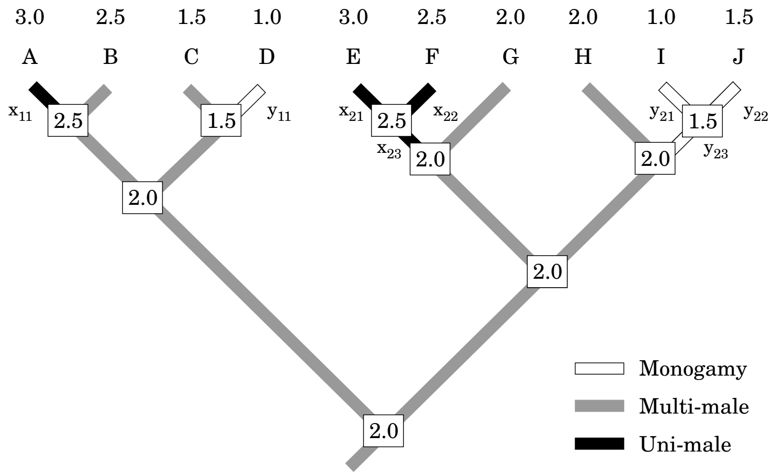

Figure 4. Common origins test. Consider the same 10 species, with the same data, as in Figure 3. For this analysis the evolution of the continuous variable also has to be reconstructed in the phylogeny, for instance by using linear parsimony reconstruction (Swofford & Maddison, 1987). The node values given by this reconstruction are indicated in boxes on each node. One data point in this test is derived by analysing the direction of change after a transition in mating system. In this example we have four such transitions; one for the species A, one for D, one for the clade including E&F, and one for the clade including I&J. For A, the direction of size evolution is given by Δx_{11}, which is calculated by subtracting the value for species A (3.0) by the value for the immediately preceding node (2.5). Thus Δx_{11} has a value of 0.5 indicating that an increase in size has taken place after the transition in mating system. Similarly, Δy_{11} has a value of -0.5 indicating that a decrease has taken place. Where there are more than one species in a clade, the sum of all included changes are taken as the typical trend representative for the clade. Thus, the value representing the clade E&F is given by $\Delta x_{21}+\Delta x_{22}+\Delta x_{23}$ which is 1.0, indicating an increase in size. Similarly, the value for I&J is -1.0, indicating a decrease in size. In this example we thus have four common origins of mating systems, two indicating that after increased polygyny size increases, but also two indicating that after a decrease in polygyny size decreases.

taking place along the internal branches. Note, however, that this average is unduly influenced by the addition of more branches. To see the nature of this problem, picture a case where there is a clear and phylogenetically identifiable increase in sexual selection pressure. In a situation where the evolutionary response in size and size dimorphism was immediate, all variation after the first speciation event could possibly be due to other factors besides sexual selection. If you sum these changes, positive and negative variation will tend to cancel out. If you average them, however, the average value indicating change will approach zero the more branches are added. This without any theoretical justification.

Because linear parsimony reconstruction of continuous characters cannot be done satisfactorily on ‘soft’ polytomies (i.e. dichotomous branching assumed but solution unknown) (Maddison & Maddison, 1992), two alternative trees were constructed for the common origins test. In one tree polytomies were resolved by removing the more polygynous species with large dimorphism and the less polygynous species with small dimorphism, and in the other tree the opposite was done. In this manner we got two trees, one most supporting the sexual selection hypothesis, and one least supporting it. These two alternative trees together with the two extreme resolutions of mating system gave four different solutions with sometimes different statistical results reported throughout the paper.

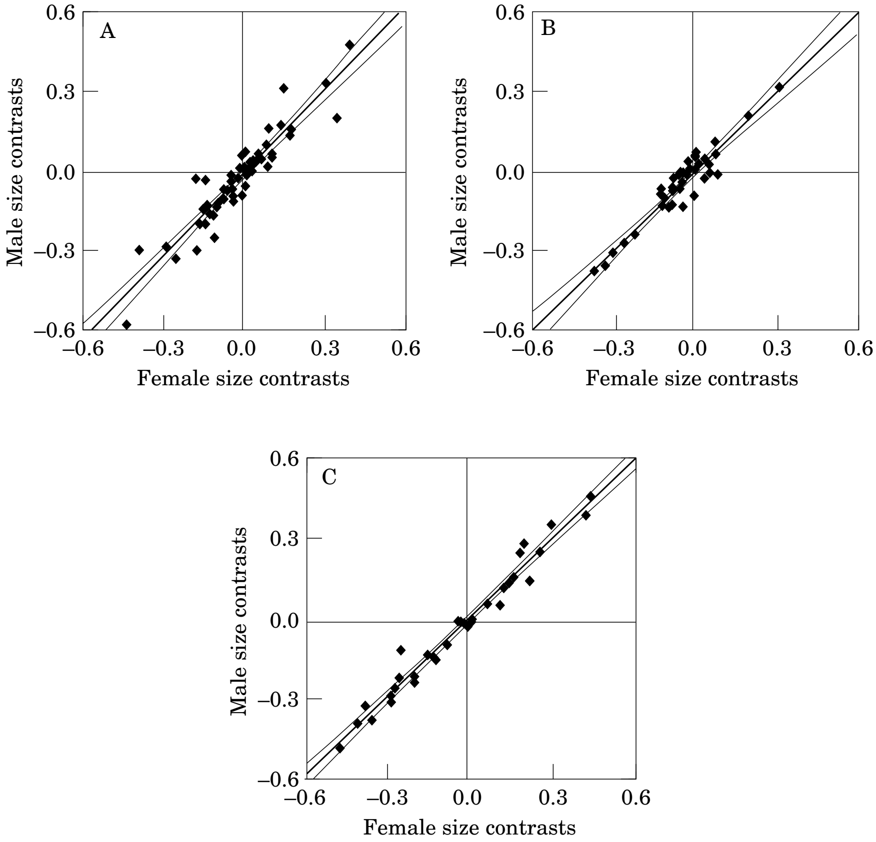

Figure 5. The relationship between contrasts in male size and female size. One data point in these graphs is an independent contrast. Regressions gave for (A) catarrhines b = 1.064, r^2 = 0.864, P = 0.000, n = 66; for (B) platyrrhines b = 1.008, r^2 = 0.870, P = 0.000, n = 47; and for (C) strepsirhines b = 0.974, r^2 = 0.966, P = 0.000, n = 34. The thin lines indicate the 95% confidence intervals which all overlap with one. Male and female size evolution are thus tightly correlated and not significantly different in magnitude.

For some reconstructions, the distribution of branch change values was heteroscedastic, so the non-parametric Mann–Whitney U-test and Wilcoxon matched-pairs test were used instead of *t*-tests. In some cases sign tests were used in combination with paired *t*-tests to check the possible effects of a few data points with a large influence (Höglund & Sillén-Tullberg, 1994).

RESULTS

Independent contrasts

Independent contrast analysis on log(male weight) and log(female weight) revealed that dimorphism does seem to increase with size (i.e. has a regression slope, b, larger than 1) in catarrhines (regression slope, b = 1.064), and similarly, but less so, in platyrrhines (regression slope, b = 1.008), while it apparently decreases with size in strepsirhines (regression slope, b = 0.974) (Fig. 5). However, the 95% confidence interval of these regression slopes all overlap with one. To further analyse the relationship, and to control if the regression slopes significantly deviate from one, we followed the approach of Abouheif & Fairbairn (1997) and compared male and female contrasts using a paired *t*-test on the standardized contrasts. Since each contrast estimates the standardized evolutionary divergence as one hypothetical ancestor diverged to two daughter species, a significant *t*-value where male contrasts exceed female contrasts would indicate consistency with Rensch's rule. We found that male and female weight contrasts are not significantly different in any group; catarrhines (one-tailed paired *t*-test: $P = 0.164$, $n = 66$), platyrrhines (one-tailed paired *t*-test: $P = 0.359$, $n = 47$) and strepsirhines (one-tailed paired *t*-test: $P = 0.696$, $n = 34$). In conclusion, this analysis shows that size evolution is highly correlated between the sexes and that dimorphism is not a necessary product of size increase. We can thus find no grounds for using residual dimorphism, calculated from a regression slope other than one, in our calculations.

Non-directional analysis: matched-pairs comparison

Having thus to some degree separated the causal connection between size and dimorphism we now turn our attention to the evolution of dimorphism itself. The matched pairs used in the analyses are presented in Appendix 2. In the reconstruction of mating systems the multi-male system turns out to be ancestral in the primate clade. There were no identified changes in mating system in lorises, while lemurs were reconstructed as having 3–7 transitions to monogamy and 0–4 transitions to polygyny, depending on the reconstructed state of the equivocal branches. Haplorhines on the other hand, had a more complex pattern of mating system evolution. In the platyrrhine primates, where we find many monogamous (in some species facultative polyandrous) callitrichids, there have been 2–3 transitions to monogamy. Only one platyrrhine species has in the literature been described as uni-male; *Cebus capucinus* Linnaeus. As it is in uni-male species where we expect the strongest sexual selection, the platyrrhines should therefore be expected to be less size dimorphic than other haplorhines. In Cercopithecinae and Colobinae, all species except two are described as polygynous. Thus, most contrasts in these groups are between uni-male and multi-male primates. The situation for the hominoids is more uncertain because of an original equivocal reconstruction of ancestral state. This group contains species exhibiting mating systems of all states used in this analysis; monogamous hylobatids, monogamous (and uni-male) humans, multi-male chimpanzees, uni-male (and multi-male) orang-utans and uni-male gorillas. In total, we found 25 transitions in mating system in the primate clade; 7 in strepsirhines, 5 in platyrrhines and 13 in catarrhines. This makes available 22 matched pairs for comparisons; 7 in strepsirhines (lemurs), 5 in platyrrhines and 10 in catarrhines (Appendix 2). Species groups which had no appropriate contrasting sister clades had to be excluded from the matched-pairs comparisons; these were lorises, tarsiers, macaques, and the colobus monkeys. The same groups also had polygynous mating systems descending from the original primate mating system and were therefore also not included in

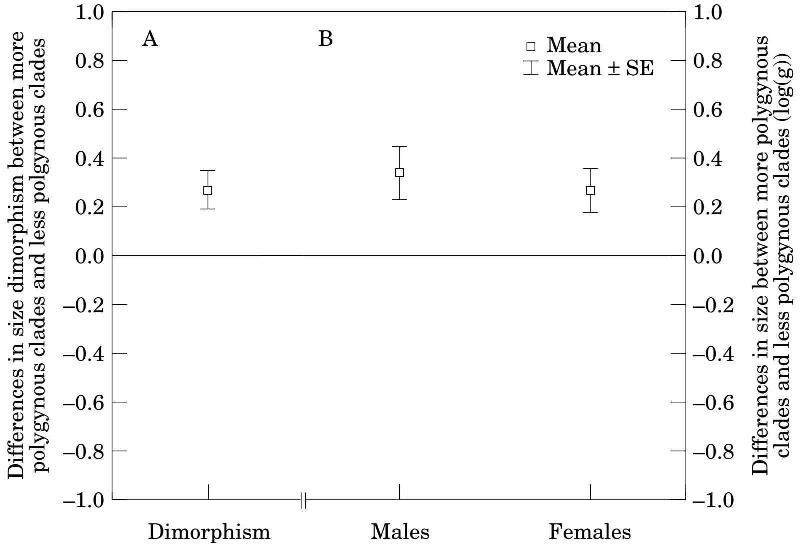

Figure 6. Matched-pairs comparisons for Haplorhini. A, species in more polygynous clades are commonly more dimorphic than species in the less polygynous sister clades (one-tailed pairwise *t*-test: $P = 0.002$; one-tailed sign test: $P = 0.004$, 13 of 15). B, species in more polygynous clades are also commonly larger than species in their less polygynous sister clades. This is true both for males (one-tailed pairwise *t*-test: $P = 0.003$; one-tailed sign test: $P = 0.018$, 12 of 15) and females (one-tailed pairwise *t*-test: $P = 0.006$; one-tailed sign test: $P = 0.018$, 12 of 15). There is also a difference between matched-pairs comparisons in size for males and matched-pairs comparisons in size for females (one-tailed paired *t*-test: $P = 0.001$; one-tailed sign test: $P = 0.004$, 13 of 15) which matches the pattern for dimorphism. None of these relationships holds true for strepsirhines.

the common origins test. Thus, analyses of strepsirhines and haplorhines rely on information extracted from the lemurs and most of the anthropoids, respectively.

Independent matched-pairs comparisons of dimorphism for all primates show that species in more polygynous clades are more dimorphic than species in their less polygynous sister clades (one-tailed paired *t*-test: $P = 0.002$; one-tailed sign test: $P = 0.008$, 17 of 22). If we investigate this closer, however, we can see that the pattern is present in haplorhines (Fig. 6A, legend), while absent in strepsirhines (one-tailed paired *t*-test: $P = 0.315$, one-tailed sign test: $P = 0.500$, 4 of 7). This far in the analysis we therefore need to acknowledge that there seems to be different processes going on in haplorhines and strepsirhines and thus analyse them separately hereafter. Thus, we conclude that in haplorhines there is a significant difference in dimorphism in accordance with the expected intensity of sexual selection as indicated by mating system.

In haplorhines, separate analyses of each sex interestingly show that both male and female size is significantly larger in more polygynous clades (Fig. 6B). This pattern is not found in strepsirhines (males—one-tailed paired *t*-test: $P = 0.641$; one-tailed sign test: $P = 0.500$, 4 of 7) (females—one-tailed paired *t*-test: $P = 0.671$; one-tailed sign test: $P = 0.500$, 4 of 7). The same pattern is thus present concerning size evolution as we saw earlier for the evolution of size dimorphism; haplorhine but not strepsirhine size has been changed by sexual selection.

If we subdivide the haplorhine clade further, into platyrrhines and catarrhines, we see that the same patterns for dimorphism more or less hold true for both these

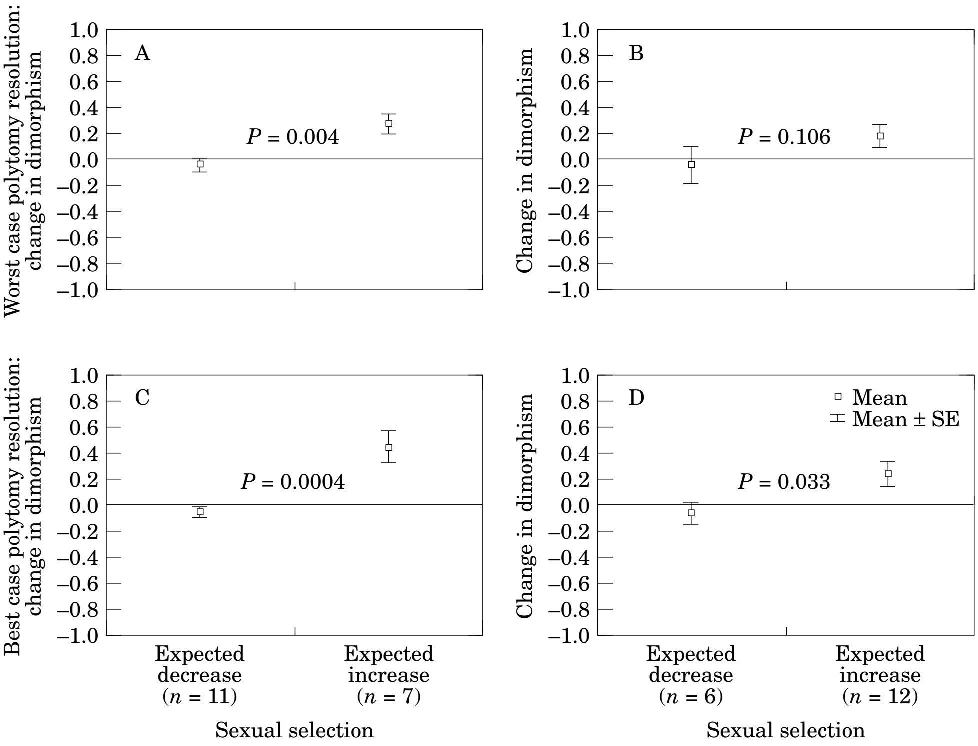

Figure 7. Changes in dimorphism in haplorhines after transitions in intensity of sexual selection. The graphs each represent one of four alternative resolutions using parsimony reconstruction. Reconstruction assuming maximum number of transitions to an expected (A) decrease and (B) increase in sexual selection with the worst case polytomy reconstruction; and to an expected (C) decrease and (D) increase in sexual selection with the best case polytomy reconstruction. See text for a more thorough explanation of the alternative reconstructions. One data point is the sum of changes along a set of branches within a clade with a common origin of mating system. The *P*-values given in the figure were obtained with one-tailed Mann–Whitney U-tests, testing the difference between the two groups ‘expected decrease’ and ‘expected increase’ in each alternative reconstruction.

groups which we found in haplorhines as a whole: there is a difference in dimorphism in accordance with the expected intensity of sexual selection as indicated by mating system (platyrrhines—one-tailed paired *t*-test: $P=0.058$, one-tailed sign test: $P=0.188$, 4 of 5) (catarrhines—one-tailed paired *t*-test: $P=0.004$, one-tailed sign test: $P=0.011$, 9 of 10). In doing this subdivision, however, we are lowering the number of data points, especially for platyrrhines, to a level where single deviations from the norm get an unwarranted influence on the statistical result. Hence we get some results which are not significant. For size as such, the patterns are similar; the general pattern that larger species are found in more polygynous clades holds true, but there are again instances which are not significant (platyrrhines, males—one-tailed paired *t*-test: $P=0.032$, one-tailed sign test: $P=0.031$, 5 of 5; females—one-tailed paired *t*-test: $P=0.033$, one-tailed sign test: $P=0.031$, 5 of 5) (catarrhines, males—one-tailed paired *t*-test: $P=0.028$, one-tailed sign test: $P=0.172$, 7 of 10; females—one-tailed paired *t*-test: $P=0.050$, one-tailed sign test: $P=0.172$, 7 of 10).

To really examine size dimorphism, however, we are interested in how matched-pairs for size in both sexes deviate from each other. If the male matched-pairs show a larger difference than the female matched-pairs, such a difference would reveal that it is the males who have been under the heavier selection pressure, and not the females. This is indeed the case for haplorhines (Fig. 6, legend). The pattern is also present for the subdivisions of haplorhines, if necessarily to a lesser degree; for platyrrhines (one-tailed paired *t*-test: $P = 0.054$; one-tailed sign test: $P = 0.188$, 4 of 5), and catarrhines (one-tailed paired *t*-test: $P = 0.004$; one-tailed sign test: $P = 0.011$, 9 of 10). In strepsirhines, however, we find no such pattern (one-tailed paired *t*-test: $P = 0.307$; one-tailed sign test: $P = 0.500$, 4 of 7). Thus, the pattern is clear; in haplorhines we find that species in more polygynous clades are larger as well as more dimorphic, and that this difference is due to male size change, but in strepsirhines we find none of these correlations.

Directional analysis: common origins test

The presence of differences between groups differing in mating system gives us a correlation type answer to the hypothesis of sexual selection. To attempt to find a causal relationship we now attempt to answer the question: How does the difference in dimorphism between mating systems come about? To analyse this, we made an analysis of the direction of dimorphism evolution using the common origins test. Identifying mating system transitions in haplorhines and dividing them into two groups, ‘expected increase’ and ‘expected decrease’ of sexual selection, we found that after a change in mating system the two groups differed predictably in inferred changes of dimorphism, if not significantly so in all reconstructions (one-tailed Mann-Whitney U-test: $0.0004 < P < 0.106$) (Fig. 7). In some of the alternative reconstructions there were no independent transitions to polygyny in strepsirhines, and only one transition to monogamy in platyrrhines, so no separate tests could be carried out on these groups because of a lack of data points. Thus, we analyse only haplorhines in this test. The pattern is clear in haplorhines that after an inferred switch in selection pressure dimorphism is increasing with increased sexual selection, but also decreasing with decreased sexual selection.

Again examining the direction of change as reconstructed in the phylogeny we now turn to an analysis of how size itself is changed by sexual selection. In haplorhines, the analysis indicates a tendency, in both males and females, for size to increase after transitions to mating systems with an expected higher sexual selection, but also for size to decrease after transitions to mating systems with lower sexual selection (males: one-tailed Mann–Whitney U-test: $0.010 < P < 0.090$) (females: one-tailed Mann-Whitney U-test: $0.013 < P < 0.106$) (Fig. 8). If sexual selection is the cause of this pattern, we should expect such a difference between the sexes concerning size changes, so that male size changes would be more influenced by increases in sexual selection pressure. By testing the differences between males and females in the ‘expected increase’ group, we find such a difference (one-tailed Wilcoxon matched pairs test: $0.009 < P < 0.025$), while no such difference exists for the ‘expected decrease’ group (one-tailed Wilcoxon matched pairs test: $0.212 < P < 0.458$). Thus, we can see clear effects of sexual selection on inferred male size as compared to female size, and this difference shows how dimorphism originates.

Visual inspection of Figure 7 shows that the calculated increase in dimorphism in clades with an increased sexual selection is higher than the decrease in clades

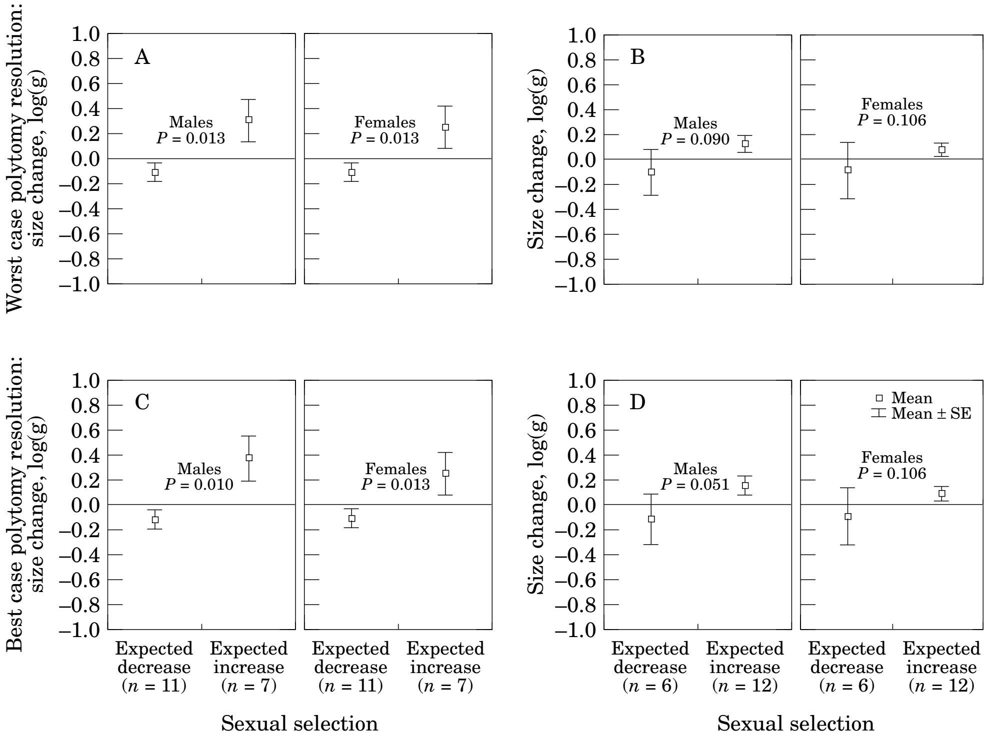

Figure 8. Changes in size in haplorhines for each sex after changes in intensity of sexual selection. The graphs each represent one of four alternative resolutions using parsimony reconstruction. Reconstruction assuming maximum number of transitions to an expected (A) decrease and (B) increase in sexual selection with the worst case polytomy reconstruction, and to an expected (C) decrease and (D) increase in sexual selection with the best case polytomy reconstruction. See text for a more thorough explanation of the alternative reconstructions. One data point is the sum of changes along a set of branches within a clade with a common origin of mating system. The *P*-values given in the figure were obtained with one-tailed Mann–Whitney U-tests, testing the difference between the two groups 'expected decrease' and 'expected increase' in each alternative reconstruction. Using one-tailed Wilcoxon matched pairs tests, we also found significant differences between changes in male and female size in the group 'expected increase' in all four alternative reconstructions (A: $P=0.009$, B: $P=0.025$, C: $P=0.009$, D: $P=0.014$). No such differences could be found in the group 'expected decrease' (A: $P=0.429$, B: $P=0.458$, C: $P=0.212$, D: $P=0.232$).

with a lower sexual selection. Also, in the two reconstructions assuming a maximum number of transitions to an expected decrease in sexual selection (Fig. 8A, C), the inferred increase in size in the more sexually selected clades seems higher than the decrease in size in the less sexually selected clades. This pattern is not, however, present in the graphs representing the two reconstructions assuming a maximum number of transitions to an expected increase in sexual selection (Figs 8B, D), where the reconstructed increase in the more sexually selected clades is more or less equal to the decrease in the less sexually selected clades. The common trend in these figures is nevertheless that the selection for large male size and, as a consequence, large female size and high dimorphism, is stronger than the selection against. The possible causes and consequences of this pattern are discussed further below.

DISCUSSION

The effects of sexual selection on primate size evolution has left a clear imprint in the haplorhine section of the primate phylogeny. Our reconstructions consistently show that benefits for males of large relative size when competing over females has over time pulled size upwards in those clades where succeeding in such competition is most advantageous for the winner. Primarily, male size is inferred to have changed, but also, to a lesser degree, female size. As benefits of increased size for females have been absent or lower than those for males, this difference in selection pressures between the sexes has produced sexual size dimorphism. All these effects are, however, strangely absent in strepsirhines, an issue which is elaborated on below. These results were partly reached using matched-pairs comparisons, a non-directional phylogenetic comparative method independent of the reconstruction of ancestral states of size, but dependent on the reliability of the phylogeny and the data as well as reconstructions of ancestral states of mating systems. In order to closely examine what specifically happens to size during different selection regimes, however, we used a directional phylogenetic analysis which is also dependent on the reconstructions of ancestral states of body size.

Some readers of this paper might hold the view that weight is such a variable character that a reconstruction of its evolutionary path would be rendered impossible. It is our opinion, however, that although size fluctuates a lot, its evolution over time can generally be uncovered and analysed with parsimonious methods. Species with close ancestry tend to be of similar size (e.g. Leutenegger & Cheverud, 1982, 1985; Appendix 1). A reconstruction of size evolution from data on present day species, however, can of course never find patterns as indicated by the recently extinct gorilla-sized lemur *Megaladapis* (Martin *et al.*, 1994), or the newly discovered ancient giant *Protopithecus*, a 25 kg New World primate (Hartwig & Cartelle, 1996). Both of these are examples of species larger than any extant species in their respective lineages. As fossil data become more complete concerning size and size dimorphism there would certainly be considerable benefits in including them within an analysis of the kind done here. The corresponding information on mating systems and thus on presumed sexual selection pressures, however, have probably disappeared forever, making such an analysis difficult, bordering on impossible. If there are grand patterns hidden away in the phylogeny which can testify to evolutionary mechanisms, we will therefore need to rely on methods making use of extant species data. We have here presented one such method to use when investigating data where the dependent variable is continuous while the independent variable is discrete: the common origins test.

In her review of mammalian species with females larger than males, Ralls (1976) stated that “the degree of sexual dimorphism in size in a mammalian species is the result of the difference between the sum of all selective pressures affecting the size of the female and the sum of all those affecting the size of the male.” We have in this study thus attempted to isolate the effects of one such selection pressure which differs between the sexes, namely sexual selection on males due to male intrasexual competition. It was our purpose to examine Darwin’s (1871) theory of sexual selection, and consequently the hypothesis that the specifically male need for large size relative to other males would over time change male size so that they would become larger than females. This selection on male size ultimately also changes female size if, for instance, there is a correlation between the sexes concerning size-controlling genes. This path to dimorphism and large size would have the consequence that the path to dimorphism would be size increase. We examined these predictions in turn.

Allometry

The question of an eventual non-adaptive allometric relationship between size and size dimorphism (Leutenegger & Cheverud, 1982, 1985), needed examination because if dimorphism had turned out to be directly tied to size somehow, then the residual dimorphism, after the effect of size had been removed, would have been the correct variable to examine. Since we are using relative size change as the variable, a product of calculating with log values, we can clearly see that an increase in size is not automatically coupled with an increase in dimorphism (Fig. 5). Thus, dimorphism increase does not automatically follow on size increase. Many previous authors have, however, found such a relationship (e.g. Abouheif & Fairbairn, 1997, and references cited therein). All of these studies used a smaller sample, including Abouheif and Fairbairn's (1997) own test (most probably on haplorhines) which was the only of these studies that controlled for phylogeny. To test whether the difference between the results reported in our study and theirs depended on the method and computer program chosen, we put our data through the treatment described in their paper, and still got similar results. Thus, the difference between this study and theirs most probably depends on the larger sample included here ($n = 116$ as compared to $n = 37$).

In doing this part of the analysis we consequently also found that Rensch's rule, a tendency for dimorphism to increase with size, was not confirmed for primates in the sense that dimorphism and size should be directly related. Rensch's rule is on the other hand not contradicted, but confirmed in the sense that most large primates tend to be dimorphic. However, this is due to reasons other than a mere allometric relationship between size and dimorphism. Rensch himself never thought that the relationship was direct, considering the most important evolutionary mechanism to be sexual selection for male secondary sexual characteristics other than size (Rensch, 1959: 212). We have here instead explored a more common hypothesis, that selection is for male size directly.

The association between absolute size and size dimorphism can be due to two, not mutually exclusive, explanations. First, there might be a threshold beneath which dimorphism is unlikely to evolve (Martin *et al.*, 1994). No such obvious threshold can be found, however, as there are small species exhibiting dimorphism (e.g. *Saimiri vanzolinii* Ayres: size <1 kg, male to female ratio >1.4), and larger species with no dimorphism (e.g. *Hylobates hoolock* Harlan: size >6 kg, male to female ratio $=1$). A second and more probable reason, which this study also supports, is that sexual selection increases size and not only size dimorphism. In fact, our results show that there is a significant influence of sexual selection on size, especially for males, which lends support to Lande's (1980, 1987) hypothesis of how sexual selection influences the size of the two sexes. Note, however, that this effect of sexual selection is true only for haplorhines.

Strepsirhini

As been shown before (Jenkins & Albrecht, 1991; Kappeler, 1990, 1991), strepsirhines exhibit little or no size dimorphism. This is not mainly because of a lack of sexual selection, even if it is weaker in general since no harem-holding species exists in this group. Still, about two thirds of strepsirhines are polygynous, about the same proportion as in haplorhines. Of these, all lorises are polygynous and this is also the group within the strepsirhines which exhibits most size dimorphism, however little. Strepsirhine species are on average smaller than haplorhines and it has been suggested that size might be a limiting factor on strepsirhine dimorphism since haplorhines in the same size range are not dimorphic (Kappeler, 1990). The lack of strepsirhine dimorphism is, however, not merely due to a lack of the larger, recently extinct, species in this group. Fossil data, although uncertain (Jenkins & Albrecht, 1991), indicate that the recently extinct large-bodied lemurs were mostly monomorphic (Martin *et al.*, 1994; Kappeler, 1991). Also, the analyses presented here show that even though strepsirhine size ranges over two orders of magnitude, there is no relationship between size and dimorphism, a fact also pointed out by Kappeler (1990). Causes for the lack of strepsirhine dimorphism have to be sought for elsewhere.

Female social dominance has been hypothesized to be connected to the lack of dimorphism in lemurs, females needing large size to dominate males (Richard, 1987). Sex has, however, no consistent effect on agonistic interactions in all lemur species (Kappeler, 1991; Pereira *et al.*, 1990), which indicates that this is not valid as a general explanation for this group. In some specific species it might still apply though, e.g. *Lemur catta* Linnaeus (Richard, 1987). The lack of strepsirhine dimorphism has also been attributed to phylogenetic inertia (Cheverud *et al.*, 1985), although this, as discussed above, is not an ultimately causal reason which also lacks clear support as most of the variation in dimorphism mainly occurs among congeneric species (Kappeler, 1990, 1991). Alternatively, speed and agility, rather than size and strength, might be favoured by sexual selection (Kappeler, 1990; Clutton-Brock, 1985). There could also be strong selection for increased female size (Kappeler, 1990; Clutton-Brock, 1985), as the costs of reproduction have been shown to be unusually high for lemurid females (Jolly, 1984). There is also a unique seasonality of resource abundance on Madagascar (Hladik, 1980) which has no similarity with the habitats of dimorphic haplorhine primates. This is an environmental stress which also could have effects on size. The most extensive investigator of this question, Kappeler (1990), believes that a combination of small body size (a cause contradicted by this study), fecundity selection on females, and selection for male agility rather than large size are the combined causes which probably explain the lack of male biased size dimorphism.

Our reconstructions of the ancestral state for all strepsirhines suggest that the ancestral strepsirhine had small, but existing, size dimorphism, comparable to the more dimorphic extant *Galago* species. The inferred existence of some degree of dimorphism is in line with fossil findings of Adapidae, a group which exhibits some sexual dimorphism and which possibly contains the ancestors of lemurs and lorises (Beard *et al.*, 1988; Szalay *et al.*, 1987; both cited in Kappeler, 1991). Overall in extant species, size differs more consistently between the sexes in the nocturnal polygynous lorises than in lemurs. Dimorphism thus seems to have decreased in the lemurid lineage and been stable in the loris lineage. Since the main effect of sexual selection which we detected in haplorhine primates is dimorphism increase, and since the main event in the strepsirhine lineage is dimorphism decrease, could it be that our analysis could not detect the influence of sexual selection in strepsirhines? Probably not, because if there has been a consistent effect of sexual selection, or lack thereof, it would definitely have shown up in the matched-pairs comparisons, which are more sensitive and thus less rigorous than the common origins test. What our analysis supports is that on average, sexual selection has had little or no influence on the evolution of size and size dimorphism in strepsirhines.

Haplorhini

For haplorhines, the results of this study show that sexual size dimorphism is clearly the result of sexual selection. Thus, this phylogenetic study confirms the results of earlier non-phylogenetic comparative studies on this matter (e.g. Alexander *et al.*, 1979; Clutton-Brock & Harvey, 1977; Gaulin & Sailer, 1984; Harvey & Harcourt, 1984). This conclusion is based on three results from this study; (1) size dimorphism is not a mere allometric response to size increase (Fig. 5), (2) an expected increase in sexual selection increases size (Figs 7, 8) and, (3) an indicated increase in sexual selection increases dimorphism by pushing up male size more than female size (Figs 6–8).

The result that size dimorphism in haplorhines is created by a larger size increase in males than in females argues against the hypothesis of Martin *et al.* (1994) that dimorphism would generally be a product of female size decrease rather than male size increase. Possible additional selection pressures to explain the patterns of size dimorphism in the primate clade are, however, numerous. For example, there is a difference between platyrrhine (New World) and catarrhine (Old World) primates in that there are no terrestrial platyrrhine species, and it is in terrestrial catarrhine primates where we can find the most pronounced dimorphism. It is certainly possible to be large and still live in trees (e.g. orang-utan) but most often arboriality seems to be a limiting factor. The found patterns of size change under different mating systems would not be predicted if one were instead to explore a niche divergence hypothesis (Shine, 1989)—the sexes diverging in size because of intersexual competition over resources. Under such a hypothesis the sizes of the sexes would diverge in different directions with equal probability, which is clearly not the case. Niche divergence would, in the scenario described here, only serve as an amplifier of sexual size differences originating for other reasons, i.e. sexual selection. The hypothesis of niche divergence has not received much attention in primates, however, mostly because there are small niche differences between the sexes in most primates.

Predator defence, a selection pressure proposed as an alternative or complementary cause of sexual size dimorphism in primates (Leutenegger & Kelly, 1977; Rowell & Chism, 1986), would not give the pattern of size decrease in less sexually selected species. Under the predator defence hypothesis, there would be no apparent cause for change towards smaller size when sexual selection pressures are relaxed, unless predation pressures are tightly correlated with male intrasexual competition. This is not an unlikely association in haplorhine primates, however, since uni-male primates are commonly terrestrial and terrestrial species hypothetically have a larger need for predator defence. It would therefore be an interesting continuation of this study to look at the influences that predation alone might have.

In our reconstruction there is, in haplorhines, a detectable decrease in size after sexual selection pressure has decreased. This indicates that there is some cost associated with being of large size which applies to both sexes, not only to females. That a sex specific cost is probable for females is indicated by the result that as sexual selection drives size upwards, dimorphism originates. Thus some selective force keeps female size down, for example energy reallocation from investment in body mass to investment in litter mass or earlier breeding opportunities. That a cost is present also for males is indicated by the result that as sexual selection pressures are relaxed, male size decreases. If there were no cost associated with large size for males, then male size would be stable, unless a genetic correlation between the sexes would make selection for small female size also pull that of the males down. In such a scenario, however, female size would decrease more than male size, as this would be where the main selection pressure was. This is not the case, however; instead, size decrease is more or less equal for both sexes. Thus, it is definitely expensive also for males to be large. This pattern also indicates that females are the more optimally sized sex for their environment in sexually selected species. In a sense, females are pulled away from their more optimal size by male intrasexual competition.

Cope's rule

There might seem to be something inconsistent with the result that size and dimorphism do not vary together, but that sexual size dimorphism nevertheless is created by size increase. However, size varies for a lot of reasons, sexual selection being one, and if we study size variation we see that size varies a lot without creating dimorphism (Fig. 5). This would be expected if the reasons for size variation mostly lay in optimizing size in the current environment. If we, on the other hand, limit the analysis of size variation to that influenced by sexual selection and the lack thereof, there is indeed a relationship between size and dimorphism, as predicted by Lande (1980, 1987). The results here imply that sexual selection is a large driving force for both male and female size evolution in haplorhines.

It is interesting to note that size and size dimorphism are pushed upwards by sexual selection in haplorhines while they are not pulled down to a similar degree when selection pressures are relaxed (Figs 7, 8A, C). If our original hypothesis was correct, that when sexual selection was relaxed size and size dimorphism would return to the original level (Fig. 2), then we should find that the degree of increase and decrease of size and size dimorphism would be equal, as is indeed the case in some of the alternative reconstructions of size (Fig. 8B, D). The common trend from these figures is, however, that the decrease in size and size dimorphism is less than the increase. This can be due to one methodological and one evolutionary reason. First, some of the clades included in the group 'expected decrease' are multi-male. In these groups, sexual selection has not disappeared, only weakened. Even when removing the multi-male clades from the analysis, however, the pattern remains. Secondly, it could be because the cost of being large when there is no intrasexual competition is not as big as the benefit of being large when there is such competition.

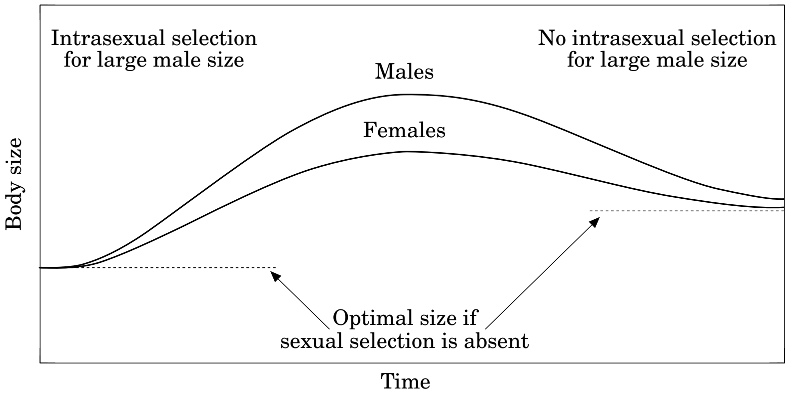

Figure 9. The path to and from sexual size dimorphism when it is caused by sexual selection for male size and a genetic correlation between the sexes. Just as in Fig. 2, size increases over the optimal species value and size dimorphism originates and is maintained due to a difference in benefits for the sexes. Also, when there is a later change in mating system so that sexual selection decreases, size decreases. However, as large size has been maintained for a long time, new adaptations related to larger size may have come into existence. Over time, such 'ons and offs' in sexual selection could increase the absolute size in a lineage.

A cause of this could be that over time new adaptations related to larger size have come into existence (Fig. 9).

If this scenario is correct, then it is a possible explanatory mechanism behind Cope's rule (1896); a tendency for body size to increase progressively over evolutionary time in many separate lineages (e.g. Bonner, 1988; but see Jablonski, 1997). Not only does sexual selection increase size, but when this selection pressure is relaxed, large size to some degree remains. Over time, such 'ons and offs' in sexual selection may increase the absolute size in a lineage more than would be expected in a random 'Brownian motion' scenario. The validity of this pattern outside haplorhines would have to be tested for its generality. As we have seen here, it is not valid for a large part of the primate order, namely strepsirhines, where sexual selection has had no influence on size. However, it seems possible for the pattern to be fulfilled for more animal lineages outside primates. As a recent study shows (Abouheif & Fairbairn, 1997), many animal lineages are in agreement with Rensch's rule, hypothetically mainly because of sexual selection. It is thus not an unreasonable hypothesis that sexual selection could be the main driving force behind a general pattern of size increase, as it is for haplorhines. The pattern in primates, however, that in one lineage sexual selection has had great impact on size while in another it has had none, cautions against any introduction of generality. It is clearly not that simple. However, it is still worthwhile examining a number of additional animal taxa to see exactly how general the pattern is.

ACKNOWLEDGEMENTS

We thank Olof Leimar, Sören Nylin, Mark Pagel, Fredrik Ronquist, Lars Werdelin, Christer Wiklund and two anonymous reviewers for valuable comments on previous drafts of the manuscript. This study has been financially supported by the Swedish Natural Science Research Council.

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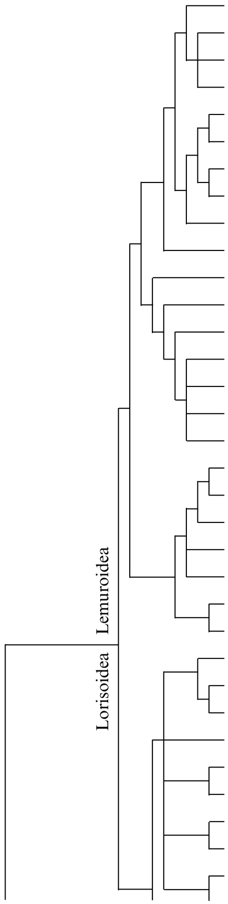
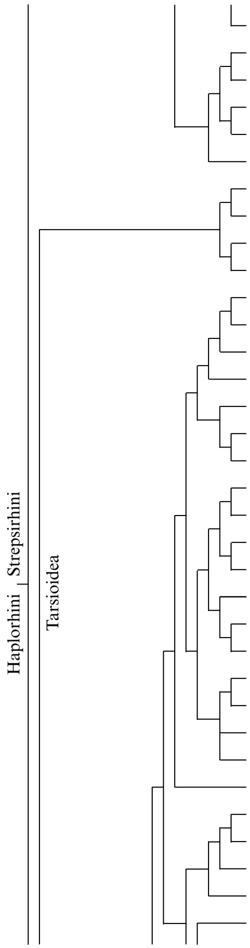
APPENDIX 1
MATING SYSTEMS, WEIGHTS AND REFERENCES



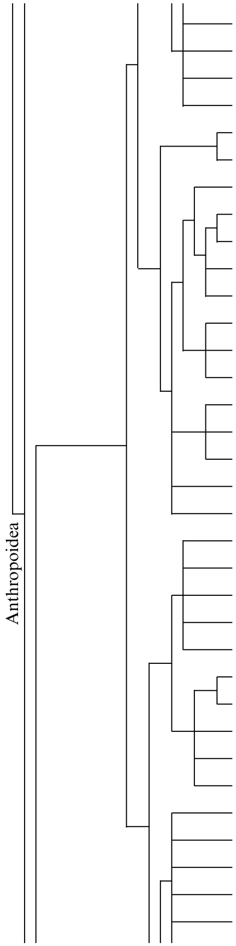
Species	Mating system	Female weight (kg)	Male weight (kg)	Ratio male/female	Mating system reference	Weight data reference
Lemur catta	MM	2.68	2.71	1.01	Hrdy & Whitten, 1987	Kappeler, 1991
Hapalemur aureus		1.18	1.25	1.06		Kappeler, 1991
Hapalemur griseus	Mon	0.89	0.94	1.05	Kappeler, 1990	Kappeler, 1991
Hapalemur simus		1.30	2.15	1.65		Kappeler, 1991
Petterus coronatus	MM	1.69	1.71	1.01	Smuts et al., 1987	Kappeler, 1991
Petterus mongoz	Mon	1.66	1.68	1.01	Kappeler, 1990	Kappeler, 1991
Petterus fulvus	MM	2.40	2.40	1.00	Richard, 1987	Kappeler, 1991
Petterus macaco	MM	2.49	2.40	0.97	Smuts et al., 1987	Kappeler, 1991
Petterus rubriventer	Mon	2.14	2.27	1.06	Kappeler, 1990	Kappeler, 1991
Varecia variegata	Mon	3.51	3.47	0.99	Kappeler, 1990	Kappeler, 1991
Lepilemur mustelinus	UM or MM	0.59	0.62	1.04	Kappeler, 1990	Kappeler, 1991
Daubentonia madagascarensis	UM or MM	2.57	2.76	1.07	Kappeler, 1990	Kappeler, 1991
Avahi laniger	Mon	1.32	1.03	0.78	Kappeler, 1990	Kappeler, 1991
Propithecus verrauxi	MM	3.70	3.64	0.98	Richard, 1987	Kappeler, 1991
Propithecus diadema	Mon	5.90	5.63	0.96	Richard, 1987	Kappeler, 1991
Propithecus tattersalli	UM and MM	3.17	3.04	0.96	Kappeler, 1990	Kappeler, 1991
Indri indri	Mon	6.25			Richard, 1987	Kappeler, 1991
Microcebus murinus	UM or MM	0.11	0.09	0.83	Richard, 1987	Kappeler, 1991
Microcebus rufus	UM or MM	0.05	0.05	1.02	Kappeler, 1990	Kappeler, 1991
Mirza coquereli	UM or MM	0.30	0.31	1.02	Kappeler, 1990	Kappeler, 1991
Cheirogaleus major	UM or MM	0.44	0.58	1.30	Kappeler, 1990	Kappeler, 1991
Cheirogaleus medius	UM or MM	0.28	0.28	1.00	Kappeler, 1990	Kappeler, 1991
Allocebus trichotis		0.09	0.09	1.08		Kappeler, 1991
Phaner furcifer	Mon	0.40	0.44	1.10	Richard, 1987	Harvey et al., 1987
Galago alleni	UM or MM	0.27	0.23	0.85	Bearder, 1987	Harvey et al., 1987
Galagoides demidoff	UM or MM	0.07	0.08	1.17	Bearder, 1987	Kappeler, 1991
Galagoides zanzibaricus	Mon and UM	0.14	0.16	1.17	Bearder, 1987	Kappeler, 1991
Galago granti						
Galago moholi	UM or MM	0.16	0.18	1.17	Bearder, 1987	Kappeler, 1991
Galago senegalensis	UM or MM	0.21	0.24	1.14	Bearder, 1987	Harvey et al., 1987
Otolemur crassicaudatus	UM or MM	1.24	1.50	1.20	Bearder, 1987	Kappeler, 1991
Otolemur garnettii	UM or MM	1.03	1.21	1.18	Bearder, 1987	Kappeler, 1991
Euoticus elegantulus		0.28	0.29	1.04		Harvey et al., 1987

APPENDIX 1—*continued*



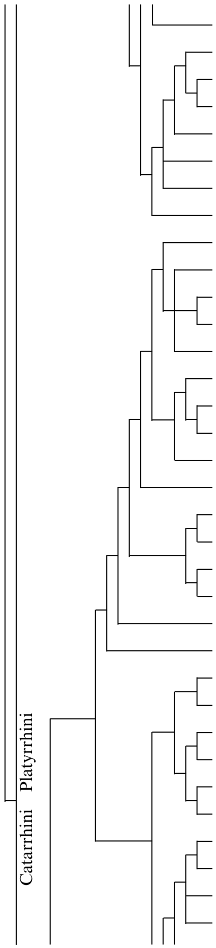
Species	Mating system	Female weight (kg)	Male weight (kg)	Ratio male/female	Mating system reference	Weight data reference
Euoticus inustus						
Loris tardigradus	UM or MM	0.19	0.19	0.99	Kappeler, 1990	Kappeler, 1991
Arctocebus calabarensis	UM or MM	0.30	0.32	1.07	Kappeler, 1990	Kappeler, 1991
Nycticebus coucang	UM or MM	1.20	1.21	1.01	Kappeler, 1990	Kappeler, 1991
Nycticebus pygmaeus	UM or MM	0.38	0.46	1.23	Kappeler, 1990	Kappeler, 1991
Perodicticus potto	UM or MM	0.99	0.95	0.96	Bearder, 1987	Kappeler, 1991
Tarsius bancanus	Mon and UM	0.13	0.13	1.01	Bearder, 1987	Kappeler, 1991
Tarsius syrichta	UM and MM	0.12	0.13	1.15	Kappeler, 1990	Kappeler, 1991
Tarsius pumilus						
Tarsius spectrum	Mon	0.20	0.20	1.00	Bearder, 1987	Harvey et al., 1987
Callithrix argentata		0.32	0.36	1.12		Ford, 1994
Callithrix humeralifer	Mon (and PA)	0.31	0.28	0.90	Ferrari & Digby, 1996	Ford, 1994
Callithrix jacchus	Mon (and PA)	0.24	0.26	1.08	Ford, 1994	Ford, 1994
Cebuella pygmaea	Mon (and PA)	0.13	0.13	1.03	Ford, 1994	Ford, 1994
Leonthopithecus chrysomelas		0.54	0.62	1.16		Ford, 1994
Leonthopithecus chrysopygus						
Leonthopithecus rosalia	Mon	0.60	0.62	1.04	Baker & Dietz, 1996	Dietz, Baker & Miglioretti, 1994
Saguinus bicolor		0.43	0.43	1.00		Ford, 1994
Saguinus midas	Mon (and PA)	0.43	0.59	1.36	Ford, 1994	Ford, 1994
Saguinus leucopus						
Saguinus oedipus	Mon (and PA)	0.43	0.41	0.96	Hrdy & Whitten, 1987	Ford, 1994
Saguinus imperator	Mon (and PA)				Goldizen, 1987	
Saguinus labiatus	Mon (and PA)	0.47	0.45	0.97	Goldizen, 1987	Ford, 1994
Saguinus mystax	Mon (and PA)	0.56	0.58	1.03	Goldizen, 1987	Ford, 1994
Saguinus fuscicollis	Mon (and PA)	0.40	0.39	0.96	Goldizen et al. 1996	Ford, 1994
Saguinus tripartitus						
Saguinus inustus						
Saguinus nigricollis	MM	0.48	0.47	0.98	Møller, 1988	Ford, 1994
Callimico goeldii	Mon	0.53	0.65	1.23	Pryce, 1996	Harvey et al., 1987
Cebus albifrons	MM	1.81	2.48	1.37	Robinson & Janson, 1987	Ford, 1994
Cebus capucinus	UM	2.67	3.87	1.45	Robinson & Janson, 1987	Ford, 1994
Cebus olivaceus	UM and MM	2.40	2.97	1.24	Robinson & Janson, 1987	Ford, 1994
Cebus apella	MM	2.39	3.05	1.28	Hrdy & Whitten, 1987	Ford, 1994
Saimiri bolivensis	MM	0.70	1.02	1.45	Dixson, 1987	Ford, 1994

APPENDIX 1—*continued*



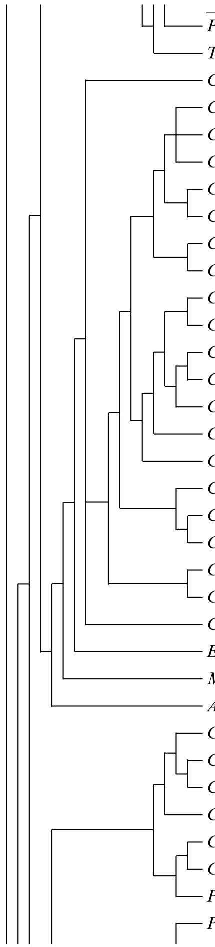
Species	Mating system	Female weight (kg)	Male weight (kg)	Ratio male/female	Mating system reference	Weight data reference
Saimiri oerstedii	MM	0.70	0.83	1.19	Robinson & Janson, 1987	Ford, 1994
Saimiri sciureus	MM	0.68	0.85	1.26	Sillén-Tullberg & Möller, 1993	Ford, 1994
Saimiri ustus		0.80	0.91	1.14		Ford, 1994
Saimiri vanzolinii		0.65	0.95	1.46		Ford, 1994
Aotus trivirgatus	Mon	0.95	0.92	0.97	Ford, 1994	Ford, 1994
Aotus azarae	Mon	0.78			Robinson, Wright & Kinzey, 1987	Ford & Davis, 1992
Callicebus brunneus	Mon	0.81	0.85	1.06	Robinson et al., 1987	Ford, 1994
Callicebus cinerascens						
Callicebus moloch	Mon	0.86	1.00	1.16	Robinson et al., 1987	Ford, 1994
Callicebus personatus	Mon	1.29	1.33	1.03	Robinson et al., 1987	Ford, 1994
Callicebus hoffmannsi		0.92				Ford & Davis, 1992
Callicebus calligatus						
Callicebus cupreus		1.12	1.01	0.90		Ford, 1994
Callicebus dubius						
Callicebus donacophilus			0.80			Ford & Davis, 1992
Callicebus oenanthe						
Callicebus olallae						
Callicebus modestus						
Callicebus torqatus	Mon	1.31	1.30	0.99	Robinson et al., 1987	Ford, 1994
Pithecia aequatorialis	Mon				Robinson et al., 1987	
Pithecia albicans	Mon		3.00		Robinson et al., 1987	Ford & Davis, 1992
Pithecia irrorata	Mon	1.88	2.01	1.07	Robinson et al., 1987	Ford, 1994
Pithecia monachus	Mon	1.90	2.80	1.47	Robinson et al., 1987	Ford, 1994
Pithecia pithecia	Mon	1.52	1.73	1.14	Robinson et al., 1987	Ford, 1994
Cacajao calvus	MM	2.88	3.45	1.20	Harcourt, Purvis & Liles, 1995	Ford, 1994
Cacajao rubicundus	MM				Hrdy & Whitten, 1987	
Cacajao melanocephalus		2.74				Ford & Davis, 1992
Chiropotes albinasus	MM	2.51	3.02	1.20	Hrdy & Whitten, 1987	Ford, 1994
Chiropotes satanas	MM	2.60	3.10	1.19	Ford, 1994	Ford, 1994
Alouatta belzebul		5.53	7.27	1.32		Ford, 1994
Alouatta caraya	UM and MM	4.61	6.80	1.48	Crocket & Eisenberg, 1987	Ford, 1994
Alouatta fusca	MM	4.55	6.18	1.36	Dixson, 1987	Ford, 1994
Alouatta palliata	MM	5.35	7.15	1.34	Crocket & Eisenberg, 1987	Ford, 1994
Alouatta seniculus	UM and MM	5.60	7.20	1.29	Crocket & Eisenberg, 1987	Ford, 1994

APPENDIX 1—*continued*



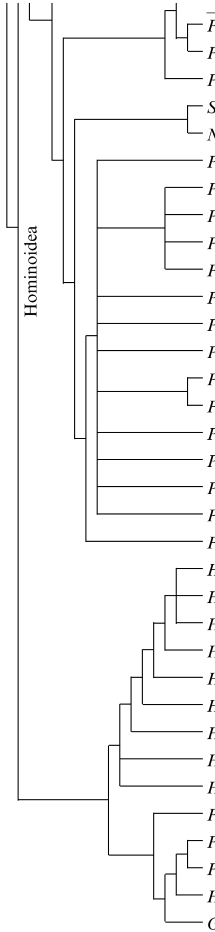
Species	Mating system	Female weight (kg)	Male weight (kg)	Ratio male/female	Mating system reference	Weight data reference
Alouatta villosa	UM and MM	6.43	11.35	1.76	Crocket & Eisenberg, 1987	Ford, 1994
Ateles belzebuth	MM	8.11	8.53	1.05	Robinson & Janson, 1987	Ford, 1994
Ateles fusciceps	MM	8.80	8.89	1.01	Robinson & Janson, 1987	Ford, 1994
Ateles geoffroyi	MM	7.46	8.21	1.10	Robinson & Janson, 1987	Ford, 1994
Ateles paniscus	MM	8.75	7.46	0.85	Robinson & Janson, 1987	Ford, 1994
Lagothrix flavicauda	MM	7.70	7.90	1.03	Robinson & Janson, 1987	Robinson & Janson, 1987
Lagothrix lagothricha	MM	5.75	8.34	1.45	Robinson & Janson, 1987	Ford, 1994
Brachyteles arachnoides	MM	9.45	12.13	1.28	Sillén-Tullberg & Möller, 1993	Ford, 1994
Macaca arctoides	MM	8.00	9.20	1.15	Melnick & Pearl, 1987	Harvey et al., 1987
Macaca assamensis	MM				Smuts et al., 1987	
Macaca radiata	MM	3.70	6.60	1.78	Melnick & Pearl, 1987	Harvey et al., 1987
Macaca sinica	MM	3.16	5.71	1.81	Melnick & Pearl, 1987	Mitani et al., 1996
Macaca thibetana		14.10	18.25	1.29		Zhao, 1994
Macaca cyclopsis	UM and MM	4.95	6.00	1.21	Leutenegger & Cheverud, 1982	Leutenegger & Cheverud, 1982
Macaca fuscata	MM	9.10	11.70	1.29	Melnick & Pearl, 1987	Harvey et al., 1987
Macaca mulatta	MM	3.00	6.20	2.07	Melnick & Pearl, 1987	Harvey et al., 1987
Macaca fascicularis	MM	3.50	5.50	1.57	Melnick & Pearl, 1987	Mitani et al., 1996
Macaca nemestrina	MM	7.80	10.40	1.33	Hrdy & Whitten, 1987	Harvey et al., 1987
Macaca maurus		5.10	9.50	1.86		Harvey et al., 1987
Macaca tonkeana		9.25	10.47	1.13		Watanabe et al., 1987
Macaca nigra	MM	6.60	10.40	1.58	Dixson, 1987	Harvey et al., 1987
Macaca ochreata						
Macaca silenus	MM	5.00	6.80	1.36	Melnick & Pearl, 1987	Harvey et al., 1987
Macaca sylvanus	MM	10.00	11.20	1.12	Melnick & Pearl, 1987	Harvey et al., 1987
Cercocebus albigena	MM	6.40	9.00	1.41	Hrdy & Whitten, 1987	Harvey et al., 1987
Cercocebus aterrimus	MM				Dixson, 1987	
Cercocebus galeritus	MM	5.50	10.20	1.85	Smuts et al., 1987	Harvey et al., 1987
Cercocebus torquatus	MM	5.50	8.00	1.45	Hrdy & Whitten, 1987	Harvey et al., 1987
Mandrillus leucophaeus	UM	10.00	17.00	1.70	Stammbach, 1987	Harvey et al., 1987
Mandrillus sphinx	UM	11.50	25.00	2.17	Stammbach, 1987	Harvey et al., 1987
Papio anubis	MM	14.70	24.00	1.63	Melnick & Pearl, 1987	Strum, 1991
Papio papio	MM				Melnick & Pearl, 1987	
Papio cynocephalus	MM	11.20	23.10	2.06	Melnick & Pearl, 1987	Leutenegger & Cheverud, 1982
Papio ursinus	MM	14.63	28.80	1.97	Melnick & Pearl, 1987	Mitani et al., 1996

APPENDIX 1—*continued*



Species	Mating system	Female weight (kg)	Male weight (kg)	Ratio male/female	Mating system reference	Weight data reference
Papio hamadryas	UM	9.40	21.50	2.29	Stammbach, 1987	Harvey et al., 1987
Theropithecus gelada	UM	13.95	26.10	1.87	Stammbach, 1987	Mitani et al., 1996
Cercopithecus aethiops	MM	3.56	5.08	1.43	Galat-Luong et al., 1996	Mitani et al., 1996
Cercopithecus ascanius	UM and MM	2.90	4.20	1.45	Hrdy & Whitten, 1987	Harvey et al., 1987
Cercopithecus cephus	UM	2.90	4.10	1.41	Smuts et al, 1987	Harvey et al., 1987
Cercopithecus erythrotis	UM				Dixson, 1987	
Cercopithecus erythrogaster	UM				Cords, 1987	
Cercopithecus petaurista	UM				Cords, 1987	
Cercopithecus mitis	UM	4.15	6.90	1.66	Hrdy & Whitten, 1987	Mitani et al., 1996
Cercopithecus nictitans	UM	4.20	6.60	1.57	Cords, 1987	Harvey et al., 1987
Cercopithecus campbelli	UM				Smuts et al., 1987	
Cercopithecus mona	UM	2.50	4.40	1.76	Cords, 1987	Harvey et al., 1987
Cercopithecus denti	UM				Cords, 1987	
Cercopithecus wolfi	UM				Cords, 1987	
Cercopithecus pogonias	UM	3.00	4.50	1.50	Smuts et al., 1987	Harvey et al., 1987
Cercopithecus neglectus	Mon and UM	3.96	7.00	1.77	Leutenegger & Lubach, 1987	Harvey et al., 1987
Cercopithecus hamlyni	UM				Cords, 1987	
Cercopithecus diana	UM				Cords, 1987	
Cercopithecus dryas	UM				Cords, 1987	
Cercopithecus salongo	UM				Cords, 1987	
Cercopithecus lhoesti	UM	4.70	8.50	1.81	Cords, 1987	Harvey et al., 1987
Cercopithecus preussi	UM				Cords, 1987	
Cercopithecus solatus	UM				Cords, 1987	
Erythrocebus patas	UM	6.50	12.40	1.91	Galat-Luong et al., 1996	Galat-Luong et al., 1996
Miopithecus talapoin	MM	1.12	1.38	1.23	Hrdy & Whitten, 1987	Jungers, 1985
Allenopithecus nigroviridis	MM				Dixson, 1987	
Colobus angolensis	MM	8.20	10.20	1.24	Struhsaker & Leland, 1987	Hayes et al., 1996
Colobus guereza	UM and MM	8.70	10.60	1.22	von Hippel, 1996	Hayes et al., 1996
Colobus polykomos	UM and MM	7.90	9.60	1.22	Smuts et al., 1987	Hayes et al., 1996
Colobus satanas	UM and MM	9.20	11.00	1.20	Smuts et al., 1987	Hayes et al., 1996
Colobus badius	MM	7.10	9.90	1.39	Hrdy & Whitten, 1987	Hayes et al., 1996
Colobus kirkii						
Procolobus verus	MM	3.80	4.30	1.13	Hayes et al., 1996	Hayes et al., 1996
Pygathrix avunculus						

APPENDIX 1—*continued*



Species	Mating system	Female weight (kg)	Male weight (kg)	Ratio male/female	Mating system reference	Weight data reference
Pygathrix brelichi						
Pygathrix roxellana	MM				Zhixiang et al., 1980	
Pygathrix nemaeus	UM and MM				Sillén-Tullberg & Möller, 1993	
Simias concolor	Mon and UM	6.80	8.80	1.29	Tenaza & Fuentes, 1995	Tenaza & Fuentes, 1995
Nasalis larvatus	UM and MM	9.90	20.30	2.05	Struhsaker & Leland, 1987	Harvey et al., 1987
Presbytis aurata						
Presbytis comata	UM	6.20	6.30	1.02	Struhsaker & Leland, 1987	Harvey et al., 1987
Presbytis frontata	UM and MM	5.66	5.60	0.99	Leutenegger & Cheverud 1982	Leutenegger & Cheverud, 1982
Presbytis melalophos	UM and MM	6.60	6.70	1.02	Struhsaker & Leland, 1987	Harvey et al.. 1987
Presbytis rubicunda	UM and MM	5.90	6.25	1.06	Leutenegger & Cheverud 1982	Leutenegger & Cheverud, 1982
Presbytis cristata	UM	8.10	8.60	1.06	Struhsaker & Leland, 1987	Harvey et al., 1987
Presbytis francoisi						
Presbytis geei		8.10	8.60	1.06		Harvey et al., 1987
Presbytis johnii	UM	12.00	14.80	1.23	Struhsaker & Leland, 1987	Harvey et al., 1987
Presbytis vetulus	UM	7.80	8.50	1.09	Struhsaker & Leland, 1987	Harvey et al., 1987
Presbytis obscura	UM and MM	6.50	8.30	1.28	Hrdy & Whitten, 1987	Harvey et al., 1987
Presbytis phayeri						
Presbytis pileatus	UM	10.40	12.75	1.23	Struhsaker & Leland, 1987	Gaulin & Sailer, 1984
Presbytis potenziani	Mon	6.40	6.50	1.02	Hrdy & Whitten, 1987	Harvey et al., 1987
Presbytis entellus	UM and MM	11.70	18.50	1.58	Hrdy & Whitten, 1987	Mitani et al., 1996
Hylobates agilis	Mon	5.82	5.88	1.01	Smuts et al., 1987	Geissmann, 1993
Hylobates lar	Mon	5.34	5.90	1.10	Hrdy & Whitten, 1987	Geissmann, 1993
Hylobates muelleri	Mon	5.35	5.71	1.07	Smuts et al., 1987	Geissmann, 1993
Hylobates moloch	Mon	6.25	6.58	1.05	Smuts et al., 1987	Geissmann, 1993
Hylobates pileatus	Mon	5.44	5.50	1.01	Smuts et al., 1987	Geissmann, 1993
Hylobates klossi	Mon	5.89	5.67	0.96	Smuts et al., 1987	Geissmann, 1993
Hylobates hoolock	Mon	6.88	6.87	1.00	Smuts et al., 1987	Geissmann, 1993
Hylobates syndactylus	Mon	10.71	11.88	1.11	Hrdy & Whitten, 1987	Geissmann, 1993
Hylobates concolor	Mon	7.62	7.77	1.02	Smuts et al., 1987	Geissmann, 1993
Pongo pygmaeus	UM and MM	38.70	86.30	2.23	Rodman & Mitani, 1987	Markham & Groves, 1990
Pan paniscus	MM	33.20	43.00	1.30	Hrdy & Whitten, 1987	Jungers, 1985
Pan troglodytes	MM	35.20	42.00	1.19	Hrdy & Whitten, 1987	Mitani et al., 1996
Homo sapiens	Mon (and UM)	40.10	47.90	1.19	Hrdy & Whitten, 1987	Harvey et al., 1987
Gorilla gorilla	UM	97.70	159.20	1.63	Hrdy & Whitten, 1987	Mitani et al., 1996

Notes: Mating systems: UM = Unimale, MM = Multimale, Mon = Monogamous, PA = Facultative polyandrous. Species with single sex weight values were not included in the analyses.

APPENDIX 2
MATCHED-PAIR COMPARISON OF SISTER TAXA

Paired Taxa	Average male size, log(gram)	Average female size, log(gram)	Average dimorphism, male weight/female weight
Strepsirhini (Lemuriformes)			
1. More polygynous: *Lemur catta*	3.43	3.43	1.01
Less polygynous: *Hapalemur griseus*	2.97	2.95	1.05
2. More polygynous: *Petterus coronatus*	3.23	3.23	1.01
Less polygynous: *Petterus mongoz*	3.23	3.22	1.01
3. More polygynous: *Petterus fulvus*, *P. macaco*	3.38	3.39	0.98
Less polygynous: *Petterus rubriventer*	3.36	3.33	1.06
4. More polygynous: *Lepilemur mustelinus*	2.79	2.77	1.04
Less polygynous: *Varecia variegata*	3.54	3.55	0.99
5. More polygynous: *Daubentonia madagascarensis*	3.44	3.41	1.07
Less polygynous: *Avahi laniger*	3.01	3.12	0.78
6. More polygynous: *Propithecus tattersalli*, *P. verrauxi*	3.52	3.53	0.97
Less polygynous: *Propithecus diadema*	3.75	3.77	0.96
7. More polygynous: *Microcebus murinus*, *M. rufus*, *Mirza coquerli*, *Cheirogaleus major*, *C. medius*	2.27	2.26	1.03
Less polygynous: *Phaner furcifer*	2.64	2.60	1.10
Haplorhini, Platyrrhini			
8. More polygynous: *Saguinus nigricollis*	2.67	2.68	0.98
Less polygynous: *Saguinus fuscicollis*	2.59	2.60	0.96
9. More polygynous: *Cebus olivaceus*, *C. apella*, *Saimiri bolivensis*, *S. oerstedii*, *S. sciureus*	3.59	3.43	1.45
Less polygynous: *Callithrix humeralifer*, *C. jacchus*, *C. pygmaea*, *Leontopithecus rosalia*, *Saguinus midas*, *S. oedipus*, *S. labiatus*, *S. mystax*, *Callimico goeldii*	3.39	3.26	1.37
10. More polygynous: *Cebus capucinus*	3.16	3.05	1.28
Less polygynous: *Cebus albifrons*	2.60	2.57	1.07
11. More polygynous: *Cacajao calvus*, *Chiropotes albinasus*, *C. satanas*	3.50	3.42	1.20
Less polygynous: *Pithecia irrorata*, *P. monachus*, *P. pithecia*	3.33	3.24	1.23
12. More polygynous: *Alouatta caraya*, *A. fusca*, *A. palliata*, *A. seniculus*, *A. villosa*, *Ateles belsebuth*, *A. fusciceps*, *A. geoffroyi*, *A. paniscus*, *Lagothrix flavicauda*, *Brachyteles arachnoides*	3.91	3.82	1.25
Less polygynous: *Aotus trivirgatus*, *Callicebus brunneus*, *C. moloch*, *C. personatus*, *C. torqatus*	3.03	3.01	1.04
Haplorhini, Catarrhini			
13. More polygynous: *Theropithecus gelada*	4.31	4.03	1.94
Less polygynous: *Cercocebus albigena*	3.96	3.74	1.65
14. More polygynous: *Mandrillus leucophaeus*, *M. sphinx*	4.42	4.14	1.87
Less polygynous: *Cercocebus galeritus*, *C. torquatus*	3.95	3.81	1.41
15. More polygynous: *Papio hamadryas*	4.33	3.97	2.29
Less polygynous: *Papio anubis*, *P. cynocephalus*, *P. ursinus*	4.40	4.13	1.89
16. More polygynous: *Cercopithecus ascanius*, *C. cephus*, *C. mitis*, *C. nictitans*, *C. l'hoesti*	3.76	3.57	1.58
Less polygynous: *Cercopithecus aethiops*	3.71	3.55	1.43

continued

APPENDIX 2—*continued*

Paired Taxa	Average male size, log(gram)	Average female size, log(gram)	Average dimorphism, male weight/female weight
17. More polygynous: *Cercopithecus mona*, *C. pogonias*	3.65	3.44	1.63
Less polygynous: *Cercopithecus neglectus*	3.84	3.60	1.77
18. More polygynous: *Erythrocebus patas*	4.09	3.81	1.91
Less polygynous: *Miopithecus talapoin*	3.14	3.05	1.23
19. More polygynous: *Nasalis larvatus*	4.31	3.99	2.05
Less polygynous: *Simias concolor*	3.94	3.83	1.29
20. More polygynous: *Presbytis comata*, *P. frontata*, *P. melelophos*, *P. rubicunda*, *P. creistata*, *P. johnii*, *P. vetulus*, *P. obscura*, *P. pileatus*	3.91	3.87	1.11
Less polygynous: *Presbytis potenziani*	3.81	3.81	1.02
21. More polygynous: *Pongo pygmaeus*, *Gorilla gorilla*	5.07	4.79	1.93
Less polygynous: *Hylobates agilis*, *H. lar*, *H. muelleri*, *H. moloch*, *H. pileatus*, *H. klossii*, *H. hoolock*, *H. syndactylus*, *H. concolor*	3.82	3.81	1.04
22. More polygynous: *Pan paniscus*, *P. troglodytes*	4.63	4.53	1.24
Less polygynous: *Homo sapiens*	4.68	4.60	1.19