Phylogenetic Analyses of Dimorphism in Primates: Evidence for Stronger Selection on Canine Size Than on Body Size

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ABSTRACT   Phylogenetic comparative methods were used to analyze the consequences of sexual selection on canine size and canine size dimorphism in primates. Our analyses of previously published body mass and canine size data revealed that the degree of sexual selection is correlated with canine size dimorphism, as well as with canine size in both sexes, in haplorhine but not in strepsirrhine primates. Consistent with these results, male and female canine size was found to be highly correlated in all primates. Since canine dimorphism and canine size in both sexes in haplorhines were found to be not only related to mating system but also to body size and body size dimorphism (characters which are also subject to or the result of sexual selection), it was not apparent whether the degree of canine dimorphism is the result of sexual selection on canine size itself, or whether canine dimorphism is instead a consequence of selection on body size, or vice versa. To distinguish among these possibil-ities, we conducted matched-pairs analyses on canine size after correcting for the effects of body size. These tests revealed significant effects of sexual selection on relative canine size, indicating that canine size is more important in haplorhine male-male competition than body size. Fur-ther analyses showed, however, that it was not possible to detect any evolutionary lag between canine size and body size, or between canine size dimorphism and body size dimorphism. Additional support for the notion of special selection on canine size consisted of allometric relation-ships in haplorhines between canine size and canine size dimorphism in males, as well as between canine size di-morphism and body size dimorphism. In conclusion, these analyses revealed that the effects of sexual selection on canine size are stronger than those on body size, perhaps indicating that canines are more important than body size in haplorhine male-male competition. Am J Phys Anthro-pol 130:50–59, 2006.   © 2005 Wiley-Liss, Inc.

Canine size dimorphism is a common occurrence among primates, with males in general having larger canines than females (Plavcan, 2004; Appendix A). For example, in many baboons (*Papio* sp.) and macaques (*Macaca* sp.), male canines are more than twice as large as those of females. However, species in which females have larger canines also exist, e.g., the eastern brown mouse lemur (*Microcebus rufus*), but this is rare. Within primates, there are some general differences between taxonomic sub-groups, in that canine dimorphism is most common among haplorhine primates (more pronounced in catarrhines than in platyrrhines), while most strepsirrhine primates have either monomorphic or only slightly dimorphic ca-nines (Plavcan et al., 1995; Kappeler, 1996; Plavcan, 2001).

Canine size dimorphism in anthropoids is typically attributed to sexual selection (Leutenegger and Kelly, 1977; Harvey et al., 1978; Leutenegger, 1982; Leutenegger and Cheverud, 1982, 1985; Kay et al., 1988; Greenfield, 1992; Plavcan and van Schaik, 1992; Plavcan, 1993, 1999, 2001; Plavcan et al., 1995; Jablonski and Ruliang, 1995; Hayes et al., 1996). Several researchers used mating sys-tem as an indicator of the intensity of intrasexual selec-tion, and demonstrated that canine size dimorphism is more pronounced in polygynous species (Leutenegger and Kelly, 1977; Harvey et al., 1978; Leutenegger, 1982; Leute-negger and Cheverud, 1982, 1985). An alternative meas-ure of the intensity of sexual selection (competition levels), facilitating tests of both intra- and intersexual competi-tion, yielded similar conclusions (Kay et al., 1988; Green-field, 1992; Plavcan and van Schaik, 1992; Plavcan, 1993, 1999, 2004; Plavcan et al., 1995).

Given the fact that sexual selection in species with intense male-male competition typically has effects on male traits (Darwin, 1871; Andersson, 1994), the expecta-tion is that male canines are larger in more polygynous species, while the same should not be true for females. If canine size is a polygenic and autosomally coded trait, however, selection for larger male canines should also result in the expression of larger canines in females (Maynard Smith, 1978; Lande, 1980, 1987; Lande and Arnold, 1983; Greenfield, 1992, 1996).

Even though sexual selection is correlated with canine dimorphism in haplorhines, the same relationship has not been found in strepsirrhine primates (Plavcan et al., 1995; Kappeler, 1996). This may be the result of weak intrasexual selection on canines, if canine size, for exam-

ple, is of little importance in male-male competition in strepsirrhines (Kappeler, 1996). Alternatively, canine size in strepsirrhines may be a highly genetically correlated character, thus constraining the expression of canine dimorphism (Plavcan, 1998).

Besides sexual selection, there are several alternative (if not mutually exclusive) hypotheses for how canine dimorphism has evolved. Examples include predator defense (Harvey et al., 1978; Hayes et al., 1996; Plavcan and van Schaik, 1992; Plavcan et al., 1995), diet (Hayes et al., 1996), activity rhythm (Leutenegger and Cheverud, 1982, 1985), and allometric ties with body or canine size (Leutenegger and Cheverud, 1982, 1985). Also, the results of Plavcan et al. (1995) indicated that the intensity of intrasexual competition not only in males, but also in females, needs to be considered to explain the degree of canine dimorphism. In species where the outcomes of fights are typically decided by coalitions between individuals, however, canine dimorphism was found to be low, in spite of intensive competition (Plavcan et al., 1995).

Canine size does not seem to be free to vary independently of body size. There are several different ways to highlight this relationship. For example, canine size was shown to covary with body size (Harvey et al., 1978; Gingerich and Smith, 1985; Greenfield, 1992; Plavcan, 1993). Also, canine dimorphism covaries with body size dimorphism (Leutenegger and Kelly, 1977; Leutenegger, 1982; Plavcan and van Schaik, 1992; Kappeler, 1996) and body size in anthropoids (Plavcan and Schaik, 1992), but not in strepsirrhines (Kappeler, 1996). Given these correlations, an obvious question arises of whether there are any effects of sexual selection that are unique to canines, or whether all effects of sexual selection are shared with body size evolution.

To investigate this question, we conducted several comparative analyses of canine size and body size evolution. Our general aim was to examine correlations between sexual selection and canine size evolution that could not be attributed to sexual selection on body size in general. We realize, however, that the converse reasoning can hold true just as well: any correlations between effects of sexual selection on body size and canine size evolution can (theoretically) equally well be attributed to sexual selection solely on the canines and a correlated response in body size. Alternatively, sexual selection may act equally strongly on canine size as on body size.

Hence, our tests first centered on analyzing whether effects of sexual selection previously shown for body size evolution (e.g., Lindenfors and Tullberg, 1998) could be replicated for canine size. Primarily, three questions were investigated: 1) if detectable effects of sexual selection on canines are present in haplorhine primates and absent in strepsirrhine primates, 2) if there is an allometric relationship between canine size and canine size dimorphism, and 3) whether the intensity of sexual selection is correlated with both canine size dimorphism and canine size *per se* in both sexes.

We also investigated whether some effects of sexual selection are uniquely attributable to selection on either canines or body size. This could be indicated by, for example, 1) if relative canine size could be found to be larger (indicating stronger selection on canine size) or smaller (indicating stronger selection on body size) in species with more intense sexual selection, or 2) if we could identify an evolutionary lag between canine size

and body size, or between canine size dimorphism and body size dimorphism, indicating that changes in one trait lag behind changes in the other trait. The presence of the latter pattern would be consistent with the interpretation that one trait is the primary target of selection and not the other, but the evidence would in this case only be circumstantial.

MATERIALS AND METHODS

The phylogeny used in all analyses utilizing branch lengths was that of Purvis (1995), which includes node dates, while the undated phylogeny of Purvis and Webster (1999) was used for matched-pairs comparisons (see below). Both these phylogenies were made with a "supertree" technique combining earlier phylogenies based on both molecular and morphological data, making them the phylogenies supported by the most comprehensive data set. Mating systems were used to estimate degree of sexual selection, classifying species into three groups: unimale (UM), multimale (MM), and monogamous (Mon), where UM species are expected to be subject to the most intense sexual selection, whereas Mon species are expected to be at the other end of the scale. Mating systems were taken from Lindenfors (2002), except for *Lepilemur mustelinus* (unknown: Zinner et al., 2003), *Cheirogaleus medius* (Mon: Müller, 1998) and *Propithecus diadema* (Mon: Pochron et al., 2002).

Measurements of canine dimensions were taken from Kappeler (1996), Plavcan (1999), and Swindler (2002), whereas data on body mass were from Smith and Jungers (1997) (Appendix A). The measure of dimorphism used throughout this paper was male size/female size. All continuous variables, including these ratios, were $\log_{10}$-transformed prior to analysis. Since haplorhines and strepsirrhines were previously shown to respond very differently to sexual selection (Kappeler, 1990, 1991, 1996; Plavcan et al., 1995; Lindenfors and Tullberg, 1998), these two groups were analyzed separately.

Canine measurements are given in the literature as 1) length, defined as the greatest mesiodistal diameter of the maxillary canine; 2) width, defined as the greatest buccolingual diameter perpendicular to the mesiodistal length at the base of the tooth; and 3) height, defined as the measurement from the apex to the cementum-enamel junction on the mesiobuccal face of the tooth. From these three measurements, an estimated volume was calculated using the formula of an elliptic cone: volume $= \frac{1}{3} \cdot$ height $\cdot \frac{1}{2} \cdot$ length $\cdot \frac{1}{2} \cdot$ width $\cdot \pi$. This measurement was deemed the best possible estimate of canine size (capturing in one number variation in all the three others), and also having the benefit that it varies on the same scale as body size, making it possible to correct directly for body mass. Independent contrast analyses showed, however, that all measures of canine size were highly correlated with each other ($P < 0.001$). Also, we here report results using all these measures of the canines, except in cases where the analyses also involve body mass, because only canine volume varies on the same scale as body mass. The results using these different measures of canine size all point to the same general conclusions.

Mating system classifications were preferred over more fine-grained measures of the intensity of intrasexual selection, such as operational sex ratio (Mitani et al., 1996), harem size (Lindenfors et al., 2002), or competition levels (Plavcan and van Schaik, 1992; Plavcan et al., 1995), as operational sex ratios and harem sizes are avail-

able only for a limited number of species, and because concerns about the *ad hoc* nature of some competition level classifications remain unresolved (Lindenfors, 2002).

Since related species in a branching phylogeny cannot be treated as independent units of information in statistical tests, the use of an accurate method to analyze comparative data, correcting for phylogeny, is of great importance (Felsenstein, 1985; Harvey and Pagel, 1991). In this study, three phylogenetic comparative methods were used: matched-pairs comparisons (Møller and Birkhead, 1992; Wickman, 1992), independent contrasts (Felsenstein, 1985), and the comparative method of Deaner and Nunn (1999) for detecting evolutionary lag. These methods are all based on the insight that even though a species is not an independent testimony of its evolutionary history, the difference ("contrast") between two closely related species, or species groups, is. This difference between the two most closely related species, or species groups, has evolved since their last common ancestor and is therefore independent from changes in the rest of the phylogeny.

Matched-pairs comparisons (Møller and Birkhead, 1992; Wickman, 1992) were used to analyze the effects of sexual selection on canine size and canine size dimorphism. Mating system (used as an indicator of degree of sexual selection) was used to divide species into two groups: "more polygynous" and "less polygynous." Since a multimale species theoretically is more polygynous than a monogamous species while less polygynous than a unimale species, multimale species could end up on different sides of these comparisons, depending on the mating system of the species, or species group, to which they were compared (Lindenfors and Tullberg, 1998; Lindenfors, 2002; Lindenfors et al., 2002) (Appendix B). When a group contained more than one species, the average value of those species was used (Møller and Birkhead, 1992; Wickman, 1992).

Phylogenetic independent contrasts (Felsenstein, 1985), as implemented in the program PDAP, were used to analyze relationships between two continuous variables. Branch lengths were set to arbitrary lengths as described by Grafen (1989), and then $\log_{10}$-transformed to receive equal weighting in subsequent analyses. This standardization of branch lengths best transformed the contrasts adequately for statistical purposes (Garland et al., 1992). Results using different branch lengths, such as those given in Purvis (1995), did not differ markedly from the results presented here. Nevertheless, the branch length adjustments described above removed some trends caused by unjustifiably large differences at the basal parts of the phylogeny (Garland, 1992; Garland et al., 1993). All contrasts were statistically analyzed with major axis regressions through the origin, as we had no a priori expectations about causal relationships for these analyses.

We used the phylogenetic method described in Deaner and Nunn (1999) to test for evolutionary lag in haplorhines between canine volume and body mass, as well as between canine volume dimorphism and body mass dimorphism. The method works by first calculating independent contrasts using only contrasts involving extant species. Only these contrasts are used, because the method relies heavily on accurate estimates of time since divergence and equal amounts of evolutionary change on both branches of each contrast. Contrasts were then "positivized," where one first gives positive signs to all contrasts on the X-axis, simultaneously switching the sign, if needed, of the contrasts on the Y-axis (Garland et al., 1992). Residuals are calculated from a regression through the origin and then regressed on time

since the taxa diverged. An evolutionary lag is indicated by larger residuals on contrasts characterized by longer branches, which indicates that relative to changes in the X-variable, the Y-variable increases when there is more time available for change to take place. In other words, we tested whether the Y-variable is larger than expected on longer branches and smaller than expected on shorter branches. For a more detailed description of the test, see Deaner and Nunn (1999).

RESULTS
Matched-pairs analyses

In total, five matched pairs for strepsirrhines and 11 for haplorhines were available for comparison (Appendix B). Of these, all of the strepsirhine contrasts were between polygynous and monogamous species, while 3 of the 11 haplorhine contrasts were between polygynous species (i.e., multimale vs. unimale; pairs 4–6 in Appendix B). In all results of the matched-pairs analyses presented below, these three comparisons were in the expected direction as relating to the hypotheses, indicating that the degree of sexual selection on canines differs within polygynous species and not, as sometimes suggested (e.g., Leutenegger and Kelly, 1977; Harvey et al., 1978; Plavcan, 2004), only between monogamous and polygynous species. Using mating system as indicative of sexual selection only gives us three data points with which to back his pattern up, which is too low a number for any statistical backing of this in the current study. However, Mitani et al. (1996) showed the existence of a significant effect of sexual selection on body size also within polygynous species. We thus find no theoretical or empirical reason not to include the comparisons between polygynous species.

Matched-pairs comparisons revealed significant differences in canine dimorphism in haplorhines between species classified as "more polygynous" and those classified as "less polygynous" (Fig. 1). In strepsirrhines, however, "more polygynous" species did not exhibit more canine dimorphism than "less polygynous" species (Table 1).
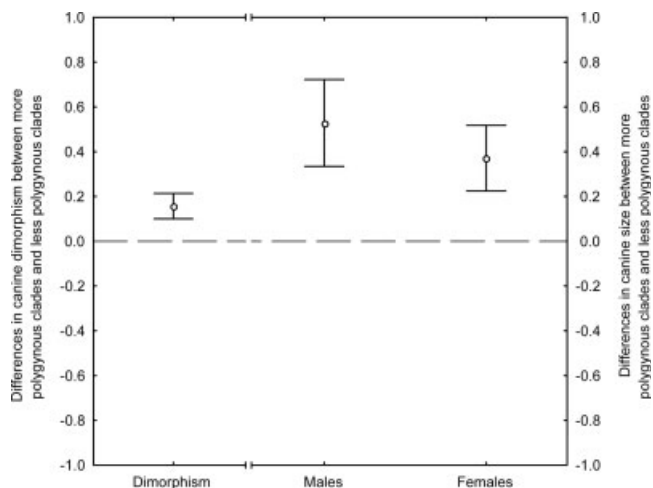
Fig. 1. Matched-pairs comparisons of relative canine volume in Haplorhini. Values represent means ± SE of differences between "more polygynous" clades and "less polygynous" clades in canine size dimorphism and canine size of males and females. Species in "more polygynous" clades are significantly more dimorphic in canine size than species in their "less polygynous" sister clades. Species in "more polygynous" clades also have significantly larger canines in both sexes.

TABLE 1. Results of matched-pairs analyses on haplorhines (n = 11) and strepsirrhines (n = 5)[1]

	Canine dimorphism				Male canine volume				Female canine volume			
	Vol	MD	Hgt	BL	Vol	MD	Hgt	BL	Vol	MD	Hgt	BL
Strepsirrhines	0.357	0.320	0.340	0.582	0.265	0.335	0.372	0.171	0.217	0.282	0.309	0.124
Haplorhines	0.009	0.000	0.007	0.011	0.006	0.008	0.005	0.011	0.012	0.010	0.031	0.024

[1] Vol, volume; MD, mesiodistal length; Hgt, height; BL, buccolingual width. All numbers are *P*-values from paired *t*-tests. Haplorhine species classified as "more polygynous" because of their mating system and phylogenetic placement exhibit significantly higher canine dimorphism, as well as larger male and female canines, than those designated as "less polygynous." None of this is true for strepsirrhines, however.

TABLE 2. Results of independent contrast analyses of male and female canine measures[1]

	Volume	Mesiodistal length	Height	Buccolingual width
Strepsirrhines	b = 1.020	b = 1.048	b = 1.039	b = 0.970
	$R^2 = 0.936$	$R^2 = 0.945$	$R^2 = 0.915$	$R^2 = 0.932$
	n = 28	n = 28	n = 28	n = 28
	$P_0 < 0.001$	$P_0 < 0.001$	$P_0 < 0.001$	$P_0 < 0.001$
	$P_1 = 0.704$	$P_1 = 0.330$	$P_1 = 0.526$	$P_1 = 0.566$
Haplorhines	b = 1.386	b = 1.287	b = 1.532	b = 1.301
	$R^2 = 0.807$	$R^2 = 0.837$	$R^2 = 0.620$	$R^2 = 0.816$
	n = 74	n = 79	n = 74	n = 79
	$P_0 < 0.001$	$P_0 < 0.001$	$P_0 < 0.001$	$P_0 < 0.001$
	$P_1 < 0.001$	$P_1 < 0.001$	$P_1 < 0.001$	$P_1 < 0.001$

[1] These revealed that male and female canine sizes are significantly correlated in both strepsirrhines and haplorhines. Only in haplorhines, however, are slopes of these relationships significantly different from slopes of 1.0, indicating that in haplorhines, canine dimorphism increases with increasing canine size. P_0 = significance value when testing for difference with slope of 0.0. P_1 = significance value when testing for difference with slope of 1.0.

Separate analyses of each sex in haplorhines similarly revealed that both males and females have larger canines in "more polygynous" compared to "less polygynous" clades (Fig. 1). Replicating the pattern for size dimorphism, however, neither strepsirrhine males nor females exhibited larger canines in "more polygynous" clades (Table 1).

Separate matched-pairs analyses of each sex in haplorhines revealed that males, but not females, had larger relative canine size (canine volume/body mass) in "more polygynous" compared to "less polygynous" clades (paired *t*-test, males, $P = 0.046$; females, $P = 0.468$; n = 11). As before, no effects of sexual selection could be found in strepsirrhine primates (males, $P = 0.458$; females, $P = 0.845$; n = 5).

Independent contrast analyses

Independent contrast analyses on canine volumes revealed that male and female canine size is correlated in both strepsirrhines and haplorhines. It is only in haplorhines, however, that canine size dimorphism increases with increasing canine size, i.e., has a regression slope significantly larger than 1.0, while the same is not true for strepsirrhines (Table 2, Fig. 2).

Further contrast analyses revealed that canine volume is significantly correlated with body size in both males and females in haplorhines (males: b = 1.381, $R^2 = 0.677$, $P < 0.001$; females: b = 1.249, $R^2 = 0.607$, $P < 0.001$; n = 71) and in strepsirrhines (males: b = 1.138, $R^2 = 0.821$, $P < 0.001$; females: b = 1.100, $R^2 = 0.806$, $P < 0.001$; n = 27) (Fig. 3). While the slopes for strepsirrhines scaled isometrically ($P > 0.05$), the slope of male canine size on male body size in haplorhines was significantly different from a slope of 1 ($P < 0.0002$), as was female canine size on female body size ($P = 0.05$).

Independent contrast analyses on canine size dimorphism and body size dimorphism showed, however, that canine size dimorphism is correlated with body mass dimorphism in haplorhines (b = 2.551, $R^2 = 0.408$, $P < 0.001$, n = 71) (Fig. 4), but not in strepsirrhines ($P > 0.05$, n = 27). Moreover, in haplorhines, canine size dimorphism increased significantly with increasing body mass dimorphism, in that the regression line of canine dimorphism on body size dimorphism differs significantly from a slope of 1 ($P < 0.001$).

Evolutionary lag

In total, 22 contrasts involving extant species were available in haplorhines to investigate evolutionary lag. From these contrasts, residuals of canine size were calculated from the regression of canine volume on body size. However, these canine volume residuals were not correlated with divergence date. Thus, canine size was not found to lag behind body size evolution (males, $P = 0.420$; females, $P = 0.212$). The analyses were repeated, testing the reversed scenario. Here, body size residuals were calculated from a regression of body size on canine size. Consistent with the results above, however, body size was not found to lag behind canine size evolution (males, $P = 0.967$; females, $P = 0.902$).

For examining whether canine size dimorphism possibly lags behind body size dimorphism, 22 contrasts involving extant species were again available for analyses. From these contrasts, canine volume size dimorphism residuals were calculated from the regression of canine size dimorphism on body size dimorphism. No evolutionary lag could be detected between the two variables ($P = 0.474$). These analyses were repeated, with body size dimorphism as the dependent variable. The resulting body size dimorphism residuals were again uncorrelated with divergence date ($P = 0.501$).

DISCUSSION

Canine size dimorphism was found to be larger in more polygynous clades, as was both male and female canine
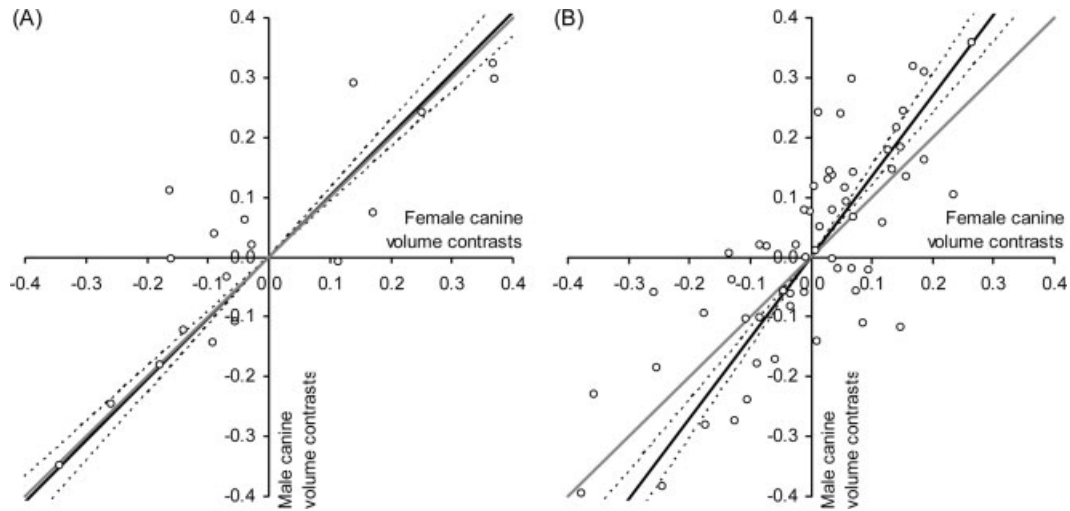
Fig. 2. Relationship between independent contrasts in male and female canine volume for (**A**) strepsirrhines and (**B**) haplorhines. Canine size evolution is highly correlated between males and females across all primates. One data point in graph represents an independent contrast, while dashed lines show 95% confidence intervals, which overlap with a slope of 1.0 (grey lines) in strepsirrhines, but not in haplorhines. Thus, in Haplorhini, canine size dimorphism increases with increased canine size.
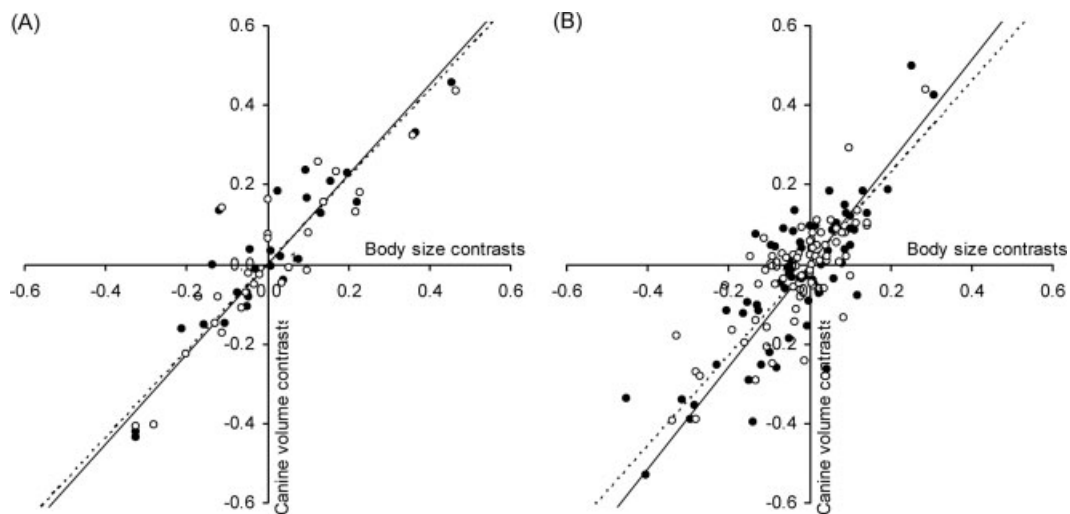

Fig. 3. Relationship between contrasts in body size and canine volume in males (solid circles and solid lines) and females (open circles and dashed lines) in (**A**) strepsirrhines and (**B**) haplorhines. One data point in graph represents an independent contrast. Canine volume is significantly correlated with body size across all primates in both sexes. Slopes of male and female canine size on male and female body size, respectively, in haplorhines were significantly different from a slope of 1.0.

size. This has resulted in an allometric relationship between male and female canine size. As is the case for body size (Kappeler, 1990, 1991; Lindenfors and Tullberg, 1998), however, these effects of sexual selection could only be found in haplorhine primates, but not in strepsirrhines.

Canine size was significantly correlated with body size in both sexes, although the relationship was allometric for both sexes in haplorhines and isometric in strepsirrhines. Also, canine dimorphism was significantly correlated with body size dimorphism, the relationship again being allometric in haplorhines and isometric in strepsirrhines. Also, matched-pairs analyses of relative canine size revealed that more polygynous species, or species groups, had larger canines than their less sexually selected sister species, or species groups, thus indicating special selection on canine size. An evolutionary lag could not be found, however, between canine size and body size, or between canine dimorphism and body size dimorphism. Taken together, these results indicate that the effects of sexual selection on canine size are stronger than those on body size, perhaps indicating that canines are more important than body size in haplorhine male-male competition.

Consistent with previous studies (Plavcan et al., 1995; Kappeler, 1996), our results showed that the intensity of intrasexual selection, as indexed by mating system categories, has had no significant effect on canine size or canine size dimorphism in strepsirrhines. This lack of canine dimorphism was suggested to be due to a strong genetic correlation between males and females, which would constrain the expression of canine dimorphism, or equal selection pressures on both sexes (Plavcan, 1998). These theories, however, do not explain why sexual selection has had no effect on male and female canine size *per se*.
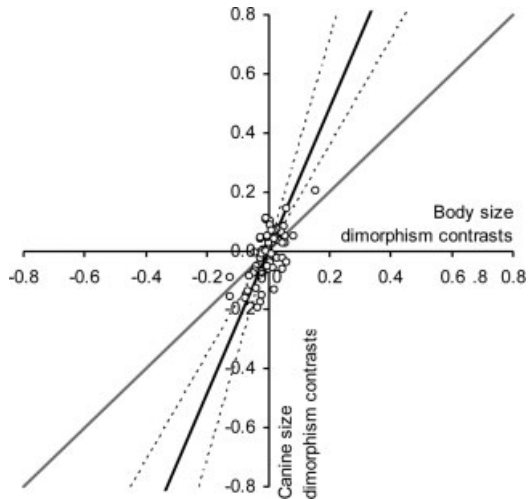
Fig. 4. Relationship between contrasts in canine size dimorphism and body size dimorphism in Haplorhini. Canine dimorphism is significantly correlated with body size dimorphism. One data point in graph represents an independent contrast, while dashed lines show 95% confidence intervals, which do not overlap with a slope of 1.0 (grey line). Thus, in Haplorhini, canine size dimorphism increases with increasing body size dimorphism.

A more probable hypothesis is therefore weak intrasexual selection on canine size in strepsirrhines (Kappeler, 1996). Neither canine size nor body size may be of importance for strepsirrhine males when competing for access to mates. It is possible that the reproductive success of males depends primarily on mechanisms that do not involve physical contest, such as agility (Kappeler, 1996; Lindenfors, 2002; Lawler et al., 2005), sperm competition (Kappeler, 1997), pheromonal suppression (Perret, 1992; Kraus et al., 1999), or coalition formation (Ostner and Kappeler, 2004). Finally, it should not be underestimated how little we know about strepsirrhine mating systems, especially about nocturnal species. For example, recent field work revealed that presumably solitary and polygynous taxa, such as *Cheirogaleus medius* and *Lepilemur ruficaudatus*, are in fact pair-living (Fietz et al., 2000; Zinner et al., 2003). Moreover, some of these pair-living taxa (e.g., *C. medius* and *Phaner furcifer*) exhibit high rates of extrapair copulations and paternity without exhibiting expected morphological adaptations (Schülke et al., 2004), creating a complete mismatch between mating system, reproductive system, and sexually selected morphological adaptations. Results from comparative studies of strepisirrhines should therefore be considered preliminary until their mating systems can be characterized with more confidence and in more detail.

If sexual selection is the driving force behind the evolution of canine size dimorphism in haplorhines, dimorphism should be more pronounced among more polygynous species, where one or a few males deny other males access to a group of breeding females (Darwin, 1871; Andersson, 1994). As predicted, and as already shown in a number of studies (Leutenegger and Kelly, 1977; Harvey et al., 1978; Leutenegger, 1982; Leutenegger and Cheverud, 1982, 1985; Kay et al., 1988; Greenfield, 1992; Jablonski and Ruliang, 1995; Plavcan and van Schaik, 1992; Plavcan, 1993, 1999, 2001; Plavcan et al., 1995;

Hayes et al., 1996), canine size dimorphism increases with more intense intrasexual selection among males.

Our results also revealed, however, that sexual selection does not only affect male canine size in haplorhines, but also female canine size, if to a lesser degree. Consistent with this result, male and female canine size evolution is highly correlated. This correlation can be due to a possible genetic correlation of canine size (Maynard Smith, 1978; Lande, 1980, 1987; Lande and Arnold, 1983), or less parsimoniously, through a tight relationship between body size and canine size and a genetic correlation between the sexes in genes controlling body size. Greenfield (1996) suggested that female canines in haplorhine primates are poorly designed to be used as weapons, which (if correct) would support the notion that there is no special selection on female canine size for use in conflict situations (but see Plavcan et al., 1995; Plavcan, 1998; McGraw et al., 2002).

Consistent with former studies, we also found that canine size is tightly correlated with body mass (Leutenegger and Kelly, 1977; Harvey et al., 1978; Gingerich and Smith, 1985; Greenfield, 1992). Additionally, we found that male canine size scales allometrically with body size in haplorhines. Thus, an increase in male body size is coupled with a corresponding larger increase in canine size. These relationships reflect on the degree of dimorphism in canine size that is also highly correlated with body size. This latter relationship is also allometric, however, rather than isometric, in haplorhines. These two allometric relationships, taken together with the results of the matched-pairs analysis on relative canine size in males, indicate exclusive sexual selection on canines.

To investigate this further, analyses used for detecting evolutionary lag (Deaner and Nunn, 1999) were used to attempt to pry apart what character changed first: body size or canine size. It was impossible to detect any evolutionary lag between canine size and body size, or between canine size dimorphism and body size dimorphism (in either direction). This indicates that the evolution of canine and body size occurred simultaneously, either because both traits were selected simultaneously, or because they were so tightly genetically correlated that selection in one trait led to change in both traits.

The results presented here are especially interesting in the context of Rensch's rule: the pattern that large body size dimorphism is correlated to large body size across many animal taxa (Rensch, 1950, 1959). His own proposal for how this relationship came to be so general was sexual selection on male secondary characters other than size, with correlated responses in body size of both sexes (Rensch, 1959, p. 212). Though not supported directly by our results, the fact that sexual selection has had larger effects on canine size than body size in male haplorhine primates definitely supports the notion that the weaponry of males is of larger importance than body size *per se*. The generality of our results has to await further analyses of other mammals. An obvious candidate group is the artiodactyls, who (like primates) carry weaponry mainly used for male-male competition.

ACKNOWLEDGMENTS

APPENDIX A. Data on mating systems, body mass and canines in primates[1]

Species	Mating system	Female mass (kg)	Male mass (kg)	Female canine mesiodistal length (mm)	Male canine mesiodistal length (mm)	Female canine height (mm)	Male canine height (mm)	Female buccolingual width (mm)	Male buccolingual width (mm)
Lemur catta	MM	2.21	2.21	5.1	5.68	9.16	10.86	2.31	2.6
Hapalemur griseus	Mon	0.903	0.987	4.14	4.16	5.91	5.94	2.6	2.56
Eulemur coronatus	MM	1.62	1.69	4.64	5.15	8.48	9.43	2.15	2.13
Eulemur mongoz	Mon	1.61	1.63	4.09	4.85	8.06	9.63	1.97	2.26
Eulemur fulvus	MM	2.077	2.0	5.38	6.12	10.09	11.87	2.36	2.72
Eulemur macaco	MM	2.51	2.37	5.68	6.01	10.34	10.58	2.39	2.69
Eulemur rubriventer	Mon	1.94	1.98	5.46	5.68	9.98	10.49	2.72	2.76
Varecia variegata	Mon	3.51	3.47	6.56	6.44	12.6	13.08	2.88	2.91
Lepilemur mustelinus				3.98	4.87	5.15	6.86	2.04	2.27
Avahi laniger	Mon	1.32	1.03	3.33	3.2	3.79	3.58	1.9	1.95
Propithecus verreauxi	MM	2.95	3.25	5.46	5.93	7.93	8.41	2.83	3.01
Propithecus diadema	Mon	6.26	5.94	5.75	6.01	9.1	8.01	3.39	3.15
Indri indri	Mon	6.84	5.83	6.71	6.79	7.79	7.76	3.88	3.79
Microcebus murinus	UM	0.063	0.059	1.45	1.42	2.08	2.07	0.88	0.85
Microcebus rufus	UM	0.042	0.043	1.43	1.39	2.13	2.0	0.93	0.86
Cheirogaleus medius	Mon	0.282	0.283	2.27	2.19	3.98	3.75	1.41	1.42
Galago alleni	UM	0.269	0.277	2.08	2.3	3.6	4.0	1.41	1.52
Galagoides demidoff	UM	0.06	0.063	1.36	1.55	2.35	3.0	0.89	1.03
Galagoides zanzibaricus	UM	0.137	0.149	1.8	1.91	3.29	3.64	1.21	1.33
Galago moholi	UM	0.173	0.187	1.91	2.04	3.45	3.67	1.16	1.23
Galago senegalensis	UM	0.199	0.227	2.03	2.25	3.61	4.01	1.29	1.42
Otolemur crassicaudatus	UM	1.11	1.19	4.03	5.07	7.28	8.95	2.42	2.86
Otolemur garnettii	UM	0.734	0.794	3.65	4.0	6.04	6.53	2.33	2.54
Euoticus elegantulus	UM	0.261	0.287	2.49	2.47	4.66	4.96	1.66	1.64
Loris tardigradus	UM	0.193	0.192	2.6	2.87	4.57	4.5	1.81	1.93
Arctocebus calabarensis	UM	0.306	0.312	1.94	2.08	3.96	3.96	1.57	1.74
Nycticebus coucang	UM	0.626	0.679	3.52	3.75	6.8	7.05	2.5	2.59
Nycticebus pygmaeus	UM	0.376	0.462	2.52	2.62	4.57	5.08	1.83	1.96
Perodictus potto	UM	0.836	0.83	4.17	4.25	7.03	7.1	2.71	2.74
Cebuella pygmaea	Mon and PA	0.122	0.11	1.63	1.64	2.99	3.06	1.35	1.34
Saguinus midas	Mon and PA	0.575	0.515	2.84	2.8	5.42	5.38	2.24	2.31
Saguinus oedipus	Mon and PA	0.404	0.418	2.9	2.9	5.65	5.65	2.33	2.42
Saguinus fuscicollis	Mon and PA	0.358	0.343	2.83	2.77	5.47	5.66	2.3	2.31
Cebus olivaceus	MM and UM	2.52	3.29	6.1	7.49	9.12	14.35	5.57	6.2
Cebus apella	MM	2.52	3.65	6.32	7.49	9.7	13.67	5.48	6.45
Saimiri oerstedii	MM	0.68	0.897	2.86	3.81	4.5	7.58	2.96	3.3
Saimiri sciureus[2]	MM	0.662	0.779	3.25	3.94	5.02	7.1	2.83	3.26
Aotus trivirgatus	Mon	0.736	0.813	3.13	3.19	4.8	5.62	2.71	2.69
Callicebus moloch	Mon	0.956	1.02	2.89	2.84	4.04	4.36	2.75	2.75
Callicebus torquatus	Mon	1.21	1.28	3.46	3.5	4.1	4.28	3.09	3.18
Pithecia pithecia	Mon	1.58	1.94	4.26	5.0	6.77	8.93	3.84	4.6
Cacajao calvus	MM	2.88	3.45	7.08	8.15	10.82	13.58	5.85	7.26
Chiropotes satanas[2]	MM	2.58	2.90	6.24	6.59	9.35	11.18	5.16	5.7
Alouatta caraya	MM and UM	4.33	6.42	6.22	8.58	9.56	14.24	4.32	5.6
Alouatta palliata[2]	MM	6.6	7.8	6.46	8.16	9.14	13.79	4.6	5.81
Alouatta seniculus	MM and UM	5.3	6.873	6.64	8.64	8.96	13.42	4.8	6.65
Ateles geoffroyi	MM	7.29	7.78	5.71	6.38	7.5	11.43	5.14	5.17
Ateles paniscus	MM	8.44	9.11	5.94	6.6	7.73	12.12	4.95	5.29
Lagothrix lagothricha	MM	7.02	7.28	5.78	7.43	8.05	14.23	5.39	6.54
Macaca sinica	MM	3.2	5.68	5.79	9.05	9.96	19.69	4.9	6.38
Macaca fuscata	MM	8.03	11.0	6.58	10.2	9.59	19.57	5.25	6.46
Macaca mulatta[2]	MM	5.37	7.71	6.1	8.67	8.13	16.97	4.65	6.42
Macaca fascicularis	MM	3.59	5.36	6.21	9.73	10.67	24.09	4.53	6.43
Macaca nemestrina[2]	MM	6.5	11.2	7.42	12.29	12.24	28.89	5.77	7.8
Macaca tonkeana		9.0	14.9	7.77	11.07	12.72	24.66	5.76	7.63
Macaca nigra	MM	5.47	9.89	6.79	11.55	11.38	29.73	5.24	7.95
Lophocebus atterimus	MM	5.76	7.84	5.92	8.25	8.82	16.73	4.71	5.69
Cercocebus galeritus	MM	5.26	9.61	6.0	9.7			4.8	6.6
Cercocebus torquatus[2]	MM	6.2	11.0	6.46	10.35	9.53	23.53	4.99	7.04
Mandrillus leucophaeus	UM			8.6	17.89	11.7	49.97	6.24	11.02
Papio anubis	MM	12.5	23.15	8.83	16.1	15.95	35.43	6.96	11.57
Papio cynocephalus[2]	MM	9.75	17.2	6.46	9.72	9.13	25.57	4.87	7.16
Papio ursinus	MM	14.8	29.8	8.71	17.0	12.12	46.53	6.12	10.72
Papio hamadryas	UM	10.65	18.95	7.85	14.14	11.17	30.64	6.35	10.66
Theropithecus gelada	UM	11.7	19.0	7.88	14.89	12.27	39.62	5.79	9.32
Cercopithecus aethiops[2]	MM	2.98	4.26	5.17	7.37	9.76	17.66	3.96	5.14
Cercopithecus ascanius	MM and UM	2.92	3.7	5.23	6.8	10.3	16.13	3.9	4.51

APPENDIX A. (Continued)

Species	Mating system	Female mass (kg)	Male mass (kg)	Female canine mesiodistal length (mm)	Male canine mesiodistal length (mm)	Female canine height (mm)	Male canine height (mm)	Female buccolingual width (mm)	Male buccolingual width (mm)
Cercopithecus cephus	UM	2.88	4.29	4.85	6.89	9.21	16.32	3.78	4.62
Cercopithecus mitis	UM	4.363	7.697	5.22	8.29	9.77	19.24	4.33	5.62
Cercopithecus nictitans	UM	4.26	6.67	5.54	8.5	11.22	18.1	4.19	5.6
Cercopithecus mona	UM			5.34	7.82	9.32	17.76	3.79	5.03
Cercopithecus wolfi	UM	2.87	3.91	4.9	7.41	9.59	18.06	3.71	4.95
Cercopithecus pogonias	UM	2.9	4.26	5.27	7.01	10.1	15.73	4.0	4.65
Cercopithecus neglectus	Mon and UM	4.13	7.35	5.68	8.56	11.64	20.02	4.04	5.72
Cercopithecus diana	UM	3.9	5.2	6.19	8.45	12.33	19.94	4.34	5.43
Cercopithecus lhoesti	UM	3.45	5.97	5.6	8.39	10.82	19.93	4.16	5.76
Cercopithecus preussi				5.25	8.25	10.66	18.91	3.93	5.0
Erythrocebus patas	UM	6.5	12.4	6.88	10.58	12.17	26.5	4.49	6.72
Colobus angolensis	MM	7.57	9.68	7.05	9.3	9.57	17.66	5.03	6.66
Colobus guereza	MM and UM	9.2	13.5	8.19	9.84	13.85	20.31	6.21	6.71
Colobus polykomos	MM and UM	8.3	9.9	8.05	9.2	10.81	19.13	6.18	6.68
Colobus satanas	MM and UM	7.42	10.4	6.81	7.86	9.16	16.08	6.23	6.2
Colobus badius	MM	8.21	8.36	6.78	8.3	9.32	17.6	5.11	6.28
Procolobus verus	MM	4.2	4.7	5.25	7.19	7.43	14.9	4.62	5.58
Pygathrix nemaeus	MM and UM	8.44	11.0	5.82	8.04	8.54	16.59	4.98	6.27
Simias concolor	Mon and UM	6.8	9.15	5.54	7.63	8.07	13.91	4.77	5.57
Nasalis larvatus	MM and UM	9.82	20.4	6.9	9.23	10.42	22.96	5.19	6.75
Presbytis comata	UM	6.71	6.68	5.94	6.75	9.23	13.93	5.0	5.0
Presbytis melalophos	MM and UM	6.47	6.59	5.82	6.4	8.15	13.95	4.93	4.51
Presbytis rubicunda	MM and UM	6.17	6.29	5.69	5.89	8.48	12.73	4.46	4.2
Presbytis cristata	UM	5.76	6.61	6.77	8.12	10.94	18.57	5.8	6.39
Presbytis johnii	UM	11.2	12.0	6.4	8.3			5.3	6.8
Presbytis vetulus	UM	5.9	8.17	6.11	7.82	9.34	16.96	5.04	6.04
Presbytis obscura	MM and UM	6.26	7.9	6.14	7.62	8.51	15.1	5.36	5.75
Presbytis phayeri		6.3	7.87	6.9	6.6			5.6	5.1
Presbytis pileatus	UM	9.86	12.0	6.91	9.09	10.52	19.85	5.85	6.66
Presbytis potenziani	Mon	6.4	6.17	6.71	7.25	9.56	13.56	5.63	5.33
Presbytis entellus[2]	MM and UM	6.91	11.4	7.29	9.58	10.82	19.08	5.96	6.87
Hylobates agilis	Mon	5.82	5.88	6.9	7.2			4.9	5.3
Hylobates moloch	Mon	6.25	6.58	7.6	7.4			5.0	5.5
Hylobates klossi	Mon	5.92	5.67	7.64	7.71	16.63	15.72	5.43	5.41
Hylobates hoolock	Mon	6.88	6.87	7.69	8.42	17.09	17.75	5.61	5.92
Hylobates syndactylus	Mon	10.7	11.9	8.45	9.72	17.61	20.94	6.06	6.68
Hylobates concolor	Mon	7.62	7.79	7.69	8.14	16.49	19.11	5.14	5.31
Pongo pygmaeus	(MM and) UM	35.7	78.2	13.33	17.5	15.95	27.0	10.41	14.26
Pan paniscus	MM	33.2	45.0	9.37	11.44	11.24	15.57	6.89	8.88
Pan troglodytes[2]	MM	45.8	59.7	11.94	15.3	15.26	21.72	9.48	11.81
Homo sapiens	Mon (and UM)	54.8	62.2	8.24	9.29	9.97	10.85	7.82	8.4
Gorilla gorilla[2]	UM	71.5	170.4	15.09	23.67	17.4	30.26	11.3	16.8

[1]Data sources: mating systems: Kappeler, 1997; Müller, 1998; Lindenfors, 2002; Pochron et al., 2002; Zinner et al., 2003; body mass: Smith and Jungers, 1997; canine size: Kappeler, 1996; Plavcan, 1999; Swindler, 2002.
[2]Data for these species were matched on a subspecies or population level.

APPENDIX B. Matched-pairs comparisons of sister taxa[1]

Strepsirhini
1. MP: *Lemur catta*
   LP: *Varecia variegata*
2. MP: *Eulemur coronatus*
   LP: *Eulemur rubriventer*
3. MP: *Eulemur fulvus and E. macaco*
   LP: *Eulemur mongoz*
4. MP: *Propithecus verreauxi*
   LP: *Indri indri*
5. MP: *Microcebus murinus and M. rufus*
   LP: *Cheirogaleus medius*

Haplorhini
1. MP: *Cebus olivaceus, C. apella, Saimiri oerstedii, and S. sciureus*
   LP: *Cebuella pygmaea, Saguinus midas, and S. oedipus*
2. MP: *Cacajao calvus and Chiropotes satanas*
   LP: *Pithecia pithecia*
3. MP: *Alouatta caraya, A. palliata, A. seniculus, Ateles geoffroyi, A. paniscus, and Lagothrix lagothricha*
   LP: *Aotus trivirgatus*

4. MP: *Papio hamadryas*
   LP: *Papio anubis, P. cynocephalus, and P. ursinus*
5. MP: *Theropithecus gelada*
   LP: *Lophocebus atterimus, Cercocebus galeritus, and C. torquatus*
6. MP: *Cercopithecus lhoesti*
   LP: *Cercopithecus aethiops*
7. MP: *Cercopithecus mona, C. wolfi, and C. pogonias*
   LP: *Cercopithecus neglectus*
8. MP: *Nasalis larvatus*
   LP: *Simias concolor*
9. MP: *Presbytis comata, P. melalophos, P. rubicunda, P. cristata, P. vetulus, P. obscura, and P. pileatus*
   LP: *Presbytis potenziani*
10. MP: *Pongo pygmaeus and Gorilla gorilla*
    LP: *Hylobates klossi, H. hoolock, H. syndactylus, and H. concolor*
11. MP: *Pan paniscus and P. troglodytes*
    LP: *Homo sapiens*

[1] MP, more polygynous; LP, less polygynous.

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