

Sexually antagonistic selection on primate size

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Abstract

Male intrasexual selection in haplorhine primates has previously been shown to increase male size and to a lesser degree also female size. I address the following questions: (1) why does female size increase when the selection is on males, and (2) why does female size not increase to the same extent as that of males. The potential for correlational selection on females through increased resource competition was analysed with independent contrasts analyses. No such effect was found, nor did matched pairs comparisons reveal females to increase in size because of selection to bear larger male offspring. Instead further matched pairs analyses revealed higher female postpartum investment, as indicated by a longer lactation period, in more sexually selected species, also after correcting for body weight. Concerning the second question, independent contrast analyses showed that large size has had negative effects on female reproductive rate across the primate order. Matched-pairs analyses on haplorhines revealed that females of species in more polygynous clades have lower reproductive rates than females of species in less polygynous clades. This is also true after the effects of body weight are removed. These results, both when correcting for body weight and when not, suggest that sexual selection has shifted female size from one favouring female lifetime fecundity to one favouring male success in competition. This depicts antagonistic selection pressures on female size and a trade-off for females between the ecologically optimal size of their foremothers and the larger size that made their forefathers successful.

Introduction

Darwin (1859) pointed out the general pattern that larger females can carry and provide for more eggs and/or offspring and therefore hypothesized that fecundity selection on females consequently would push body size up over time. Fecundity selection would in this scenario *always* be present so that larger individuals at all times would have a fecundity advantage. In mammals, however, interspecific comparisons have shown that the relationship is generally the opposite (e.g. Boyce, 1988), although examination of intraspecific variation might suggest the opposite correlation because of environmental influences on body size or maternal effects that mask this trade-off (e.g. Stearns, 1992). Furthermore, theoret-

ical models generally predict that there is a trade-off between somatic growth and reproduction (e.g. Charnov, 1993). So why are many mammals so large if fecundity goes down with size (Harvey *et al.*, 1989)?

Body size is a correlate of many life-history characters in animals in general (e.g. Roff, 1992; Stearns, 1992), and in primates in particular (e.g. Harvey & Clutton-Brock, 1985; Harvey *et al.*, 1987). These relationships are often thought of as being physiologically constrained as growth to larger size takes more time and energy, resulting in a trade-off between body size and reproduction (Roff, 1992; Stearns, 1992; Charnov, 1993). The correlation between size and life-history characters constrains the evolution of both, and evolutionary change along the regression lines describing the allometric relationships between them are therefore usually explained by two different lines of argument: (1) either one or more life-history variables are under selection, and size may change as a consequence (e.g. MacArthur & Wilson,

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1967), or (2) size itself is the variable under selection (e.g. Andersson, 1994, pp. 251–255 and references cited therein).

For example, high mortality rates are generally believed to select for animals that reproduce earlier (e.g. Williams, 1966). As Charnov (1993; but see Kozowski & Weiner, 1997) has modelled the process, earlier maturation in turn influences body size because animals that mature early do not have time to grow for a long time and thus cannot become as large as animals with later maturation. Effects of size then feed back into the reproductive rate because growing larger offspring takes longer time, which leads to the expectation of lower reproductive rates for larger animals. The prediction from this theory would thus be that larger animals should be expected to be less fecund.

There are, however, also a lot of potential advantages of large size, e.g. dominance in competitive situations, better predator defence, secondary effects on other crucial characters linked to size such as weaponry, that can be invoked to explain size increase in mammals (Andersson, 1994). In a recent study of one of these factors – the effects of male intrasexual competition – Lindenfors & Tullberg (1998) showed that increases in male intrasexual competition, as indicated by changes in mating system, have caused increases in male size in haplorhine primates. This is a pattern in full accordance with Darwin's (1871) sexual selection theory.

In haplorhines, however, Lindenfors & Tullberg (1998) found that *female* size also increases after increases in male competition, although to a lower degree. Dimorphism resulted from a reduced response in female size compared with male size (see also Gaulin & Sailer, 1985). In both sexes size was also found to decrease when male competition decreased. The increase in female size as a response to a selection pressure on males is not predicted by sexual selection theory, but fits as an explanation for Rensch's rule (Rensch, 1950, 1959); that more dimorphic species also are larger. A correlated response in females to selection in males is also predicted to occur by quantitative genetic models (Maynard Smith, 1978; Lande, 1980, 1987; Lande & Arnold, 1983), but only initially until natural selection slowly brings female size back to its original, theoretically optimal level.

Thus, the increase in female size in haplorhines introduces two questions that need to be answered: (1) why does female size increase when the selection seemingly is on males? and (2) what constrains females to be of a smaller size than males, i.e. why dimorphism at all? These two questions are the focus of this article.

Hypotheses and tests

Concerning the first question of what causes the response in female size to selection on males, there are three possible hypotheses: (1) the underlying factor causing a change in mating system, or a factor correlated with

mating system, also causes a size increase in females, (2) females are selected to be larger to be able to produce larger sons or larger offspring in general or (3) there is a genetic correlation between the sexes concerning size-controlling genes so that selection in one sex also induces changes in the other sex (Maynard Smith, 1978; Lande, 1980, 1987; Lande & Arnold, 1983), that is, temporary (if considerably long-lasting) changes in female body size that then, for some reason, become permanent. The first two hypotheses involve selection factors that are correlated to sexual selection whereas the last hypothesis involves a correlated response in females to sexual selection on males. There are more hypotheses than these, however, that have been invoked to explain the related pattern of general covariation between size and size dimorphism. In a thorough review of allometry for sexual size dimorphism, Fairbairn (1997) lists eight proposed causes. Of these, however, some have proven wrong and others are not applicable for primates.

To test the first hypothesis – that there is some underlying factor either causing, or that is correlated with, changes in mating system – the first task is to identify such a potential factor. It is, however, unfortunately not known exactly what lies behind changes in primate mating systems although a number of hypotheses have been forwarded (e.g. Rutberg, 1983; Ridley, 1986; van Schaik & Dunbar, 1990; van Schaik & Hörstermann, 1994; van Schaik & Kappeler, 1997; see also Smuts, 1987; Wrangham, 1987 for discussions), making an analysis of an underlying factor somewhat difficult. There is thus no one factor that can be said to be the cause of primate mating system transitions. Hence, although factors such as diet, activity period, group defence, substrate use and female ability to resist males' advances all may have a substantial influence on body size (e.g. Leutenegger & Kelly, 1977; Rowell & Chism, 1986; Harvey *et al.*, 1987; Ford, 1994; Plavcan & van Schaik, 1997), they do not covary consistently with mating systems but may instead function as separate selection factors on size (personal observations).

Although differences in size and size dimorphism are also found between uni-male and multi-male species, the largest differences can be found in comparisons between monogamous and polygynous species (e.g. Alexander *et al.*, 1979; Mitani *et al.*, 1996). Comparisons between monogamy and polygyny, however, constitute differences not only in mating system but also in social system, as polygyny in most haplorhine primates also means female group living, while monogamy almost exclusively does not. As social grouping increases the possibilities of resource competition, I here investigate the effects of group size on female body weight using an independent contrast analysis. An increased group size could indicate a higher degree of within-group competition that in turn could select for larger overall size for both sexes. This is in contrast to sexual selection where it is the mating system, not social system that is the crucial variable. Although

social life among primates involves a fragile balance between cooperation and competition, group living primates often form dominance hierarchies, females as well as males, that are useful predictors, if not strict determinants, of resource acquisition (Walters & Seyfarth, 1987). Even if body size is only a part of the complex web of causes determining dominance rank, its influence on resource acquisition could potentially result in a strong phylogenetic signal.

The predictions of the second hypothesis – that females are selected to be larger to be able to produce larger sons or larger offspring in general – are that more sexually selected, and thus larger, species would have larger sons, or invest more in their offspring of both sexes, than their less sexually selected sister species. To test this hypothesis, independent contrast analyses are first carried out to establish the possible correlations between body size and different offspring characters. Then matched pairs analyses are used to test if there are effects of sexual selection on these offspring characters, both size dependent but also possible effects that go above those of size alone.

The third possible hypothesis – that there is a genetic correlation between the sexes concerning size-controlling genes so that selection in one sex also induces changes in the other sex – cannot be tested directly with the data currently available in the literature. Instead, the circumstantial evidence for such a genetic correlation is discussed in the discussion part of this paper.

The second question of what constrains females to a smaller size than males deal with the factors antagonistic to sexual selection that can explain the female side of size dimorphism. Here I conduct a phylogenetic life-history analysis using independent contrasts and matched-pairs analyses to investigate if there are possible detrimental effects of larger size and sexual selection on female fecundity. Lande's model (1980, 1987) predicts that natural selection will bring female size down to its initial level after an initial size increase because of sexual selection on males. Natural selection would in this case most probably act on characters that determine the rate of female reproduction: mainly age at first birth and birth rate (Cole, 1954; Charnov, 1993). It is of general interest to identify the components of natural selection invoked by Lande (1980, 1987) to explain the female side of dimorphism. The results presented here are also a potential key to understanding the lack of size dimorphism in polygynous strepsirhines.

Materials and methods

Data for body weights were taken from Smith & Jungers (1997) who have reviewed the literature for wild primate weights and compiled them for the explicit purpose of using in comparative studies. Sex-specific neonate body weights were taken from Smith & Leigh (1998). To increase sample size, these were complemented with non-sex-specific neonate weights when calculating the

influence of female body weight and sexual selection on general neonate weight. In these analyses, the averages of the sex-specific neonate weights of Smith & Leigh (1998) were used as species values. Where dimorphism was used as a separate variable, it was everywhere calculated as $\log(\text{male weight}) - \log(\text{female weight})$.

Information on life-history variables and group sizes were compiled from various literature sources (see web materials). In cases where different values were found for the same variable, data originating from wild populations were given precedence over those from captive populations. Where several values, or a range, was given in a data source, the mean of these values, or of the range limits, was used. The two life-history variables that have the largest influence on female fecundity: the age at first birth and the birth rate (the number of offspring per year for a mature individual) (Cole, 1954; Charnov, 1993), are complemented by several other variables being their component parts: age at sexual maturity, gestation length, the number of offspring per litter and the interbirth interval. These are included in order to more closely examine where selection acts. The maximum recorded life-span is also included as it also determines female fecundity even if it is of much less importance as a selection factor (Cole, 1954; Charnov, 1993). Measured weaning weights were unfortunately not available to the extent required by a phylogenetic analysis, so estimated weights calculated from growth curves were used instead (Lee, 1999). Foetal growth rate was calculated as litter mass divided by gestation length, whereas postnatal growth rate was taken from Ross (1991) where it was computed as litter mass at weaning minus litter mass at birth, all divided by the age at weaning. All continuous variables were log-transformed prior to statistical analysis. The variables are presented as supplementary material (Appendix 2).

Mating system, divided into three discrete groups, uni-male, multi-male and monogamous, was used as a discrete variable indicating the strength of male intra-sexual competition. The ancestral states of this variable were parsimoniously reconstructed using the computer program MacClade (Maddison & Maddison, 2000). Note that mating systems as used here are a classification based on the number of individuals of one sex that typically mates with an individual of the other sex. It is thus a different categorization than social system although the two often coincide in primates. For example, many lorises lead solitary lives where there is no clear group structure, but where the mating system nonetheless is of harem type (uni-male) because males defend territories that overlap the territories of several females and thus exclude other males from mating access.

Mating system categories are admittedly crude as a lot of information is lost when squeezing the diversity of primate mating patterns into a mere three variables, but these variables still contain a lot of information by indicating fundamental differences in sexual selection

pressures. Mating systems were preferred over the more fine-tuned measures of operational sex ratios as the latter are available only for a very limited number of species (Mitani *et al.*, 1996). Mating systems were also considered a superior choice over the 'competition levels' of Plavcan & van Schaik (1992, 1997), because of the way these competition levels are calculated.

The 'competition levels' (Plavcan & van Schaik, 1992, 1997) are invoked from two ranking variables, male competition intensity (whether males are tolerant or intolerant towards each other) and competition frequency (whether there is one male or several males in a breeding group). More intensely competing species are classified in groups 3 and 4, whereas the less intensely competing species are classified in groups 1 and 2. Further, if a species typically has more males in a breeding group, then the species is classified in groups 2 or 4, or if it typically has one male in a breeding group it is classified in groups 1 or 3. In this way harem-holding species should end up in groups with supposedly less sexual selection pressure than multi-male promiscuous species, in total contrast to the normal expectation of sexual selection theory. This is not always the case (Plavcan & van Schaik, 1992, 1997), however, indicating that the classification scheme is not strictly adhered to. Also, for monogamous pair-bonding species that exhibit high intensity male-male competition, an *ad hoc* correction (for mating system!) is made because monogamy predicts lower sexual selection pressure. Given these weaknesses of the 'competition levels' classification I preferred not to correct for mating system but instead to use it as a reliable variable indicating sexual selection pressure.

The phylogeny used in all analyses was a composite phylogeny by Purvis & Webster (1999), made with a 'super-tree' technique using phylogenies based on both molecular and morphological data. Most analyses were also carried out on an older phylogeny (Purvis, 1995) but the results did not differ in any meaningful way to those presented here.

To analyse the influence of body weight on all life-history variables, phylogenetically independent contrasts (Felsenstein, 1985) were calculated using the computer program PDAP (Garland *et al.*, 1993) on data for all primates. Branch lengths were set to arbitrary lengths as described by Grafen (1989) and then log-transformed to receive equal weighting in the subsequent regression analyses. This standardization of branch lengths generally best transformed the contrasts adequately for statistical purposes, as discussed by Garland *et al.* (1992). Regression results using different branch lengths did, however, not differ markedly from each other, but the branch lengths used for the results presented here nevertheless removed trends caused by unjustifiably large differences at the basal parts of the phylogeny (Garland, 1992; Garland *et al.*, 1992).

For the analyses of the effects of sexual selection on different variables in haplorhines, closely related spe-

cies or species groups (matched pairs), differing in mating system, were compared (Appendix 1). The commonly used procedure of letting one such independent comparison constituting one data point was then adhered to (e.g. Felsenstein, 1985; Møller & Birkhead, 1992; Wickman, 1992; Tullberg & Hunter, 1996; Lindenfors & Tullberg, 1998). Unweighted species averages were used in the comparisons and polytomies therefore did not pose any problem. Matched-pairs comparisons such as these give access to phylogenetically independent 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.

Results

Why are females so large? – The 'resource competition' hypothesis

To investigate possible effects of resource competition on female body size, independent contrasts analyses were carried out on group size and female body weight. A positive relationship would indicate that within-group competition may act as a selection factor on female size. The analyses showed that group size and female body weight were close to significantly correlated in the primate order (regression $P = 0.061$, $b = 0.142$, $R^2 = 0.023$, $n = 155$). It is strepsirhines that account for this trend (regression $P = 0.067$, $b = 0.446$, $R^2 = 0.098$, $n = 34$), while group size shows no correlation with body size in haplorhines (regression $P = 0.301$, $b = 0.077$, $R^2 = 0.009$, $n = 120$). The nearly significant value for strepsirhines is, however, because of a single internal contrast. When this point is removed, the trend disappears completely (regression $P = 0.220$, $b = 0.260$, $R^2 = 0.047$, $n = 33$), as is true also for the total primate order (regression $P = 0.141$, $b = 0.107$, $R^2 = 0.014$, $n = 154$).

Why are females so large? – The 'larger investment in offspring' hypothesis

An alternative scenario that would explain female size increase in sexually selected haplorhine species would be if females in such species had been selected to be larger in order to be able to produce larger sons or larger offspring in general. Data for weight at weaning and postnatal growth rate were unfortunately only available for haplorhines. Independent contrast analyses showed that female body weight and offspring variables were significantly correlated so that larger species invest more energy in each offspring than do smaller species (Table 1).

To investigate if this larger energy investment also is correlated to sexual selection so that more sexually selected species also make larger investments, I performed matched-pairs analyses. These tests unfortunately gave

Table 1 Results from regression analyses on independent contrasts concerning different offspring traits regressed onto female weight for primates, haplorhines and strepsirhines. The relationships are highly significant for all variables, *n* refers to the number of contrasts used for the regressions.

Variable	Primates				Haplorhines				Strepsirhines			
	<i>b</i>	<i>R</i> ²	<i>P</i>	<i>n</i>	<i>b</i>	<i>R</i> ²	<i>P</i>	<i>n</i>	<i>b</i>	<i>R</i> ²	<i>P</i>	<i>n</i>
Foetal growth rate	0.586	0.746	0.000	79	0.632	0.825	0.000	54	0.490	0.590	0.000	24
Neonate weight	0.690	0.809	0.000	100	0.678	0.812	0.000	72	0.704	0.846	0.000	27
Age at weaning	0.417	0.365	0.000	95	0.441	0.336	0.000	67	0.371	0.466	0.000	27
Weight at weaning	–	–	–	–	0.529	0.597	0.000	35	–	–	–	–
Postnatal growth rate	–	–	–	–	0.485	0.638	0.000	39	–	–	–	–

Table 2 Results from matched-pairs comparisons concerning the influence of male intrasexual selection, as indicated by mating systems, on several offspring life-history traits. The age and weight at weaning are significantly longer in more sexually selected species. This is true for age at weaning even if size is corrected for. Significant values from the one-tailed Wilcoxon's matched pairs test are given in bold, *n* refers to the number of independent comparisons.

Variable	Primates			Haplorhines		
	Size-dependent Wilcoxon's matched pairs	Residuals Wilcoxon's matched pairs	<i>n</i>	Size-dependent Wilcoxon's matched pairs	Residuals Wilcoxon's matched pairs	<i>n</i>
Foetal growth rate	<i>P</i> = 0.153 <i>Z</i> = 1.022	<i>P</i> = 0.182 <i>Z</i> = 0.909	15	<i>P</i> = 0.065 <i>Z</i> = 1.511	<i>P</i> = 0.395 <i>Z</i> = 0.227	11
Neonate weight	<i>P</i> = 0.096 <i>Z</i> = 1.306	<i>P</i> = 0.345 <i>Z</i> = 0.398	15	<i>P</i> = 0.070 <i>Z</i> = 1.478	<i>P</i> = 0.480 <i>Z</i> = 0.051	10
Age at weaning	<i>P</i> = 0.007 <i>Z</i> = 2.438	<i>P</i> = 0.038 <i>Z</i> = 1.775	17	<i>P</i> = 0.005 <i>Z</i> = 2.589	<i>P</i> = 0.036 <i>Z</i> = 1.804	12
Weight at weaning	–	–	–	<i>P</i> = 0.021 <i>Z</i> = 2.028	<i>P</i> = 0.199 <i>Z</i> = 0.845	7
Postnatal growth rate	–	–	–	<i>P</i> = 0.199 <i>Z</i> = 0.845	<i>P</i> = 0.199 <i>Z</i> = 0.845	7

too few data-points for strepsirhines to treat them separately. Nevertheless, the analyses showed that age and weight at weaning were significantly influenced by sexual selection so that more sexually selected species had a higher lactation investment than did less sexually selected species (Table 2; Fig. 2).

To check for possible additional effects of sexual selection that go above those of size, matched-pairs analyses of residual values, after effects of body weight had been removed, were conducted. These showed that there was an effect on age at weaning above that which would be expected by size alone (Table 2). Thus, there are additional effects of sexual selection on top of the influence of size.

The only offspring variable where sex-specific data was available was that of neonate weight (Smith & Leigh, 1998). Matched-pairs analyses were carried out on this data but these revealed no pattern for the primate order concerning male neonate weight (one-tailed Wilcoxon's matched pairs *P* = 0.163, *Z* = 0.980, *n* = 8) or neonate dimorphism (one-tailed Wilcoxon's matched pairs *P* = 0.163, *Z* = 0.980, *n* = 8). Carrying out this test using only the data that Smith & Leigh (1998) used in their own analyses (average weights calculated from

measurements of nine or more neonates for each sex) gave only three matched-pairs comparisons to work with which were too few to draw any meaningful conclusions, although all three were in the expected direction.

Why are females so small?

To investigate why female size does not increase isometrically with male size increase, I analysed the influence of female body weight on several female life-history variables. These analyses showed that larger size affects the key life-history characters determining female reproduction, age at first birth and the birth rate, negatively for all primates (Fig. 1; Table 3). In addition, the other investigated life-history characters were also negatively correlated with large body size (Table 3). Large size consequently increases the amount of time invested in each individual offspring.

Results from this analysis are roughly similar for haplorhines and strepsirhines, except that in strepsirhines the relationship between female body weight and number of offspring as well as maximum recorded life span were nonsignificant. Note, however, the low *R*² values for the relationship between female body weight

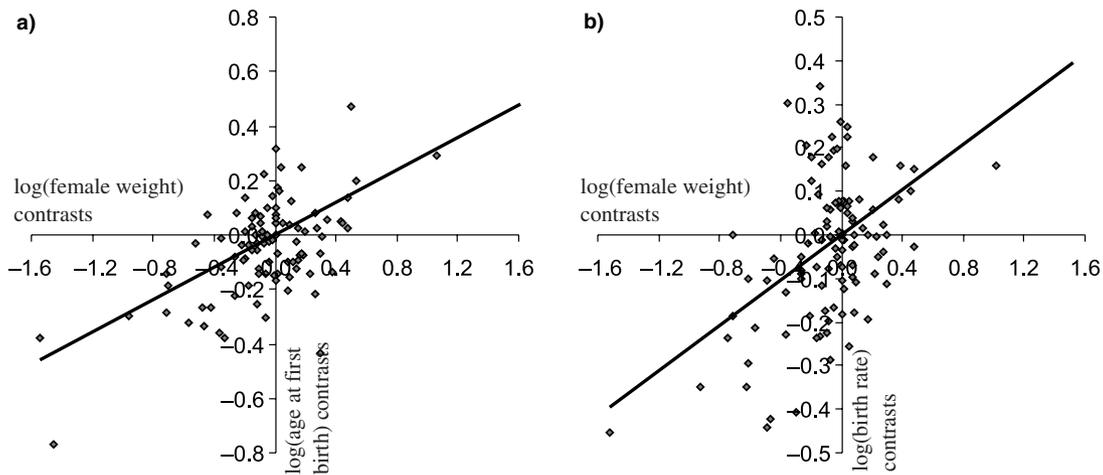


Fig. 1 Independent contrasts analyses on primates (strepsirhines and haplorhines) relating female body weight with (a) the age of female's first birth, and (b) the birth rate (the number of offspring per year for a mature individual). Both these life-history variables are significantly correlated with female body size.

Table 3 Results from regression analyses on independent contrasts concerning different female life-history traits regressed onto female weight for primates, haplorhines and strepsirhines. The two characters that are most important in determining female fecundity are given at the top of the table whereas their component parts, as well as the maximum recorded life-span, is given at the bottom. The relationships are highly significant for most variables which are given in bold, *n* refers to the number of contrasts used for the regressions.

Variable	Primates				Haplorhines				Strepsirhines			
	<i>b</i>	<i>R</i> ²	<i>P</i>	<i>n</i>	<i>b</i>	<i>R</i> ²	<i>P</i>	<i>n</i>	<i>b</i>	<i>R</i> ²	<i>P</i>	<i>n</i>
Age at first birth	0.298	0.359	0.000	99	0.302	0.353	0.000	75	0.282	0.391	0.001	23
Birth rate	-0.304	0.282	0.000	98	-0.308	0.319	0.000	75	-0.293	0.223	0.023	22
Age at sexual maturity	0.251	0.282	0.000	82	0.245	0.248	0.000	62	0.262	0.402	0.003	19
Gestation length	0.079	0.154	0.000	113	0.062	0.164	0.000	81	0.111	0.172	0.018	31
Offspring per litter	-0.049	0.060	0.005	131	-0.032	0.072	0.006	102	-0.088	0.078	0.144	28
Interbirth interval	0.260	0.260	0.000	107	0.293	0.309	0.000	82	0.192	0.160	0.042	24
Maximum life-span	0.161	0.141	0.000	101	0.201	0.184	0.000	77	0.081	0.060	0.249	23

and the number of offspring per litter in all cases. This is because of the fact that most primates have a litter size of one (Table 3).

To analyse if the pattern of highly significant correlations between female body weight and several female life-history variables possibly act as constraints on female size evolution, and thus can shed light on their part in the evolution of size dimorphism, matched-pairs analyses were carried out. As was the case previously, again this analysis unfortunately gave too few data-points for strepsirhines to treat them separately.

The comparisons on haplorhines as well as for all primates show, however, that one of the key life-history characters, the birth rate, is influenced by male intra-sexual selection so that females in more sexually selected species have a lower birth rate than do smaller species. Further tests show that this slower birth rate is because of a negative effect of sexual selection on the interbirth interval (Table 4).

To investigate if additional effects of sexual selection that go above those of size could be found, analyses of residual values after the effects of body weight had been removed were performed. These showed that there was an effect on birth rate above that which would be expected by body weight alone, again through the influence of the interbirth interval (Table 4). Thus, there are additional effects of sexual selection on female reproduction on top of the influence of size.

Discussion

Haplorhines

In haplorhine primates, sexual selection on males causes increases in the size not only of males but also of females (Lindénfors & Tullberg, 1998). This size increase for females in sexually selected species could not be shown to come as a result of more intense resource competition

Table 4 Results from matched-pairs comparisons concerning the influence of male intrasexual selection on several female life-history traits. Of the two most important life-history variables determining the rate of female reproduction – age at first birth and the birth rate – the birth rate, through the influence of the interbirth interval, is significantly longer in more sexually selected species. This is true even if size is corrected for. Significant values from the one-tailed Wilcoxon's matched pairs test are given in bold, whereas *n* refers to the number of independent comparisons.

Variable	Primates			Haplorhines		
	Size-dependent Wilcoxon's <i>P</i>	Residuals Wilcoxon's <i>P</i>	<i>n</i>	Size-dependent Wilcoxon's <i>P</i>	Residuals Wilcoxon's <i>P</i>	<i>n</i>
Age at first birth	<i>P</i> = 0.266 <i>Z</i> = 0.625	<i>P</i> = 0.455 <i>Z</i> = 0.114	15	<i>P</i> = 0.077 <i>Z</i> = 1.423	<i>P</i> = 0.187 <i>Z</i> = 0.889	11
Birth rate	<i>P</i> = 0.013 <i>Z</i> = 2.215	<i>P</i> = 0.030 <i>Z</i> = 1.874	15	<i>P</i> = 0.008 <i>Z</i> = 2.411	<i>P</i> = 0.027 <i>Z</i> = 1.922	13
Age at sexual maturity	<i>P</i> = 0.347 <i>Z</i> = 0.392	<i>P</i> = 0.291 <i>Z</i> = 0.549	12	<i>P</i> = 0.222 <i>Z</i> = 0.764	<i>P</i> = 0.323 <i>Z</i> = 0.459	10
Gestation length	<i>P</i> = 0.389 <i>Z</i> = 0.282	<i>P</i> = 0.359 <i>Z</i> = 0.717	19	<i>P</i> = 0.458 <i>Z</i> = 0.105	<i>P</i> = 0.232 <i>Z</i> = 0.734	13
Offspring per litter	<i>P</i> = 0.086 <i>Z</i> = 0.173	<i>P</i> = 0.341 <i>Z</i> = 0.411	20	<i>P</i> = 0.500 <i>Z</i> = 0.000	<i>P</i> = 0.187 <i>Z</i> = 0.879	16
Interbirth interval	<i>P</i> = 0.018 <i>Z</i> = 2.101	<i>P</i> = 0.035 <i>Z</i> = 1.817	15	<i>P</i> = 0.008 <i>Z</i> = 2.411	<i>P</i> = 0.027 <i>Z</i> = 1.922	13
Maximum life-span	<i>P</i> = 0.111 <i>Z</i> = 1.223	<i>P</i> = 0.275 <i>Z</i> = 0.596	14	<i>P</i> = 0.288 <i>Z</i> = 0.561	<i>P</i> = 0.361 <i>Z</i> = 0.356	11

in group-living species as group size is uncorrelated to female body weight. Neither is female body weight increase in sexually selected species correlated with giving birth to larger progeny. The age at weaning is, however, significantly higher in more sexually selected species, even when the effects of body weight are removed, indicating a higher postpartum energy investment in the offspring. Another possible alternative explanation to female size increase being correlated to sexual selection on males is, however, that female size increases because of a genetic correlation between the sexes concerning genes controlling size. This issue is discussed further below.

Body weight is in this study shown to be correlated with many life-history variables. This is a familiar picture where larger species have slower reproductive rates, but higher energy expenses per offspring, than do smaller species (Harvey *et al.*, 1987, 1989; Roff, 1992; Stearns, 1992). Here a potential antagonistic effect of male intrasexual competition, through its influence on size, on female reproductive rate was examined. A significant negative correlation between sexual selection and birth rate was found, through the influence on body weight. Adding to this, however, the birth rate was significantly slower in sexually selected species also when correcting for body weight. This slower birth rate is possibly a result of the higher weaning age described above.

Thus, it has been shown that sexual selection causes size increase in both sexes (Lindensfors & Tullberg, 1998), with the change in female size most probably caused by a larger postpartum investment in offspring (Table 2). I have furthermore shown that larger body size is correlated with decreased fecundity in females (Table 3) and

that there also is a negative interspecific correlation between sexual selection and female fecundity, both when correcting for body weight and when not (Table 4). These results taken together indicate that sexual selection and fecundity selection act antagonistically on size and consequently together cause sexual size dimorphism in haplorhine primates (Fig. 2).

Why are females so large?

Female size increase was hypothesized to come about through three possible processes. The first, that there is some factor that causes transitions in mating system, or at least a factor that is correlated with such transitions, was analysed indirectly through a possible influence of group size. The rationale behind this is elaborated upon in the Introduction. In any case, no such relationship was found. Other confounding factors than this are of course possible; diet, activity period or substrate, to name but a few that have not been analysed here. Although these may have substantial influence on body size, they are not in any consistent way correlated with mating system (personal observations), and were thus not included in this analysis.

The hypothesis that females in more sexually selected species would be larger because they were selected to produce larger male offspring, or even larger offspring in general, was analysed through several separate tests. These showed that no effects of sexual selection could be found for prenatal growth rate, average neonate weight or male neonate weight. Thus, no indications could be found that supported the notion of an increased energy investment before birth. Females instead probably make

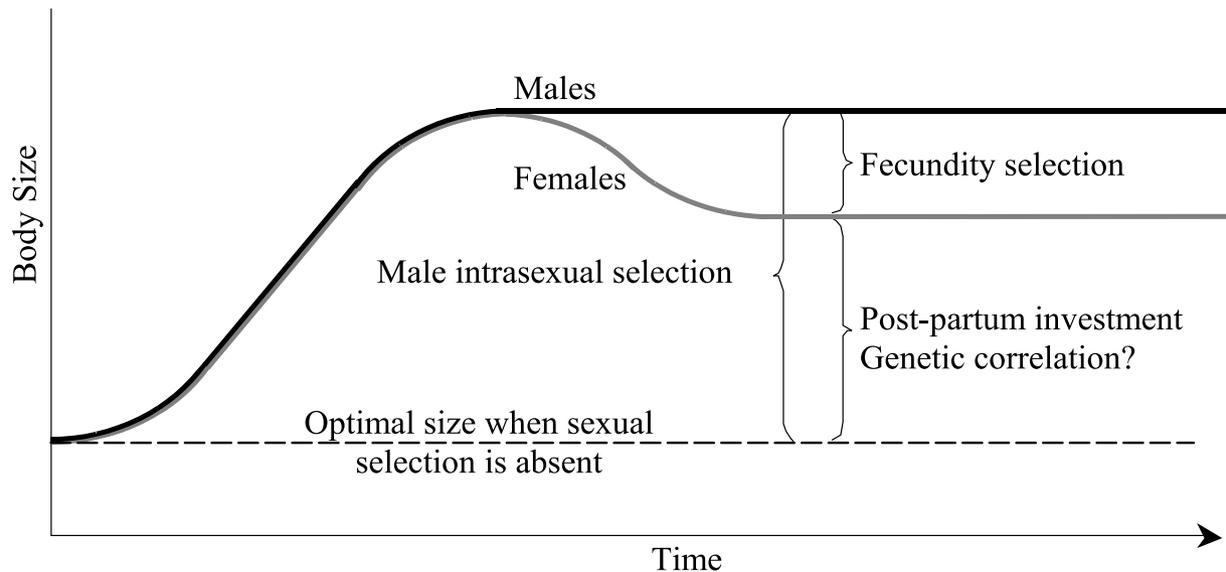


Fig. 2 An idealized graph of the evolution of sexual size dimorphism in haplorhine primates. Intrasexual competition, as indicated by mating systems, has in a previous study been shown to cause an increase in body size in males and also, but to a lesser degree, in females (Lindénfors & Tullberg, 1998). As Lande (1980, 1987) has modelled the process, female size increase can be the result of a genetic correlation between the sexes concerning size-controlling genes. Contrary to Lande's model, however, female size does not decrease to initial levels over time. The results of this study indicate that this probably is because of a higher postpartum investment, through a longer lactation period, in more sexually selected species. Fecundity selection is in this study shown to act as a constraint on female size increase. Sexual selection and fecundity selection thus act as antagonistic selection pressures on primate size. The results presented here indicate that these two selection factors are what cause sexual size dimorphism in haplorhine primates.

a larger reproductive investment in more sexually selected species *after* birth via a longer lactation period possibly resulting in a higher weaning weight. The postnatal growth rate, however, was not correlated with sexual selection, perhaps indicating that females in more sexually selected species have a longer energy investment period but not a higher energy investment rate.

The data available for weight at weaning were calculated from growth curves and not directly measured (Lee, 1999). It is thus possible that when more and better quality data becomes available for this variable, preferably sex-specific data, it will be possible to validate effects of sexual selection on weaning weight also when the effects of size are removed. That this would be expected is here indicated by the results on age at weaning. Until then, however, this remains a hypothesis. Also, better quality data on sex-specific neonate weights available in the future might show an effect of sexual selection on male birth weights. From the data currently available it certainly seems true in specific cases that more dimorphic species give birth to more dimorphic neonates (Smith & Leigh, 1998), but it appears not to be true that males are generally born larger in more sexually selected species.

Resources transferred during lactation are typically more energetically costly than the prenatal costs of gestation (Cameron, 1998) and it is also a general pattern

in mammals that female body mass is correlated to milk yield (Ofstedal, 1984). Thus, a longer suckling period could constitute a significant selection pressure on female size. Generally, larger mammal species are also more able to utilize energy reserves stored as body fat when lactating than smaller species who are more dependent on direct acquisition of resources during this period (Sadleir, 1984). This is another advantage of larger body size when the lactation period becomes prolonged. Sexual selection theory would predict, however, that the postpartum investment would be preferably made in male offspring (Trivers, 1972), but it is hard to say whether there are differences in maternal investment in male and female offspring when it comes to duration of suckling as there are no studies of sex-specific ages at weaning in primates. More and better quality data would aid in the resolution of this question.

A study on fallow-deer (Birgersson *et al.*, 1998) has shown that even when the time of suckling-bouts was held the same for both sexes, the suckling rate for male infants was higher than that of females. Thus, rearing large male offspring may be more energetically costly even if time spent on suckling does not differ between the sexes. In the present study there were, however, no detectable effects of sexual selection on the postnatal growth rate, as would then have been expected. Postnatal growth rate is, however, one of the variables with

the lowest sample size and it is possible that the data points are too few to detect any such pattern. Another obfuscation is that there might exist an extra investment in sexually dimorphic males after weaning through foraging assistance. All these topics warrant further investigation.

An alternative hypothesis explaining why female size increase is correlated to sexual selection on males is the idea that there is a genetic correlation between the sexes concerning size-controlling genes. As Lande (1980, 1987) has modelled the process, a decreased number of males participating in reproduction results in genes making successful males quickly increasing in the gene-pool, whether these genes are specific to males or not. The genetic basis of variation in metrical characters such as body size is usually polygenic (Lande, 1980 and references cited therein), so a correlated response in one sex to selection on the other is actually expected, but only initially as natural selection is expected to bring females back down to their initial, theoretically optimal size, eventually. The time required for this latter process of female size decrease could, however, according to Lande's model, be several orders of magnitude longer than the time required for the initial size increase. The potential for new adaptations pertaining to the temporarily larger female body size would therefore be large.

Empirical support for a genetic correlation in body size is available for several nonprimate species (*Drosophila*: Shaklee *et al.*, 1952; *Mus musculus*: Frankham, 1966; *Meleagris gallopavo*: Eisen & Hahnrahan, 1972; all cited in Andersson, 1994). Field studies of birds also point to genetic correlations (e.g. van Noordwijk *et al.*, 1980; Price, 1984; both cited in Andersson, 1994). Furthermore, an analysis of the genetic basis of human body size supports the existence of a genetic correlation by showing that the genetic covariances between male and female length are so high that population means of body length should respond 60 times as rapidly as population means of length dimorphism if these two selection forces were of equal strength (Rogers & Mukherjee, 1992). Thus, assuming that the human genetic makeup is not too different from that of other primates, female size will increase in sexually selected species even if it means lower reproductive rates. The observed increase of female size in sexually selected species may thus represent a shift of focus towards a more male-biased genetic makeup of the species (e.g. Rice & Chippindale, 2001; but see Rice, 1984; Shaw *et al.*, 1995).

Other genetic changes can, however, significantly speed up the evolution of sexual size dimorphism. A single factor that stops growth early in females is sufficient. Such modifier genes altering either rate or duration would be optimally placed on the sex-chromosomes (Rice, 1984). Genetic data show that the y-chromosome in primates carries a number of genes of importance in sexual selection (Roldan & Gomiendo, 1999).

There are also other indications that modifier genes, whether on the sex chromosome or not, are present in at least some species. For primates it is reported that the female brain to body size ratio in sexually selected species is larger than expected from body size alone (Willner & Martin, 1985). As the brain ceases growing earlier in the ontogeny than the body, one explanation for this pattern could be that females in these species follow the same growth curves as males, but stopped short of completion. This is not the case, however, in all haplorhine primates, as there also are studies showing that some of the dimorphism is because of differences in growth-rates between the sexes, not only growth duration (Leigh, 1992, 1995; Leigh & Shea, 1995, 1996).

Why are females so small?

It is of course still important for a female to have more offspring than her competitors, which is the probable reason why dimorphism eventually evolves. This study indicates that the effects larger size has on female fecundity constitute a selection pressure that can account for why sexual size dimorphism evolves in sexually selected species, and not only equally large size for both sexes. However, the evolution of dimorphism is a much slower process than the initial size increase (Lande, 1980, 1987; Lande & Arnold, 1983; but see Shaw *et al.*, 1995). Thus, the final degree of size dimorphism may not only be a product of the intensity of sexual selection, fecundity selection and the genetic correlation, but also of time. The much longer time-span of female size decrease might, however, be long enough for new adaptations to the larger size to evolve in females and thus 'freeze' their size to one larger than their initial.

Observe that the results presented here do not result in the prediction that smaller females will have higher reproductive rate in *within*-species studies. Although there is widespread acceptance for a trade-off between investment in body size and investment in reproductive output, maternal effects and environmental correlates can still make reproductive success vary so that larger females will be more fecund (e.g. Stearns, 1992; Charnov, 1993). This can be true even if genetic control of size is additive, which is probable (see Futuyma, 1998, p. 430, for a brief discussion of this topic). Environmental and heritable variation in female size could thus lead to different expectations concerning their reproductive output. In fact, if the variance in fitness as a result of environmental effects is larger than the variance because of genetic effects, this alone can mask genetic influence on fitness (Stearns, 1992, p. 81).

Strepsirhines

One of the great puzzles in primate size evolution is the low degree of sexual size dimorphism in sexually selected strepsirhines. Although roughly two-thirds of

the strepsirhines are polygynous, the same proportion as in haplorhines, dimorphism is low, lacking or, in some cases, even reversed. A number of hypotheses have been forwarded to explain this pattern (see, e.g. Kappeler, 1990; van Schaik & Kappeler, 1996 for brief reviews).

All lorises are polygynous and this is also the group within the strepsirhines where one finds most instances of size dimorphism, however, small. But lorises are nocturnal species that live solitary lives. They are polygynous only in the sense that male territories overlap with several female territories. Thus, the comparatively lower degree of sexual selection in lorises somewhat matches the observed degree of dimorphism, as compared with the polygynous haplorhines. The real puzzle does not concern them, but instead the diurnal sexually selected lemurs of Madagascar.

Kappeler (1990) has proposed, when reviewing the issue, that of all the proposed causes of strepsirhine monomorphism, a combination of small body size, fecundity selection on females, and selection for male agility rather than large size are the probable causes that explain the lack of male-biased size dimorphism. Small body size is, however, a cause contradicted by results in Lindenfors & Tullberg (1998) as there is no automatic allometric relationship between body size and sexual size dimorphism in primates. Also, fecundity selection is shown in the present study to select for smaller size, not larger. Thus, combining Kappeler's (1990) results with those of Lindenfors & Tullberg (1998) and the present study leaves selection for male agility as the only factor left to explain strepsirhine monomorphism in sexually selected species.

However, van Schaik & Kappeler (1996) have researched the puzzle further and forwarded the hypothesis that recent ecological changes on Madagascar, in particular the demise of large diurnal raptors, have produced a mismatch between current activity periods and adaptations to those activity periods. Their conclusion is that the social systems of non-nocturnal lemurs are best considered as formed by species adapted to live in pairs, as nocturnal lemur species commonly do. Thus the change in social system has been recent, and selection has not had time to affect body size. There is an 'evolutionary disequilibrium' between current selection pressures and the effect of those selection pressures. This hypothesis, however, needs more work in order to be evaluated in full.

Connections to earlier research

Many other factors also affect female size in haplorhines, e.g. size adaptations to different environmental factors, and consequently also the whole life-history variable complex. Small size might be important, for example, in neotropical primate species as they need to venture out on thin branches to forage (Harvey *et al.*, 1987), whereas large size might be important in terrestrial primate species as it gives increased oppor-

tunity for predator defence (Leutenegger & Kelly, 1977; Rowell & Chism, 1986). No such factor is consistently correlated with mating system, however. Similarly, life-history variables also vary a lot for other reasons besides selection on size (Roff, 1992; Stearns, 1992; Charnov, 1993), so there is still a significant amount of variation in female reproductive rate left to be explained besides the effects of sexual selection described in this study.

A previous study by Carranza (1996) has shown that sexual size dimorphism has adverse effects on litter size in mammals, a life-history consequence similar to the consequences of sexual selection and large size shown in the present study. Thus, increases in male body weight relative to female body weight were correlated with reductions in the number of offspring per litter. Most primates, however, all deliver a single offspring per litter, and there is therefore no similar pattern to be found in this order. In fact, twinning in haplorhines is a secondary adaptation (e.g. Dunbar, 1995; Ah-King & Tullberg, 2000). A similar negative effect of male intrasexual competition could nevertheless here be shown in primates for the birth rate, a variable crucial for reproductive output. This, taken together with Carranza's (1996) results concerning litter size, suggests a possible underlying general pattern in mammals of adverse influence of male competition on female reproduction, even above the effects of size. The probable underlying cause of this is an increased investment in offspring in sexually selected species as is indicated in this study by the effects of sexual selection on the duration of suckling.

The patterns reported here can also be viewed in a larger context as examples of a sexually antagonistic intragenomic conflict where traits are advantageous for one sex, whilst detrimental for the other (Rice, 1992; Arnqvist, 1994; Arnqvist & Rowe, 1995; Rice & Holland, 1997; Holland & Rice, 1998; Brooks & Jennions, 1999; Rice & Chippindale, 2001). This process is usually attributed to the discord in sexual organisms between females, who primarily invest in offspring, and males, who primarily invest in fertilization opportunities. It is often the case in such studies that the effect for males of having the trait is positive but the effect for the species (through effects on the females) is negative (Holland & Rice, 1998; Rice & Chippindale, 2001). Likewise, in this study, the effect of larger size for females is negative, resulting in a slower reproductive rate. Stronger selection on males than females, such as the case reported here, is also a probable explanation behind the phenomena that genes for male reproductive success evolve faster than genes for other types of characters (Wykoff *et al.*, 2000).

The effects of body size are the important factors found in the present study, even if the results also indicate an interesting cost of sexual selection above that of body size. But an important final point is the one expressed by Fairbairn (1997, p. 672): 'Researchers who remove body

size effects before testing functional hypotheses or include body size as one of a suite of functional variables predicting SSD may therefore be removing much of the variance that should be explained by their adaptive hypotheses.' One cannot hope to understand sexual selection for sexual size dimorphism without taking body size into account. To only correct for size is to miss the point.

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Supplementary material

The following material is available from <http://www.blackwell-science.com/products/journals/suppmat/JEB/JEB422/JEB422sm.htm>:

Appendix 2

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Appendix 1 Matched-pair comparison of sister taxa.

Strepsirhini

1. More polygynous (MP): *Lemur catta*
Less polygynous (LP): *Varecia variegata*
2. MP: *Pteropus coronatus*
LP: *Pteropus rubriventer*
3. MP: *Pteropus fulvus*, *P. macaco*
LP: *Pteropus mongoz*
4. MP: *Propithecus verreauxi*
LP: *Indri indri*
5. MP: *Propithecus tattersalli*
LP: *Avahi laniger*
6. MP: *Lepilemur mustelinus*, *Daubentonia madagascarensis*
LP: *Hapalemur griseus*
7. MP: *Allocebus trichotis*
LP: *Phaner furcifer*

Haplorhini

8. MP: *Tarsius bancanus*
LP: *Tarsius spectrum*
9. MP: *Saguinus nigricollis*
LP: *Saguinus fuscicollis*
10. MP: *Cebus capucinus*
LP: *Cebus albifrons*
11. MP: *Cebus olivaceus*, *C. apella*, *Saimiri boliviensis*, *S. oerstedii*, *S. sciureus*
LP: *Callithrix humeralifer*, *C. jacchus*, *C. pygmaea*, *Leontopithecus rosalia*, *Saguinus midas*,
S. oedipus, *S. imperator*, *S. labiatus*, *S. mystax*, *Callimico goeldii*
12. MP: *Cacajao calvus*, *C. rubicundus*, *Chiropotes albinasus*, *C. satanas*
LP: *Pithecia aequatorialis*, *P. albicans*, *P. irrorata*, *P. monachus*, *P. pithecia*
13. MP: *Alouatta caraya*, *A. fusca*, *A. palliata*, *A. seniculus*, *A. villosa*, *Ateles belzebuth*, *A. fusciceps*, *A. geoffroyi*, *A. paniscus*,
Lagothrix flavicauda, *L. lagotricha*, *Brachyteles arachnoides*
LP: *Aotus trivirgatus*, *A. azarae*
14. MP: *Mandrillus leucophaeus*, *M. sphinx*
LP: *Cercocebus galeritus*, *C. torquatus*
15. MP: *Papio hamadryas*
LP: *Papio anubis*, *P. papio*, *P. cynocephalus*, *P. ursinus*
16. MP: *Theropithecus gelada*
LP: *Cercocebus albigena*, *C. aterimus*
17. MP: *Cercopithecus lhoesti*
LP: *Cercopithecus aethiops*
18. MP: *Cercopithecus campbelli*, *C. mona*, *C. denti*, *C. wolfi*, *C. pogonias*
LP: *Cercopithecus neglectus*
19. MP: *Cercopithecus ascanius*, *C. cephus*, *C. erythrotis*, *C. erythrogaster*, *C. petaurista*, *C. mitis*, *C. nictitans*, *C. diana*,
Erythrocebus patas
LP: *Miopithecus talapoin*
20. MP: *Nasalis larvatus*
LP: *Simias concolor*
21. MP: *Presbytis comata*, *P. frontata*, *P. melalophos*, *P. rubicunda*, *P. obscura*, *P. pileatus*
LP: *Presbytis potenziani*
22. MP: *Pongo pygmaeus*, *Gorilla gorilla*
LP: *Hylobates agilis*, *H. lar*, *H. muelleri*, *H. moloch*, *H. pileatus*, *H. klossii*, *H. hoolock*, *H. syndactylus*, *H. concolor*
23. MP: *Pan paniscus*, *P. troglodytes*
LP: *Homo sapiens*